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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.

CHAPTER I

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 syncœcy (*σύν* with, *οἶκος* house), which has been suggested for certain particular cases. Syncœcy 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 *biocenoses*. 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 Sluiter⁴⁸ 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 Lunel³⁶.

The members of the genus *Physalia*, whose nematocysts are particularly urticarious, are frequently accompanied by little fishes (*Nameus 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. Coutière²² 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 Coutière²²) 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. Potts⁴⁵ 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. Borradaile⁶ 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 *Eumeson convictor*, observed by Seurat¹⁵ 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 Potts²⁶⁷ 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 Bouvier¹⁴ and by Sluiter⁴⁹. 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,

arching up on itself, can move about, dragging the polyp after it. The manner in which this association develops suggests that it must be accidental; it is however found with the same species in places as widely separate as Réunion, the Red Sea and the Malay Archipelago.

Many instances of commensalism have been observed without having been sufficiently studied in life. In the sand of the French beaches the spatangid urchin *Echinocardium cordatum* is very often accompanied by a bivalve mollusc, *Montacuta ferruginea*, which occurs near the anus of the spatangid and which lives in the same kind of association with some synaptid holothurians as does the amphipod *Urothoë marinus*. These animals probably utilize the stream of water produced by the sea urchin. In the lateral folds of the anterior region of *Balanoglossus*

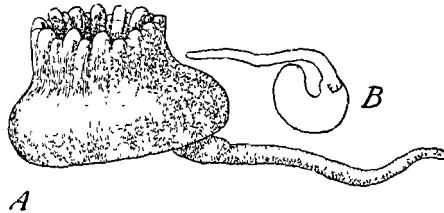


Figure 1. *Aspidosiphon* and *Heteropsammia cochlea* (after Bouvier).

A, the sipunculid moving along and dragging the polyp. *B*, the sipunculid in isolation.

(=*Ptychodera*) there regularly occurs a number of annelids, which must be attracted there by the stream of water from the gill slits of the enteropneust. Thus Giard³² has found a hesionid, *Ophiodromus herrmanni*, on *Balanoglossus* in the Glénans Islands; Gravier³³ has described a large polynoid, *Lepidasthenia digueti*, living in the same way on *Balanoglossus* in the Gulf of California; the ornamentation of the commensal makes it almost invisible on the enteropneust. Other polynoids, such as *Nychia cirrosa* and *Lenilla setosissima*, live within the tubes of *Chaetopterus*. On the species of *Balanoglossus* which in the Gulf of California is associated with *Lepidasthenia digueti* there is often found a crustacean, *Lysiosquilla*. A copepod genus, *Hersiliodes*, is represented by some species which live in the

galleries dug in sand by a clymenid or *Callianassa*. Within the tube of a large terebellid, *Loimia medusa*, of tropical seas there frequently occur porcellanid crabs of the genus *Polyonyx*. De Saint-Joseph⁴⁶ has seen numbers of them on samples of this species brought from Senegal, and I have had the opportunity of seeing the same association with *Loimia medusa* collected in the Malay Archipelago by the *Siboga* expedition. Under the same conditions *Polyonyx* associates with other annelids. Indeed, of 99 individuals of *Chætopterus* collected at Beaufort (North Carolina) on the Atlantic coast of America, Enders²⁷ found only 11 without *Polyonyx*, while 75 of the *Chætopterus* tubes contained 176 of the porcellanids. This author remarks that it is very uncommon to find the crustacean free-living, and that in the tube its death quickly follows that of the worm; it is likely that the current of water produced by the worm is essential for the crab's respiration.

This selection of examples, to which could be added many others, shows how commonly and regularly these associations occur. We shall conclude with those formed by the pagurids, on which some important researches have been carried out.

It is well known that the pagurids, or hermit crabs, take shelter in the empty shells of gastropods and are highly adapted to this habitat, as is shown by the softness and asymmetry of the abdomen, the conformation of the terminal appendages (uropods) and a number of other characters.* There are numerous commensals associated with the pagurids; we shall consider some of them.

These associations are very varied, even among the species of the French coasts. Chevreux¹⁸ has carried out a methodical examination of *Buccinum* shells occupied by *Eupagurus bernhardus* on the Normandy coast where this species is collected and used both for food and for bait. The shells often bear an anemone, *Calliactis parasitica*. Almost all are covered by a hydroid, *Hydractinia echinata*; 10 per cent. contain a polynoid, *Harmothoë cæliata*; 30 per cent. of them have *Nereilepas fucata*, which we shall discuss later on (Malaquin found 50 per cent. at Portel). In many of the shells there also lives a copepod, *Sunaristes paguri*, and, in addition, Chevreux collected 8 species

* For reversion to symmetry due to living without shelter see Bouvier, Recherches sur les affinités des Lithodes et des Lomis avec les Pagurides, *Ann. Sci. nat. Zool.*, ser. 7, 18, 1895.

of amphipods, 4 of which were common. Until then, one of the latter was believed to be a rarity, so we may conclude that its normal habitat is within the shells inhabited by the pagurids. It is very likely that further quantitative investigations, similar to those carried out by Chevreux, on other species in other localities will produce analogous results. Bonnier and Pérez¹², working in the Red Sea, have found, in shells inhabited by *Pagurus brevipes*, the schizopod crustacean *Gnathomysis gerlachei*, which is the type of a new family.

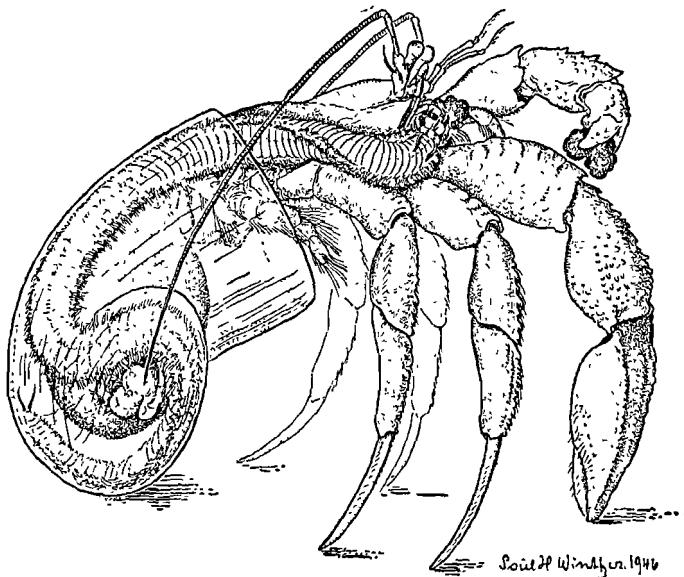


Figure 2. Hermit crab in an artificial glass shell, with its commensal *Nereilepas fucata* coming out to take part in a meal of sea urchin ovary (drawing lent by G. Thorson).

The commensalism of *Nereilepas fucata* has been the subject of interesting observations by Chevreux and Coupin²¹. First it must be noted that it is always this species that is found under these particular conditions, and no other nereids; the association is rigorously specific. The worm conceals itself in the terminal whorls of the shell where it finds shelter. It is truly a commensal in the strict sense of the term. Chevreux, indeed, when feeding *Eupagurus bernhardus* with mussels in an aquarium, observed that when the pagurid gets one, the nereid,

probably attracted by an olfactory stimulus, leaves its place inside the shell and comes up, between the mouth-parts of the crab, to seize pieces of the prey. Coupin has made analogous observations when feeding the pagurid with *Cardium*, and he remarks that the crab never attempts to devour the annelid, although this could easily be done. There is obvious toleration, which implies special reflexes and precise instincts. These details have recently been confirmed and extended by G. Thorson. He succeeded in making both partners accept artificial shells made of glass, in which the behaviour of the worm could be followed, particularly in a red light which closely conforms to the illumination of its natural home. The nereid usually remained quietly at the bottom of the shell, with its ventral surface against the glass. If the crab was given a piece of the ovary of a sea urchin and began to eat it the nereid would be seen hurrying forwards to seize its share close to the very mouth of the crab. The occurrence did not last a minute. The crab did not try to get rid of the intruder, who is a tolerated tenant admitted to the table of the landlord. In this association we see that the roles of the two partners are not equal; the nereid appropriates a share of the crab's prey and therefore lives at its expense.

The shells inhabited by the pagurids are very often covered near the aperture by the hydroids *Podocoryne* and *Hydractinia*. The polyps grow up from a mat of a horny substance which, in the case of *Hydractinia*, even extends beyond the margins of the shell and prolongs it. It appears that in this association there are reciprocal advantages: the nematocysts of the hydroid must give the pagurid some protection, and the hydroid must gain extra food as a result of the pagurid's movements in search of prey.

Let us now consider the anemones which are attached to these shells. On the French coasts *Calliactis parasitica* is associated with several species of pagurids: *Eupagurus bernhardus*, *Pagurus striatus* and *P. angulatus*; *Adamsia palliata*, on the contrary, is always commensal on *Eupagurus prideauxi*. At great depths *Pagurus pilosimanus* regularly occupies shells covered with a colonial anthozoan, *Epizoanthus parasiticus*. In the last two cases the body of the commensal grows beyond the shell, thus enlarging the pagurid's dwelling, particularly so

where *Epizoanthus* is concerned. It is noticeable that *Calliactis parasitica* and *Adamsia palliata* show very highly developed acontia, long filaments bearing nematocysts, which they discharge through lateral openings, the cinclides, and it cannot be doubted that these constitute a specialized defensive mechanism both for them and for the pagurids.

The *Calliactis*-pagurid association is much less intimate than that of *Adamsia* with *E. prideauxi*. There may be as many as seven or eight individual *Calliactis* on the same shell, necessarily occupying very varied positions. Moreover, this anemone is able to live a solitary life, though normally it associates with the pagurid, as may be seen in aquaria. Faurot³⁰ indeed has shown that if the pagurid is taken out of a shell on which a *Calliactis* is fixed, the latter will, after a few hours, spontaneously detach itself from the empty shell. The pagurids literally capture the *Calliactis* when they meet one: these tactics have been followed in detail by Cowles²⁰ on *Pagurus deformis* and *P. asper* in the Philippines, which occupy the shells of *Dolium*, *Strombus* and *Cassis*. They transplant their anemones when they change shells. The anemone lends itself to this manœuvre; it does not contract and after a few moments detaches itself; the pagurid then rolls it along and transfers it to the new shell. Faurot has noted that in none of these cases are the acontia discharged although their discharge is regularly brought about in other circumstances by a much weaker stimulus. The association therefore involves a complex of precise reflexes.

The work of numerous authors, notably Faurot³¹, has shown that with *Adamsia* the facts are much more significant. Here the pagurid, *Eupagurus prideauxi*, always lives in a shell too small to contain it; the shell serves less as a shelter than as a means of attachment for the anemone. The latter, which always occurs singly, forms the true shelter for the crab and is proportionate in size; it provides a supple covering, moulded to some extent upon its inmate and allowing it an agility of movement which distinguishes it from the pagurids associated with *Calliactis*; these are much heavier and slower. A comparison of the appendages of a number of pagurids shows clearly how perfectly those of *Eupagurus prideauxi* are adapted to its association with *Adamsia palliata*; with such a type of movement it could not live in a deep shell.

Adamsia occupies an unvarying position upon the shell, its mouth always opening on the ventral surface of the pagurid, behind the mouth of the latter; it thus often ingests a large share of the pagurid's prey without the crab's offering any resistance.

As soon as the anemone is fixed, after having been captured by the pagurid, it expands, undergoing a very great change of shape and secreting a membranous cuticle from the concave plantar surface which prolongs the shell.

It appears that *Adamsia* cannot live except in association with

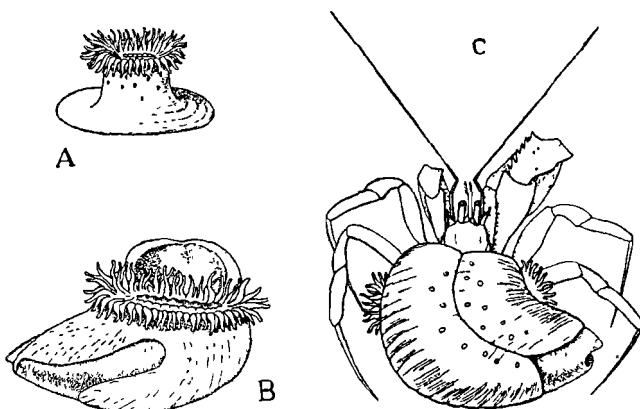


Figure 3. Association of *Eupagurus prideauxi* and *Adamsia palliata* (after Faurot).

A, the anemone alone. B, the anemone attached to a *Scaphander* shell (its mouth on the lower surface). C, the hermit crab with the anemone.

the pagurid. If, indeed, the latter is removed, the anemone rapidly detaches itself from the shell. It settles on the bottom but does not survive for long even when fed. Adaptation in these associates is reciprocal and very close. There are clear advantages for each partner: shelter and protection for the pagurid, food for the anemone. Here, undeniably, there exists mutualism between two distinct species, and each has been modified, both in structure and behaviour, by the association.

This association is one of those which have been most studied; nevertheless, it could still furnish material for many experiments. The association of *Pagurus pilosimanus* and

Epizoanthus parasiticus is probably equally intimate; unhappily it is not accessible to experiment. Many tropical pagurids could certainly provide material for observations of the same kind as those discussed above.

The pagurids are not the only Crustacea that associate with anemones. On the coasts of Chile, Burger¹⁷ has seen an analogous association between a crab, *Hepatus chilensis*, and *Actinoloba reticulata*. Out of sixty of these crabs collected at Coquimbo, only four were solitary; each of the others had its back and carapace covered with the anemones. Burger separated the animals from each other and placed them in an aquarium. The anemones first settled on the bottom, but after a few days they spontaneously detached themselves. Burger noticed that on coming into contact with a crab they attached themselves by the foot to one of its limbs and then moved up until they reached the back. Here, then, it is the anemone that takes the initiative in the association, the reverse of that which occurs with anemones and pagurids.

The preceding associations may be compared with the very curious behaviour of certain crabs that are always found holding an anemone in each claw. This singular association was first observed in the Seychelles, in 1880, by Möbius, in *Melia tessellata*. It was found again in the same species by Borradale in the Maldives, then in Hawaii; it is clear, then, that it is not fortuitous, but a normal association. Duerden²⁵ made a very interesting study of it in Hawaii, where he discovered another case in a crab, *Polydectes cupulifera*. The anemones carried by *Melia* seen to be the same in the three localities mentioned, in spite of the distance apart. There are two species, one belonging to the genus *Bunodeopsis*, the other to *Sagartia*. Duerden observes that the crab does not discriminate between them. *Polydectes* carries another anemone, of the genus *Phellia*. I shall restrict myself to a summary of the most important facts about *Melia*. The claws of the crab are very slender and are borne by the highly mobile chelipeds; their inner, opposing surfaces bear a row of sharp teeth like a saw, by means of which the anemone is carried. The claw is only half shut, so that the anemone is lightly held but it cannot be detached without being torn. The crab can, however, release it spontaneously.

The anemones have a fixed position, the mouth turned towards the dorsal surface of the crab, with the tentacles upwards. As soon as the crab is disturbed it thrusts out its claws in the direction of the intruder, brandishing the anemones as if they were a kind of weapon. Duerden has watched it eating. It uses the second pair of walking legs to put food into its mouth, but not the chelipeds even when the anemones have been removed. If the latter are offered food, such as a piece of meat, they close on it immediately, and if the morsel is small enough to be swallowed in one gulp they get the lot; if it is large and sticks out of the mouth, the crab hastily seizes it with its other

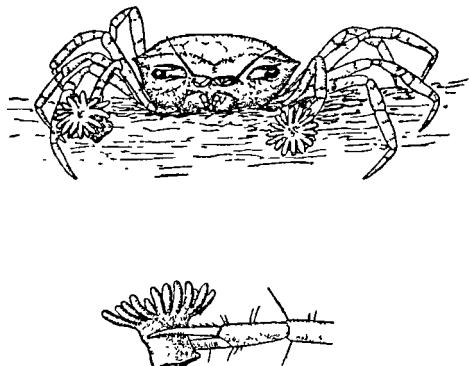


Figure 4. *Melia tessellata* holding a sea anemone in each of its chelæ (after Duerden).

limbs and eats it. It is certain that the crab feeds largely on prey stolen from the anemone after having used the latter to capture it.*

If the anemones are removed and then put separately in the aquarium containing the crab, it remains indifferent as long as it does not chance to come into contact with them. But as soon as contact has been made with one of them the crab seizes it

* Borradaille and Giard, independently of each other, compare the way in which the crab uses its anemones with the way the workers of the ant *Ecophylla smaragdina* hold a larva in their jaws (see Doflein: "Beobachtungen an den Weberameisen", *Biol. Centralbl.* vol. 25, 1905, p. 497). The larva, which has highly developed salivary glands, spins a thread of silk which the workers use for joining leaves by their edges. The adult worker has no spinning glands and therefore makes use of those of the larvæ. Giard has suggested that this kind of behaviour should be known as *biontergasy* (*βιών* living, *έργασία* work, *Rev. Scientif.*, 1905, 1st sem., p. 314).

and goes through a series of manœuvres in order to detach it from the bottom and place it within its claw, in the position already described. Even a fragment of an anemone suffices to release a series of reflex actions. Without going into further detail we can see that Duerden's interesting experiments demonstrate, in the crab at least, highly elaborate and differentiated reflexes such as occur in the pagurid-*Adamsia* association. Duerden was unsuccessful in finding isolated anemones of the genera *Melia*, *Bunodeopsis* and *Sagartia*, but he found solitary *Phellia*. His observations show that the crab benefits from the association much more than the anemone.*

In addition to the associations already discussed, pagurids commonly form another type with a monaxonid sponge, *Suberites domuncula*, which first covers the shells with a thick, fleshy mass and then resorbs the shell itself. Within the substance of the sponge, the pagurid forms a gallery which extends the original shell cavity and remains open to the exterior. The mass of the sponge provides a very secure shelter, particularly

* There is undoubtedly a link between the preceding facts and certain instincts of crustaceans which are not strictly cases of commensalism but which must arise from the same physiological mechanisms and which serve to elucidate commensalism proper. I refer to the instinct of disguising. It is particularly developed in the oxyrhyncous crabs (*Maia*, *Hyas*, etc) and is easily seen on our coasts. It also occurs in the Dromiacea. The principal facts, known for a long time, were carefully described in 1889 by Aurivillius¹¹, and their psychophysiological significance has been the subject of profound researches by Minkiewicz³⁹. The objects used by the oxyrhynchids to clothe themselves vary greatly—green or red algae, sponges, compound ascidians, hydroids, etc.—but are always selected so as to be homochromatic with the substratum on which the crab lives. *Maia* has even been seen in an aquarium disguising itself with the eggs of a cuttlefish, detaching them one by one from a cluster. These objects are attached to hooked setae on the dorsal surface and the crab uses its long chelipeds to fix them there after having torn them. Crabs can be brought to disguise themselves with non-living material such as paper or rags; if they are of different colours the animal sorts them to obtain a covering homochromous with the bottom, or else, having adopted its disguise, it moves on to a bottom matching it. Crabs still disguise themselves, but without regard to colour, when their ocular peduncles have been removed and the connectives between the cerebral ganglia and the ventral nerve cord severed. The series of reflexes is completed once the initial reflex has been released. The instinct for concealment, concludes Minkiewicz, "est un enchaînement de réflexes des appendices thoraciques antérieurs, provoqués par les tangoreceptions des pinces, dirigés par des tango- et chemoreceptions des pièces buccales et poussés par les tangoreceptions des crochets dorsaux flexibles vers leur but terminal". Colour choice is superimposed on the instinct for disguise and is determined by a "chromotropism" corresponding with the environment, compelling the animal to seek certain coloured surfaces and to avoid others. Data recently obtained on arthropod endocrinology, and the effect upon chromatophores of a gland in the eye stalk of decapod Crustacea, throw considerable light on the observation of Minkiewicz on *Maia* in which the eyes had been removed.

against octopuses. The early stages of the association are little known.*

It is obvious from the examples of commensalism given above—to which many others could be added—that under a guise of simplicity these associations involve complicated reflexes which are the culmination of long-standing adaptations just as are morphological specializations. It is only through observation of the living animals and through experiment that we can further our knowledge.

Some of these associations, like those of *Eupagurus pri-deauxi* and *Adamsia palliata*, are clear examples of mutualism; others appear to be exclusively for the benefit of only one of the associates which can accordingly be regarded, in some respects, as a parasite.

Commensalism ought not to be regarded as a rigid and clearly defined entity, but as a general term gathering together cases of extreme diversity where the relationships vary from simple proximity to well-defined associations involving precise reflexes. At the same time there may be reciprocal immunity against the secretions of each partner. Many of these associations, if carefully studied in this regard, would undoubtedly produce interesting results.

* *Suberites* is also employed as a disguise by the Dromiacea which place small pieces of the sponge on their backs where it grows and takes on the shape of the carapace.

CHAPTER II

COMMENSALISM IN TERRESTRIAL ANIMALS

IN terrestrial animals there are perhaps fewer clear-cut associations than in the marine animals already discussed; most of those which could be quoted are better dealt with as cases of parasitism. Some, however, are analogous, such as the relationships between ungulates and certain birds which follow the herds, sometimes resting on the animals and picking off the ticks and the oestrid larvæ that infest the hide. Starlings do this, also some wagtails (*Motacilla flava*) and magpies in France, *Crotophagus* in America, and *Buphagus*, the ox-pecker, in Africa. The last genus associates particularly with rhinoceros and the larger antelopes.*

It is among the social insects, particularly the ants and termites, that the greatest number and variety of facts connected with commensalism are found. Wasmann⁷¹, estimated that in 1895 there were 1,246 myrmecophilous species known, 1,177 of which were insects (including 993 beetles), 60 arachnids, and 9 crustaceans. At the same time he enumerated 109 termitophiles, 87 of which were beetles.

Amongst these various commensals he distinguished four main groups:

1. *SYNCEKETES* (*σύν* with, *οἶκος* house), or true commensals, simply sharing the subterranean dwelling of the ants and termites, and living on debris, scraps left from their hosts' food, or even corpses of the latter. The ants are indifferent to them.

* "Credited with removing these insects are the ox-peckers (*Buphagus africanus*) which, however, in the Uele district and the Bahr-el-Ghazal are far more eager to follow the herds of giant eland. It so happens that at least one of these birds always seems to be on the lookout to warn big game of the slightest danger. As the little ox-peckers rise higher and higher into the air their sharp shrill notes act as a magic whip even for the rhinoceroses. Without a moment's delay the thud of swiftly moving feet affirms the obedience shown to the tiny feathered sentinels." H. Lang, "The White Rhinoceros of the Belgian Congo"; *Bull. N. Y. Zool. Soc.*, 23, 1920, p. 89.

2. SYNECHTHRANS ($\sigmaύν$ with, $\epsilon\xi\theta\rho\sigma$ enemy), which enter the nest as robbers, feeding on the stores accumulated there or devouring the larvæ. The ants attack them and put them to death.

3. SYMPHILES ($\sigmaύν$ with, $\phi\lambda\sigma$ friend). These are the species sought by the ants and termites, even obtained by brute force, and fed by them. This group includes the myrmecoxenes and termitoxenes of Forel and Emery. Symphiles are by no means always welcome to the hosts who harbour them, as we shall see.

4. PARASITES, which we shall consider later.

The synæketes of ant-hills comprise a considerable number of species: acarines (*Trachyuropoda bostocki*, *Lelaps equitans*), spiders (*Micaria scintillaris*, *Thyreostenus biovata*, *Tetrilus arietinus*), isopods (*Platyarthrus hoffmannseggii*), Collembola (*Beckia albina*), Diptera (*Phyllomyza formica*, larvæ of phorids and syrphids, the limaciform larva of *Microdon mutabilis*), Hemiptera (*Alydus calcaratus*, *Nabis lativentris*), Micro-lepidoptera, Orthoptera (an apterous cricket *Myrmecophila*, *Attaphila*) and numerous Coleoptera; among these last are the histerids (*Hetærius*), staphylinids (*Dinarda dentata*, *D. hagensi*), larvæ of *Clytra*, Cetoninæ (*Cetonia floricola*), etc. These various species do not occur at random in the ant-hills. Most are permanently located in the nests of particular species. Thus some staphylinids, such as *Mimeciton* and *Ecitomorpha*, live with the Dorylinæ which they mimic to some extent. There are even some ants living as synæketes in the nests of other species; this is the case with *Formicoxenus nitidulus* and *Solenopsis fugax* in the nests of *Formica rufa*.

The synechthrans of ant-hills are mainly certain staphylinids, for instance, *Myrmecodia humeralis* (with *Formica rufa*), *M. funesta* (with *Lasius fuliginosus*), and *Quedius brevis*. Among the bees there are also synechthrans, such as the wax moths *Galleria melonella* and *Achræa grisella*, that lay their eggs on the combs, the larvæ living on wax and riddling it with galleries lined with silken threads, and *Acherontia atropos*, the death's head sphinx, which devours the honey as does also *Cetonia cardui*.

Symphiles are very numerous. They are principally beetles belonging to a variety of families: staphylinids (*Lomechusa*,

Atemeles, *Xenodusa*, etc.); Pselaphidæ, especially the Claviger-inæ; Paussidæ, which are completely adapted to a myrmecophilous life; Histeridæ (*Heterius*, *Tylois*, *Chlamydopsis*); Cetoniæ; and some Nitulidæ. Most of them are the specific guests of a particular species of ant or termite. The ants care for them, feed them by regurgitation and rear their larvæ. Generally the ants are attracted to the beetles by aromatic ethers of which they are very fond. These secretions are produced by glands situated at the base of tufts of hairs, usually reddish yellow in colour, called *trichomes* and located principally on the sides of the abdomen. These ethers are derived more or less directly from the fat body: they are not truly nutritive but the ants delight in them and lick them greedily from the hairs amongst which they are exuded. This sometimes leads to true aberrations of instinct.

Such is the case, for instance, with *Lomechusa*, one of the myrmecophiles which has been most studied. *Lomechusa strumosa* lives in the ant-hills of *Formica sanguinea*; the ants seek it even to the extent of seizing it from other ant-hills; they nourish it and lick it; they raise and feed its larvæ, carrying them to safety in case of danger. Now, these larvæ of *Lomechusa* are the worst enemies of the ant larvæ, which they eat, and yet the ants feed them at the expense of their own larvæ. An ant-hill of *Formica sanguinea* infested with *Lomechusa* degenerates and finally disappears. After a certain time, indeed, no more normal females develop but only some that are more or less atrophied and rather like the workers (pseudogynes): in the end the ant-hill is no more. *Lomechusa* then migrates to another. It is obvious that this guest is altogether disastrous to the ants, but all the same it is avidly sought by them. Wasmann rightly compares this aberrant instinct of the ants to the use of tobacco, opium or alcohol by man.

Lomechusa, *Atemeles* and other aleocharines have a means of defence against the ants that attack them; K. H. Jordan⁶² has shown that they possess a gland the secretion from which collects in a reservoir situated ventrally and opening beneath the fourth abdominal segment. The staphylinid, when attacked, raises its abdomen and squirts the secretion, which smells of amyl acetate, over the ant, which is stupefied by it. Amyl acetate, *in vitro*, has the same effect. This gland is not an

adaptive structure since it is found in aleocharines which are not myrmecophilous.

Atemeles, a genus containing several species, lives only with definite species of ants whose relationships with it are similar to those of other ants with *Lomechusa* but are less detrimental to the hosts since *Atemeles* does not live permanently with them. Most individuals migrate regularly from one ant-hill to another, living in spring and summer with *Formica* and in autumn and winter with *Myrmica*. *Xenodusa* is the genus which, in America, takes the place of *Atemeles*.

The Paussidæ are beetles which are gigantic compared with ants and have a very characteristic appearance, particularly as regards the antennæ; they are highly adapted to a myrmecophilous life. According to Escherich⁵⁵ they are derived from the Carabidæ. They are mainly tropical, living for the most part in the ant-hills of *Pheidole*; only two species, *Paussus favieri* and *P. turcicus*, are found in the Mediterranean region. They feed on the larvæ of the ants. When disturbed they make an explosive noise and emit a smell, and Peringuey thought that this bombardment terrified the ants which therefore tolerated the paussids. Really, however, this reaction never occurs within the ant-hills. The ants not only tolerate the paussids but lick their trichomes; they do not feed them. They tend the paussid larvæ which, according to Bœving's observations, are carnivorous like the adults. The paussids, then, although cared for by the ants, are destructive guests which well deserve the name of parasites.

The Clavigerinæ are a very large group comprising numerous genera and species; in France *Claviger testaceus* and *C. longicornis* live in the ant-hills of *Lasius flavus* and *L. niger*; their larvæ are still unknown. The adults are meticulously cared for by the ants who feed them and carry them to safety when in danger, as they do their own larvæ. They produce a secretion in a dorsal depression of the abdomen, which is licked up by the ants. *Claviger* does not appear to be harmful to its hosts like the beetles already discussed. However, *C. testaceus* has sometimes been seen vigorously biting and killing larvæ of *Lasius*.

Histerid beetles of the genus *Hetærius*, which live in many of the ant-hills of species indigenous to France (*Formica fusca*,

F. rufibarbis, and *F. sanguinea*), feed on the corpses of ants or other insects but appear never to attack the healthy larvæ of the ants.

Diptera are represented in ant-hills and termitaries by a series of types which are highly adapted, particularly with regard to their wings which are rudimentary or even completely atrophied (*Psyllomyia* living with *Dorylus*, *Commoptera*

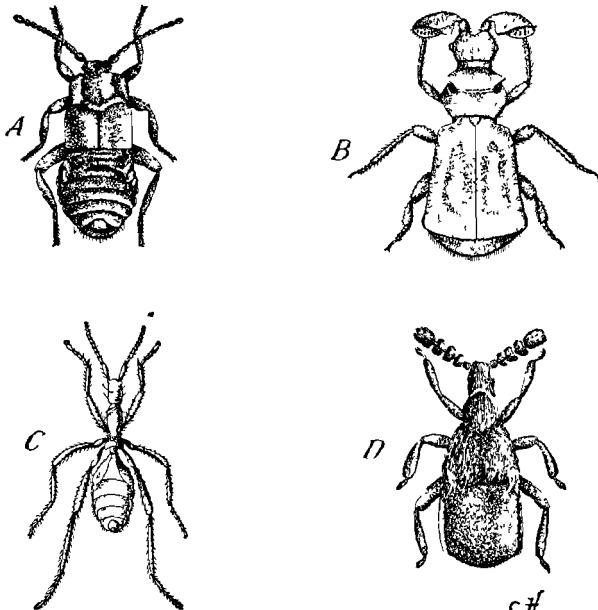


Figure 5. Insects that live as commensals with ants. .

A, *Lomechusa strumosa* (after Wheeler). B, *Paussus turcicus* (after Escherich). C, *Mimeciton pulex* (after Wasmann). D, *Claviger testaceus* (after Wheeler).

with *Solenopsis*, *Ectomyia* with *Ectiton*, etc., *Termitoxenia* in the termitaries). Many phorids live there as larvæ and some of these larvæ have very curious habits, such as those of *Metopina pachycondylæ*, which Wheeler⁷⁷ found in Texas in the ant-hills of *Pachycondyla vorax*. This larva adheres by a posterior disc to one of the ant larvæ, forming a collar round it, and when a worker presents food to the ant larva the dipterous larva elongates its anterior end and captures the morsel intended for

its host. It can pass from one larva to another and finally pupates within a cocoon of an ant larva. *Pachycondyla* does not treat it as an enemy but cleans it at the same time as its own larvæ. This behaviour recalls that of *Braula*, a pupiparous form that lives on bees, clinging to them and forcing them to disgorge drops of honey which it secures. It is not without resemblance to *Nereilepas* in relation to hermit crabs; in short, it tends towards parasitism.

Among Lepidoptera, the caterpillars of the Lycænidæ have, in general, relations with ants analogous to those between beetles and ants that we have already considered. They usually

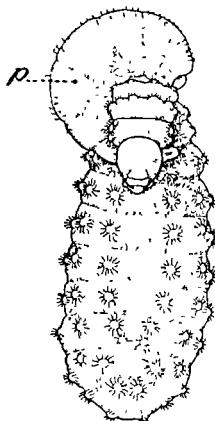


Figure 6. Larva of *Pachycondyla vorax* bearing a larva (p) of *Metopina pachycondylæ* (after Wheeler).

live on papilionaceous plants to begin with but cannot complete their development there. They are sought and captured by the ants and finish their larval life within the ant-hill. They possess abdominal glands discovered by Guénée, unpaired ones on the dorsal surface of the seventh segment and paired ones on the eighth. The ants are very greedy for the secretion from these glands, which they lick up; the caterpillars then protrude the gland openings as tubular structures which can be sucked. According to de Nicéville certain ants rear the lycænid caterpillars in flocks, constructing shelters for them where they remain during the day, and leading them out to feed at night. Other lycænids develop in galls produced by *Crematogaster* on

acacias. Some species have carnivorous caterpillars which feed on the larvæ of the ants which harbour them, as Oberthür⁶⁶ has found in *Lycæna alcon* and *L. euphemus*; nevertheless these are sought by the ants and taken into the ant-hills. Here again, then, are relationships analogous to those of *Lomechusa*. Evidently there remain many similar cases to be carefully studied, differing in detail from one species to another.

The relationships between ants and aphids are long-established classics; even Linnæus wrote "Aphis formicarum vacca". At the beginning of the 19th century Huber made detailed studies of them and his results have often been confirmed since then. Here there is true nutrition of the ant and not a search for a secretion which is simply agreeable. The aphids cannot utilize all the sugar that they extract from plants, and excrete an appreciable amount by the anus, in the form of liquid droplets ejected on to the leaves. It is this that forms the honey dew which was known already by Hesiod and which in another form constituted the manna of the Hebrews; since the 18th century it has been much studied (Réaumur, Tréviranus, Boussingault, Darwin, Büsgen, Forel, etc.). Huber had noticed that the ants induced the emission of a sugary liquid by catching the aphids and stroking the abdomen with their antennæ. This brings about the welling up of a droplet which the ants immediately absorb. They are truly milking a domestic animal. They go to milk the aphids on the leaves. The radicolæ are captured and led into the ant-hills where the ants rear them and protect them as if they were their own larvæ. In good weather *Aphis maidiradicis* is carried on to its food plants and brought back into the ant-hills on cool nights, or sometimes carried from old roots on to young ones. The aphids adopt a passive attitude to all this. This particular kind of association is known as *trophobiosis*.

Sympphilism, then, includes associations in which the relationships are very varied and which are far from being mutual.

It is always the ants that appear to play the leading part. The regularity and persistence of these events in widely separate localities show that for the species discussed this is a normal and necessary mode of life, the result of the evolution both of behaviour and of form. Wasmann⁷⁵, who has carried out the greatest number of researches on sympphilism, believes that we

have here a special instinct which has been derived from the ants' instinct for adoption. Janet⁶⁰ and Escherich⁵⁶ consider this an unsatisfactory hypothesis. The ants care for the symphiles as if they were their own offspring and it is rather the symphiles that have adapted themselves to the instincts of the ants and have exploited them for their own profit, sometimes becoming true parasites, letting themselves be fed and their progeny reared as in the case of the cuckoo. This has produced truly aberrant instincts among ants, which make them sacrifice their own larvæ and which Escherich has compared to social failings such as alcoholism in human societies.

Amongst the symphiles, adaptation extends to morphological modifications. Coleoptera living in ant-hills display characters which are clearly adaptive, as with the trichomes, and in mouth-parts where there is more or less marked reduction of the palps in species which live on food regurgitated by the ants. In *Claviger* all the palps are short; the maxillary palps are reduced to a single segment while those of the free-living pselaphids are very long. The staphylinid aleocharines (*Lomechusa*, *Atemeles*, *Xenodusa*), which are fed by the ants, also have highly abbreviated labial palps and a wide and short tongue; this is particularly marked in the termitophilous species: *Spirachtha eurymedusa* possesses only the rudiments of labial palps.* However, there are some species of *Termitomorpha* which have retained a very long maxillary palp. Wasmann⁷² explains this anomaly by the fact that the insect uses this palp to stroke the termites and thus excites them to feed it; *Lomechusa*, *Atemeles* and *Claviger* use their antennæ on the ants in the same way.

Another adaptive character found in symphiles is *physogastry*, or the more or less considerable hypertrophy of the abdomen. This is particularly marked in termitophiles but has also been observed in *Claviger*, among the myrmecophilous aleocharines (*Lomechusa*, *Atemeles*) and especially amongst the species (*Ecitochara*, etc.) found with *Eciton* in Brazil. In the termitophilous aleocharines (*Spirachtha*, *Termitobia*, *Termitomorpha*, etc.) the abdomen is so greatly hypertrophied that its segments are scarcely recognizable; it is either extended in the normal

* The same reduction of the palps is to be seen in the slave-making ants (*Anergates*) which are dependent on their slaves for food.

position (*Termitomorpha*) or rolled right up on itself with the tip turned towards the thorax (*Spirachtha*).

It is very significant to see physogastry developed not only in the aleocharines but also amongst the termitophilous carabid beetles (*Glyptus sculptus* living in Africa with *Termes bellicosus*, etc.). This is a most remarkable case of convergence. The origin of this physogastry must be alimentary. One can imagine that overfeeding by the ants or termites leads to hypertrophy of the fat body; this alteration is on the same level as the modifications of the mouth-parts.

Finally, a last peculiarity of adaptation lies in the structure of the antennæ which are modified in different ways to become very sensitive tactile organs.

As a result of these various adaptive forces a certain number of symphiles have come to resemble ants both in appearance and behaviour. Wasmann and some other workers consider them to be mimics (cf. *Mimeciton pulex*, Fig. 5C, p. 20).

Here it is convenient to add to the preceding associations others existing between different species of ants, and usually regarded as types of slavery. We know that some species of ants carry off the pupæ of others and take them into their own ant-hills where, after metamorphosis, they play the part of auxiliary workers. This phenomenon of abduction, termed *dulosis* by Forel, can be interpreted in various ways. Forel attributes its origin to the highly developed instinct of pillage possessed by ants. Darwin tried to explain it by selection. In the first place the ants would have carried off the larvæ of other species for food, then some of the pupæ which had escaped slaughter would develop into adults which, obeying their nursing instincts, would tend the larvæ of the pillaging species. This circumstance, at first accidental, would become persistent on account of the advantage it conferred on the colony. But, as in all social modifications among ants, it is not obvious how this change in instinct could be transmitted and fixed by selection since the workers are sterile. Wasmann⁷⁴ does not accept Darwin's explanation. He points out that the queen, the only fertile member of the ant colony, does not take part in the hunt for slaves and that therefore the instinct to rob cannot be inherited through her; nevertheless in seeking the explanation, we must take her as the starting point. It is necessary, on the one

hand, to take into account that the ants captured as slaves are strictly specific and, on the other hand, the circumstances in which a new ant-hill is founded.

The simplest case is when, after the nuptial flight, the queen digs underground, lays her eggs and rears the first workers without assistance. This occurs in species such as *Formica fusca* and *F. rufibarbis*. Here there is evidently a difficult initial phase in the founding of the colony. Certain other species occupy deserted nests, or install themselves near the nest of other species that they will rob. Thus *Solenopsis* settles near the nests of *Messor barbarus*. This proceeding may be termed *cleptobiosis* (Wheeler) or *lestobiosis* (Forel). The female of some other species installs herself in the nest of yet another one where she is tolerated. This is what Forel calls *parabiosis* and must be the explanation of a certain number of mixed ant-hills; the female of *Formicoxenus nitidulus* establishes herself in this way in the nests of *Formica rufa* or *F. pratensis*.

But in many species the fertilized female, incapable of founding a nest by herself, is picked up after the nuptial flight by the workers of a nest near which she has fallen. The workers of *Formica rufa* and *F. pratensis* act in this way towards their own species. Often, however, the adopted female may be of another species; thus *F. rufa* adopts females of *F. truncicola*, and in America, *F. incerta* adopts those of *F. consocius*. As a result, we find colonies which are temporarily mixed and remain so until the original workers have died out. In other cases the colonies remain mixed because the workers of the incoming species pillage the pupæ of the species to which the original auxiliary workers belong. Thus *F. sanguinea* pillages the larvæ of *F. fusca* and *F. rufibarbis*.

According to Wasmann, these adoptions were the prelude to slave-making. The species which steal pupæ to make auxiliary workers of them are those whose colony is founded by adoption, and the workers captured later always belong to the species that provided the initial workers. Slave-making would be an aberration of the instinct of adoption found in ants. The queen would participate in the evolution of this instinct through the circumstances of her adoption and one can imagine that it might be possible for her to transmit these modifications of it.

Evolution of the type of behaviour from which slave-making

results leads to morphological evolution. All or some social activities are progressively transferred to the slave workers and finally their owners are fed by them, the mouth-parts becoming so modified that it is impossible for them to feed themselves; they are thus absolutely dependent upon their slaves. Primitive adoption becomes transformed into social parasitism.

This is what happens in *Polyergus rufescens*, the Amazon ant. The members of this species have sabre-like mandibles (Fig. 7a), which are weapons of attack. They are excellent warriors and are energetic in carrying off the pupae from which they will later obtain workers. Now, the captured pupae always belong to the species (*Formica fusca*, *F. rufibarbis*) which have helped to establish the nest. The mandibles of *Polyergus* have lost their

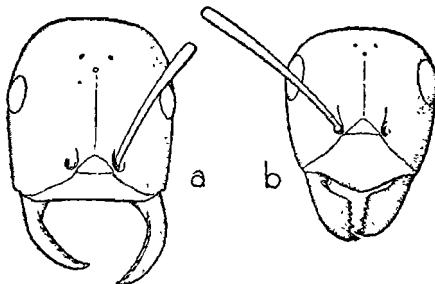


Figure 7. Head and mandibles of workers of *Polyergus rufescens* (a) and of *Formica fusca* (b) (after Bondroit).

masticating edge (cf. Fig. 7b); the workers cannot carry out the domestic work of the ant-hill; they even lose the instinct of feeding themselves directly. They depend on their slaves, whose number is always proportional to that of their masters.

Leptothorax emersoni thus parasitizes *Myrmica brevinodis*. It dies when there are no *Myrmica* to regurgitate food for it.

This line of evolution culminates in the disappearance of the workers, as in *Anergates*, of which one species, *A. atratulus*, in Europe, forms obligatorily mixed colonies with *Tetramorium caespitum*. Wheeler⁷⁸ has also noted the complete absence of workers in *Epæcus pergandei*. But slavery can lead to paradoxical aberrations of instinct in the conquered species, as has been found in *Monomorium salomonis*, which, reduced to slavery by *Wheeleriella santschii*, kills its own queen, thus con-

demning its own colony to perish. Piéron⁶⁷ considers this voluntary sterilization of the parasitized colony as a social form of parasitic castration.

Wheeler's views⁷⁸ on the origin and evolution of slavery amongst ants are somewhat similar to those of Wasmann. He starts in the same way with the founding of the colony but does not believe that it is always a question of the adoption of the female by the workers of another species: the female of *Formica sanguinea*, for instance, after the nuptial flight, conquers the larvæ which will be the first workers in the new nest. For Emery⁵⁴, too, the initial proceeding is one of violence; he considers that a female penetrating into a nest kills and disperses the workers and forms a new colony with the larvæ.*

The truth is certainly less simple than any of these general theories. It is obvious how closely these phenomena resemble commensalism and how impossible it is to distinguish clearly between them and parasitism.

We shall now examine another type of association which, under the influence of Darwinism, has occupied a prominent place in evolutionary thought. I refer to myrmecophilous plants. Fritz Müller, and later Schimper, considered them the result of special adaptation developed by natural selection. They provide shelters for ants, as in the hollow-trunked *Cecropia* (Urticaceæ) described below, or in the form of fleshy swellings which are hollow, as in various rubiaceous epiphytes (*Myrmecodia*, *Hydnophytum*), or by means of hollow spines which are large and swollen, as in *Acacia spherocephala*. Most of these plants also possess numerous nectaries. On the leaf petioles of *Cecropia* are minute structures (Müller's bodies) containing oils and albuminoids. *Acacia spherocephala* possesses minute succulent structures at the tips of the pinnules.

These various organs provide for the ants a food which attracts them and is automatically renewed. Therefore ant colonies are nearly always found on these plants. The advantage to the plants of being protected by the ants from animals that attack their foliage is said to have led by selection to the development of these special organs. Myrmecophilous plants have thus become a favourite example in the theory of natural selection. This interpretation is opposed by workers who have

* See also p. 29.

observed the ants at first hand. From amongst these we shall summarize the work carried out at São-Paolo by H. von Ihering⁵⁹ on *Cecropia* spp. (mainly *C. adenopus*, the imbauba) and the symbiotic ants of the genus *Azteca*.

According to the myrmecophilous plant theory, *Azteca* for the most part protects *Cecropia* against *Atta*, a genus of leaf-cutting ants which sometimes despoil whole trees of their foliage. Work on the habits of *Azteca* is difficult since these ants inhabit cavities within *Cecropia* and, at the least disturbance, become very aggressive and bite savagely. All the old imbauba trunks contain *Azteca* but this is by no means the case with the young trees and when they have been rid of the ants it has been observed that they do not suffer from *Atta*. Thus *Azteca* is not indispensable to them. These ants feed principally on the young growths of the tree as well as on Müller's bodies, at the base of the petioles. They penetrate into the tree in the upper region of the internodes, where there is least resistance, and establish their nests within the hollow trunk. The opening so formed has been termed a *stoma* and around it the parenchyma proliferates, forming the *stomatome*, rich in fats and sugar which provide food for the ants, so that they induce the formation of successive stomatomes as fast as the tree grows. Ihering tried unsuccessfully to produce stomatomes experimentally but the saliva of the ants seems necessary for this. In short, it is a question of gall formation.

As for *Atta*, when these ants venture on to the imbaubas they are chased off by *Azteca*, but they have no special liking for these trees and the *Azteca* ants are only concerned with protecting their own nests and remain unmoved by the attack of other animals, such as chrysomelid beetles, caterpillars and particularly sloths (*Bradypus*), which do infinitely more damage to *Cecropia*; they only attack certain species of ants and tolerate others. The imbauba is clearly the normal habitat of *Azteca*, and provides it with shelter and food. The ant exploits the tree and only protects it to protect itself. The ant is by no means indispensable to the tree and, to quote Ihering, the *Cecropia* lives without *Azteca* as easily as a dog without fleas. *Azteca* is more closely adapted to the tree. According to Wheeler, the ants perish when the tree is felled; they are really parasites on it. The same author considers that in general the

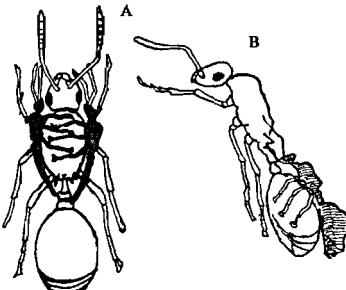
ants are adapted to the so-called myrmecophilous plants but that the converse has definitely not been established. Too many of the observations on which the theories of selection are based have been hastily made by travellers.

In the same connection, Chodat⁵² has established that in Paraguay the swellings in various plants (*Cordia*, *Acacia*) occupied by ants (*Azteca*, *Pseudomyrma*) and regarded as myrmecophilous adaptations were, in reality, galls produced by chalcids (*Eurytoma*), the emerging adults leaving exit holes through which the ants entered. The latter have only made use of a modification in the plant, which was produced independently of them, and the true adaptation here is the correlation between them and the chalcids. It would be of great interest to find out how widely such explanations apply to various myrmecophilous plants.

The few examples given in the preceding pages imply the existence of a considerable variety in associations of this type, each one of which demands a very detailed study.

Recent research in Switzerland by Stumper and Kutter⁵⁹⁶⁻⁸ has brought to light two extreme cases of parasitism in ants. The first of these concerns *Teleutomyrmex schneideri* n. sp., in colonies of *Tetramorium cæspitum*. In isolation the parasite dies. Its mandibles are atrophied, and the tarsi modified as organs of attachment. The female penetrates into the nest of the host immediately after the nuptial flight, loses her wings and attaches herself to the *Tetramorium* queen, who may carry several of these parasites (Fig. A). They are tended by the workers, become physogastric (Fig. B) and lay their eggs; the brood is mixed. There are no workers in *Teleutomyrmex*; brother and sister mating occurs.

The second parasite is *Epimyrma stumperi*. The female penetrates the nest of the host *Leptocephalum nigriceps*, and there uses her limbs to smear herself with the cutaneous secretions of the host workers. Thus disguised, she kills the queen and is adopted by the workers who tend her eggs and larvæ. The workers of *Epimyrma* live on food regurgitated by the workers of the host species.



Female of *Tetramorium* with *Teleutomyrmex* attached (after Stumper).

CHAPTER III

FROM COMMENSALISM TO INQUILINISM AND PARASITISM

INQUILINISM

WE shall now consider a different series of associations. In these one animal lives within another but without feeding entirely at its expense although finding a shelter and diverting for its own use a part of the food collected by its partner. These are not true parasitism and are often given the name of inquilinism* (*Raumparasitismus* of German authors). They form a graduated series leading to true parasitism.

A classic example is provided by the fishes belonging to the genus *Fierasfer* (family Ammodytidæ), which generally live within holothurians (they are also found in starfishes, *Culcita*, and bivalves, *Pinna*), either in the respiratory tree or even in the general body cavity when the wall of the branchial sac has ruptured. They do not actually feed on the holothurian but on small crustaceans, emerging from time to time to hunt for them. Emery⁵⁴ has studied their relationship to the host. They enter by the cloaca, meeting with some resistance from the holothurian which, in exceptional cases, even expels its viscera, but usually tolerates them and does not appear to suffer even when harbouring three or four. What *Fierasfer* seeks from its host is a shelter. When kept in an aquarium without one, and with predatory fishes, it is speedily attacked and eaten.

In the Bahamas Plate⁴³ found a similar close association between a fish (*Apogonichthys strombi*, 3-6 cm. long) and a gastropod, *Strombus gigas*; the fish shelters during the day in the mantle cavity of the mollusc, emerging at night in search of food.

Many crustaceans obtain similar shelter within the mantle cavity of bivalves; *Pontonia* lodges in *Pinna*, and Pérez⁴² found

* Inquilini, from *incolinus*, who lives within.

pairs of the prawn *Anchistus miersi* in a Red Sea *Spondylus*. Pinnotherid crabs normally occupy such a habitat; there are many species in this family and most of them lodge in the mantle cavity of bivalves, though a few are found in other animals. Semper has seen them with *Fierasfer* in holothurians. This way of life even attracted the attention of the ancients, who believed that the crab apprised the mollusc of the presence of its prey. The biology of the pinnotherids deserves careful attention. It is generally supposed that, when the mollusc's valves are half open, the crabs lie in wait for prey passing nearby, but Coupin²¹ has found that their intestine contains the same vegetable residues as that of the mollusc that shelters them.

Numerous other examples of inquiline crabs could be quoted. Semper found a crab living in the mantle cavity of *Haliotis* and a prawn in the gill cavity of a large pagurid. In various sponges, particularly hexactinellids, we find *Pontonia*, *Typton*, *Spongicola* and *Æga*, which are, moreover, considerably modified. Then there is the classic case of the barrel shrimp, *Phronima*, the female of which lives in the test of *Pyrosoma* or the branchial chamber of salps. In the gill chamber of *Lepas* are annelids of the genus *Hipponoë*. *Malacobdella*, a nemertean with suckers, lives in the mantle cavity of bivalves (*Cyprina*, *Mya*, *Pholas*). An oligochæte, *Epitelphusa catensis*, occurs regularly within the gill chamber of the freshwater crab *Telphusa*. And there are other cases.

Inquilinism merges by slow degrees into parasitism, as we can see in the copepods that parasitize ascidians. Even the true inquilines living within the branchial chamber undergo considerable malformation, at least in the case of the females. Most of them live on minute organisms and particles brought into the branchial chamber by the respiratory currents of the ascidian, and in such cases (*Notodelphys*, *Doropygus*) they still retain the biting mouth-parts of the free-living forms. But some related forms (*Enterocola*) have migrated into the stomach, or, in the case of *Enteropsis*, into the epicardial tubes, and are true parasites, their buccal apparatus being modified for sucking up liquid food provided by the host. Other genera (*Ophoseides*, *Ooneides*), of which Chatton⁴⁷ has made a particular study, are even more degenerate.

EPIZOITES

Verging on parasitism is the case of those animals which always live on the surface of another animal, sometimes attached to it, sometimes free. Permanent attachment to a support is an important factor in morphological change, and its effects are often comparable to those of parasitism. In many sedentary animals the support plays only a mechanical part and its nature varies accordingly. As, however, conditions differ from one support to another, many animals tend to become localized on more or less definite types, or rather development is more successful on some types than on others.

This is particularly so in the case of living supports where the attached animals as a rule show a very considerable degree of specificity as well as definite localizations. This leads to precise and constant associations, and epizootic animals, like epiphytic plants, form a special type of commensalism.

There are very many cases of this. Many infusoria live on marine or freshwater animals and generally on definite species. We find this in many vorticellids (*Cothurnia*, *Urceolaria*, *Trichodina*). They take nothing from their host in the way of food but utilize the currents of water it produces, feeding on the particles which are brought to them. Fauré-Frémiel²⁹ has made interesting observations on *Opercularia* attached to various freshwater animals (*Gammarus*, *Asellus*, *Cyclops* and *Notonecta*). He has noted that infusoria soon die when detached from their host, even when, for instance, the limb to which they are fixed is isolated with them. It is the movement of the host and the resulting disturbance of the water which matter to them, and most infusoria remain healthy if the isolated limb is kept moving. Different species of *Opercularia* are confined to different hosts and if they are transferred from a *Notonecta* to a *Dytiscus* they fare badly and dwindle away. They must find favourable environmental conditions on one particular host and from this there results the specific nature³⁰ of these associations.

The class Acineta, or Suctoria, all the members of which are fixed either to inanimate objects or to living organisms whether plant or animal, contains a rather high proportion of true commensals, a few tending towards inquilinism or becoming true parasites. Even on plants there are certain specific associa-

tions. Thus, as Collin¹⁹ has observed, *Discophrya cothurnata* has never been found except on the roots of *Lemna*. Others are always attached to the shells of gastropods (*Paludina*, *Limnæa*), or to the limbs of some specific aquatic beetle (*Discophrya ferrum equinum* to *Hydrophilus piceus*, *D. steinii* to *Dytiscus marginalis*, *D. cybistri* to *Cybister*). Some very peculiar forms, such as *Ophryodendron sertulariae*, live on hydroids.* A great variety of Suctoria is carried by crustaceans: *Dendrosomides paguri* on the limb setæ of pagurids, *Dendrocometes paradoxus* on the branchial plates of *Gammarus*, *Stylocometes digitatus* on the gills of *Asellus*, etc.; and *Ophryodendron annulatorum* occurs on annelids. Some have penetrated into the outer region of the internal cavities of their hosts: *Trichophrya salparum* occurs in the pharynx of salps, and at the opening of the branchial chamber in many ascidians,† sometimes together with *Hypocoma ascidiarum*.‡

Under analogous conditions certain hydroids (*Hydractinia*, *Podocoryne*) live on the skin of fish or the shells occupied by pagurids; *Stylactis* (= *Podocoryne*) *minoi*, found in the Indian Ocean by Alcock¹⁰ on *Minous inermis*, in the region of the opercular opening, has been observed by Doflein under the same conditions in Japan. In Puget Sound, Heath³⁴ found that on 25 per cent. of *Hypsagonus quadricornis* there was a rich growth of *Perigonimus pugetensis*, for the most part on the fins and belly. *Nudiclava monacanthi* lives on a fish in Indian seas. *Ichthyocodium sarcotreti* has been observed by Jungersten³⁵ on a copepod, *Sarcotrete scopeli*, itself a parasite of a *Scopelus glacialis*.

Among the Kamptozoa (Polyzoa Endoprocta), *Loxosoma* spp. live only as epizoites on a limited number of animals, such as Gephyrea, Annelida (*Aphrodite*, *Capitellidæ*, etc.). In material from the *Caudan* expedition I myself saw on an abyssal *Nephropsis* a peculiar polyzoan belonging to the Ctenostomata.

Among the Cirripedia, all fixed at least to some passive support, there are some occurring only on certain animals such

* This species is really a true parasite feeding on the outer layers of *Sertularia*.

† *Acineta tuberosa* is often very abundant on copepods.

‡ In an association between a ciliate and a suctorian there has recently been discovered the curious fact that the peritrich ciliate *Epistylis* living on the skin of a newt is in reality usually attached to a suctorian, *Tokophrya*, fixed to the newt. It is a regular association, the constancy of which has been carefully worked out by Fauré-Frémiel. *Ann. Acad. Brasil Sciencias* 20, 1948.

as whales or sharks; *Coronula* on *Megaptera*, *Tubicinella* buried in the skin of the Australian baleen whales, *Alepas* and *Anelasma squalicola* on sharks. Many species of *Scalpellum* occur on hydroids and others of the same genus on Bryozoa and sponges.

Beside the epizoites which may be properly said to be fixed must be placed the animals which also live upon another but which are unattached and feed on various scraps and waste from the animal itself: nemerteans, such as *Polia involuta* living in the midst of crab's eggs, feeding on eggs that are dying or dead but apparently not attacking healthy embryos; *Histriobdella homari* (probably a modified annelid) living similarly among the eggs of lobsters or within the gill chamber. Most caprellids remain upon other animals such as sponges (*Halichondria*), Alcyonaria, ascidians, etc., and from this group is derived *Cyamus*, the whale louse, which lives clinging to the skin of Cetacea. With all the animals living under such conditions it is necessary to ascertain precisely the conditions in which they feed; some of them are true parasites and others are just commensals.

Having to some extent separated the preceding examples from real parasites we still find that among the organisms which are generally agreed to be true parasites there are some that could also be classed with inquilines and which very probably are derived from them. These are the intestinal parasites which, properly speaking, do not feed on the actual substance of the host but on its intestinal contents, that is, on ingested material in the process of being assimilated but not yet incorporated into the organism. This is obviously a subtle distinction and these nutritive substances are undoubtedly taken at the host's expense; we can indeed consider such animals as true parasites. For example, there are the cestodes, and no one would dispute that they are authentic parasites. But within the intestine there are other organisms which feed on waste matter that the host cannot utilize, or they may even act on food substances so that these become more digestible. The normal bacterial flora of an organism plays such a part and Pasteur has questioned if an aseptic life would indeed be possible; at the end of this book we shall consider this problem. In the intestine of termites there are the trichonymphids which are always present in great numbers in the workers and are not

only harmless but assist in the digestion of wood. The vast numbers of infusoria (*Ophryoscolecidae*), which are always found in the rumen of ruminants and in the cæcum of horses, have no noxious effect in spite of their multitude and live on either vegetable debris or on the bacteria which develop in this medium. There is even good reason for believing that they help in the digestion of cellulose. In any case they are rather to be regarded as commensals or inquilines than as true parasites and they end by being digested in the small intestine. It is the same with at least some of the Protozoa in the large intestine and rectum, living as saprophytes, for instance *Opalina*, *Nyctotherus*, certain flagellates and amoebæ, such as *Chlamydophrys stercorea* which swarms as a naked amoeba in the rectum of the horse and encysts in the droppings; and also for some nematodes, such as the eelworms in cow dung.

INTERMITTENT PARASITES

One of the sources of true parasitism is gradual adaptation to an exclusive diet, monophagy. Such a habit cannot in itself be regarded as parasitism although it creates and maintains the relation of predator and prey that is essential for this. Many nudibranchs live regularly on the hydroids on which they graze, assimilating even nematocysts within their hepatic diverticula; pycnogonids are constantly found on hydroids for the same reason, *Lamellaria* on compound ascidians, *Cæloplana* on Alcyonaria. Most caterpillars are confined to a definite plant, as are aphids, and by such gradual steps we come to the gall-producing species whose status as parasites is undeniable. Such a graduated series is also shown by the blood-sucking insects. Amongst these there are some, such as the culicids, which are not exclusively blood-suckers. Many, for instance the Tabanidae, the Simuliidae and the Hemiptera, are still obviously free-living. But there are others which, in spite of appearing to be free-living, are, in fact, intermittent parasites—*Glossina*, the tsetse fly, feeds only on vertebrate blood taken from a blood vessel and, as we shall see, has undergone in both its digestive and reproductive systems modifications which are parallel to those of Diptera Pupipara, which are true parasites permanently restricted to their host, for instance, *Melophagus* on sheep,

Hippobosca on horses, *Liptotena* on deer, *Lynchia*, *Ornithomyia*, etc., on birds. Of other groups, the Muscidæ, in their larval stages, show a similar range of habits: *Auchmeromyia* lives on man and other naked mammals (the aard-vark, *Orycteropus*, and the wart-hog, *Phacochoerus*), and certain *Phormia* and *Protocalliphora* on birds. Fleas, bugs and leeches show us advanced stages of adaptation to parasitism, but retain a relatively free mode of life. Among the isopods the Cymothoidæ and *Gnathia* provide analogous series.

In all these various examples we are faced with types which are indisputably parasites but which are related, by very gradual series, to other forms that are clearly free-living although their way of life is analogous. The limits of parasitism are difficult to decide. The criterion which comes to mind is that of being established more or less permanently on an individual and specific host, as are the Pupipara and ticks; this is, however, inadequate, and it is not possible to exclude intermittent parasites passing very gradually into free-living forms.

GENERAL NATURE OF MODIFICATIONS PRODUCED BY PARASITISM

Inquilinism and parasitism, properly speaking, entail considerable morphological change which is one of the most interesting things to be studied in them, both from the point of view of comparative anatomy and evolution. These modifications are always connected with the special conditions of life of the parasite on the host and their interpretation presupposes an analysis of these conditions, in short, research into the physiology of the parasites, a study which, in general, is still in its infancy and is very often difficult to undertake. It is not surprising that here, too, morphology has largely preceded physiology.

It is out of the question to include in a few pages all the adaptive modifications shown by parasites; they are infinitely variable and, to give some idea of this, it is better to take several examples which are significant in themselves as well as by comparison with related free-living forms. Generally, these modifications may be summed up as a simplification of the organs relating the animal to the environment, that is, the sensory and

locomotory systems, and a hypertrophy of those connected with nutrition—the digestive and reproductive systems. We can by no means always directly relate to adaptation all the changes that have come to pass; many must have resulted from correlations which, acting in an orthogenetic manner, have led to extreme states in which the purpose of the adaptation is no longer recognizable: this must occur with parasitic forms just as much as with free-living ones, but here it is a matter of a secondary evolution whose point of departure is usually easy to reconstruct.

The organs of locomotion of parasites either eventually atrophy or disappear, or, on the other hand, differentiate into organs of attachment. In arthropods the distal segments of the limbs become hooked claws (*Cyamus*, *Cymothoidæ*, *Epicaridæ*, etc.). In the Myzostomaria, a group derived from the annelids and parasitic on crinoids, the parapodia are completely atrophied and represented by a pair of chætae. The leeches, also derived from annelids, have lost all vestige of appendages; however, an archaic genus, *Acanthobdella*, parasitizing salmonids in Russian lakes and rivers, possesses chætae (five groups on either side towards the anterior extremity in *A. pallidina*), indicating that parapodia were present formerly.*

The counterpart of the degeneration of appendages in parasites is the development of organs of fixation, either, as we have already said, by modification of the appendages themselves, or by the development of new structures, particularly suckers or hooks. The trematodes, cestodes and leeches provide numerous examples illustrating the first and, often at the same time, the second condition which also occurs in other groups such as the Acanthocephala.

The central nervous system of parasites is often reduced and so are the sense organs, particularly the eyes. In the digestive system there is generally a modification of the mouth-parts, which very often become adapted for sucking, and a more or less marked reduction of the hind gut since the parasite ingests little or no waste matter with its food. The alimentary canal may even disappear completely as in the cestodes and Acanthocephala where nutrition is by means of diffusion through the

* *Acanthobdella* also possesses vestiges of a spacious cœlom typical of the true annelids.

body wall of assimilable matter elaborated by the host, or, as in the Rhizocephala, by a system of roots spreading throughout the whole structure of the host. A modification of this kind also occurs in certain parasitic infusoria such as *Opalina*; they no longer ingest solid food but obtain nourishment by diffusion.

In most parasites, particularly the blood-sucking ones, ingested matter accumulates in the mid-gut, which becomes a vast pouch from which there is gradual resorption. Leeches, ticks, biting flies and bed bugs become gorged in this way at more or less widely spaced intervals of time, and similarly many parasitic crustaceans (Epicaridæ, *Gnathia*) accumulate nutritive matter sucked from the host, in the hypertrophied liver. Such methods of nutrition correspond to peculiar physiological mechanisms which are not yet well understood. Thus, most blood-sucking parasites apparently possess anticoagulants which keep the ingested blood in a liquid state. This has been found in leeches (Haycraft ³⁷⁵, Apathy ³⁷¹), where it is due to glands opening near the mouth within the sucker, in ticks (Sabatini ²⁹⁹), in the larvæ of blood-sucking cœstrid flies (Weinberg ³⁹⁰), in *Ancylostomum duodenale* (L. Lœb and A. J. Smith ³⁷⁹) and also in a parasitic annelid (*Ichthyotomus*, Eisig ¹⁸⁰) which we shall consider later. This is a significant example of a similarity of adaptations occurring in organisms living under a particular set of circumstances, even though they belong to different groups and are manifestly independent. There must be many other facts of the same nature in the physiology of digestion in parasites.

Reproduction is the process which is most sensitive to the results of parasitism and it assumes a preponderant importance: we shall study its principal modifications in a special chapter; here we shall limit ourselves to noting in general that there is hypertrophy of the ovary and an increase, often enormous, in the number of eggs, offsetting the very considerable numbers of embryos which are lost on account of the difficulties of finding the host.

Parasitism thus modifies the organism very profoundly and it is customary to say that it results in degeneration or regression. Indeed, it leads to simplification of many organs and even to their disappearance. But we must not forget that, on the other hand, it causes hypertrophy or differentiation of other organs.

It is therefore preferable to say that parasitism results in specialization rather than in degeneration; in short, certain parasites, degraded in comparison with the normal members of the group to which they belong, are marvellously adapted to the very peculiar conditions under which they live, and the evolution which they have undergone in departing from the normal type is by no means a regression but progressive modification in a definite direction.

Since the modifications resulting from parasitism vary so greatly, generalizations about them could only be vague and it will be better to examine them in the light of certain particular examples. We shall begin with parasites that have developed as an exception in groups of animals that are generally free-living. Such examples are particularly significant on account of the clear-cut comparisons which they allow.

CHAPTER IV

ADAPTATIONS TO PARASITISM IN ANNELIDS AND MOLLUSCS

POLYCHÆTES

ICHTHYOTOMUS SANGUINARIUS. The case with which I shall begin will give us an idea of the first effects of parasitism. It concerns an animal that is only slightly modified and belongs to a group in which parasitism is very exceptional, the polychæte annelids. This particular species, *Ichthyotomus sanguinarius*, was discovered and studied in great detail by H. Eisig¹⁸⁰ at Naples; it parasitizes an eel, *Myrus vulgaris*.

It is interesting to see the beginning of adaptation to parasitism in an annelid because this group is probably the stock from which the Hirudinea and Myzostomaria were derived and these consist entirely of parasites and are profoundly modified; we can imagine, then, how their modifications arose. Besides *Ichthyotomus* there are some other cases of parasitism in polychætes known to us, both in the Eunicidæ and in the Syllidæ, which we shall consider later. A. Treadwell has briefly described under the name of *Haplosyllis cephalata* a specimen that was discovered attached by the pharynx to the cirri of a eunicid already preserved in alcohol. F. A. Potts¹⁸² described as *Parasitosyllis* an annelid found under the same conditions as annelids and nemerteans from Zanzibar; its structure appears to be typical but its evaginated pharynx is firmly fastened to the body wall of the host from which it cannot be detached. It seems, then, that in both cases it is a matter of permanent attachment to a host by the pharyngeal region*, but it is essential that they should be studied alive and in large numbers. This is what Eisig was able to do under the most favourable conditions with *Ichthyotomus sanguinarius*.

* The syllids are carnivorous annelids which attack their prey by evaginating the pharynx and perforating the body wall (cf. Malaquin, Recherches sur les Syllidiens. *Mem. Soc. Sciences et Arts de Lille*, 1893, p. 246).

This animal (the adult is 7-10 mm. long), which is firmly attached to the fins (Fig. 8) of *Myrus*, and in particular to the dorsal one, looks like an ordinary annelid with well-developed parapodia, and it is its organ of fixation which, above all else, deserves the most close study. This organ consists of two stylets projecting from the mouth and turning on each other by their articulating surfaces as they diverge (Fig. 9). The distal part embedded in the skin of the host is spoon-shaped with a toothed edge which holds it firmly in position. The animal bites with its stylets close together, it then separates them from each other, so tearing the host's skin and the walls of small blood vessels.

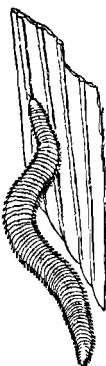


Figure 8. *Ichthyotomus sanguinarius* attached to the fin of *Myrus vulgaris* (after Eisig).

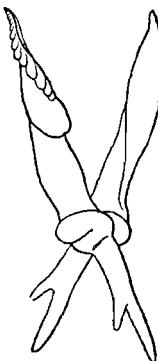


Figure 9. The stylets forming the organ of fixation in *Ichthyotomus* (after Eisig).

It is very difficult to detach an *Ichthyotomus* from its host without wounding the latter. The divergence of the stylets ensures attachment and at the same time corresponds with a resting state in the motor muscles; thus the animal is fixed when it is passive and has to exert muscular contraction to free itself. Here, therefore, is an organ of attachment that is an extremely effective and highly specialized mechanism that can be compared to the two-pronged hooks that were driven into a ceiling to hold a chandelier. We must ask how it originated. Is it by the continuous modification of an apparatus present in syllids whether they are free-living or not? At the entrance to the œsophagus many syllids possess a tooth or a ring of teeth but nothing

resembling the apparatus of *Ichthyotomus*, except, it seems, in a syllid, *Gnathosyllis diplodonta*, observed by Schmarda, which has two teeth which may perhaps be analogous. Unfortunately, the description is no more than a summary and this species has not been found since. The mechanism by which this structure

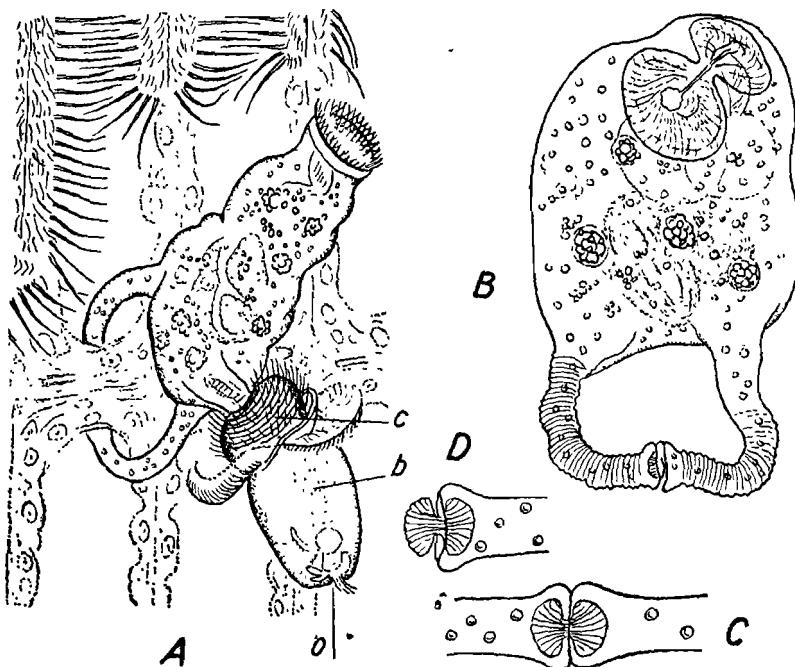


Figure 10. *Ellobiophrya donacis*.

A, the ciliate attached by its posterior limbs to a trabecula of the molluscan gill and bearing a bud, b, in an advanced stage of growth; c, aboral ciliated crown of the bud; o, oral pole of bud; B, an isolated individual of *Ellobiophrya* at the beginning of longitudinal fission (the peristome is dividing). C, D, the junction of the two limbs under normal conditions, and after rupture (after Chatton and Lwoff).

was achieved is mysterious: we can hardly invoke a lamarckian explanation; these stylets are non-living structures, they have their definitive form from the beginning and the way they work cannot influence their structure; the animal must make use of them as they are; on the other hand, we cannot reasonably accept as a matter of pure chance the sudden achievement of a

piece of apparatus which is so complicated and also well suited for attachment.* The problem will remain obscure until the discovery of related forms possessing an analogous organ but one that is less differentiated. But at present we have no knowledge of such a case apart from Schmarda's species. And this simple example shows how most of the morphological problems concerning adaptation to parasitism present themselves; at the same

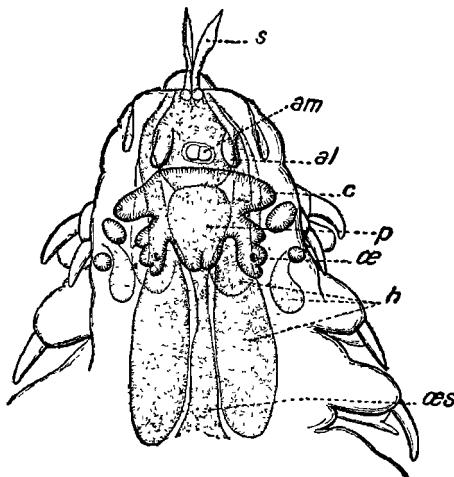


Figure 11. Anterior region of *Ichthyotomus* (after Eisig).

am, median antenna; *al*, lateral antenna (rudimentary); *c*, brain; *h*, haemophilous glands; *œ*, eye; *œs*, œsophagus; *p*, pharynx; *s*, attachment stylets.

time it shows that parasitism is far from leading only to regression or degeneration.

Adaptation in *Ichthyotomus* is shown by other characters, particularly in the anterior region which is in the process of being modified as a sucker. As the stylets tear the skin of the eel they cause bleeding at the point of attachment. The polychaete gorges

* Here we have a typical example of what Cuénot has called *coaptations*. Many cases are known amongst parasites as well as amongst free-living forms. There is a typical example in a peritrich, *Ellobiophrya donacis*, which lives on the gills of a bivalve, *Donax vittatus*, and has been thoroughly investigated by E. Chatton and A. Lwoff ⁸⁸. Two flexible cylindrical branches are given off from the posterior part of the body of the peritrich; they encircle one of the trabeculae of the molluscan gill, meet each other and adhere by a clamping device, thus forming a firm closed ring comparable to a padlock or to the ring on an earring (hence the name *Ellobiophrya*).

itself on the blood and at the same instant may be seen applying to the skin of the eel its entire anterior region which becomes concave although usually it is convex. This part, forming the temporary sucker, is the head, which in the annelids carries special appendages, antennæ, palps, etc, principally sensory in function with well-defined nervous areas on the surface of the skin corresponding to them. In the syllids, which *Ichthyotomus* obviously resembles, there are three dorsal antennæ (one median and two lateral) and two ventral palps. Now, on the head of *Ichthyotomus*, Eisig has found the nervous areas corresponding to these various appendages, but the appendages themselves have disappeared and the nervous areas are included in the sucker-forming zone. Here, we can clearly grasp the modification of the anterior extremity of the animal in relation to its mode of life; it is obviously of a regressive nature, but at the same time it constitutes a differentiation appropriate to its way of life and certainly illustrates a stage of the process of modification culminating in the Hirudinea in which the sucker has become permanent and the primitive structure of the annelid head has left no trace.

Ichthyotomus is an example of the blood-sucking parasites mentioned above (p. 38) which prevent coagulation of the blood they have ingested. Eisig has made exact observations and experiments on this subject. Although the blood simply extracted from a vessel of the fish clots very quickly, that ingested by the worm remains liquid. The absence of clotting is due to the secretion of extensive glands, the hæmophilous glands, of which there are two pairs opening to the exterior in the part of the anterior region forming the sucker. Their secretion mingles with the blood before it can reach the pharynx. Eisig has established by direct experiment their anti-coagulant action. Thanks to it the blood remains liquid and is constantly moving in the alimentary canal. Besides the effect that this has on assimilation, Eisig sees in it a modification of a respiratory nature. Indeed, the intestine gives off extensive lateral diverticula in each segment of the annelid and they extend even into the parapodia and cirri, contrary to what usually occurs in annelids. On the other hand, *Ichthyotomus* has neither vessels nor gills.

The presence of hæmophilous glands is an important adaptive character; they are probably not altogether new structures.

Other syllids possess glands on the head which are most likely to be homologous with them and at the expense of which they doubtless differentiated, both by hypertrophy and by acquiring an anti-coagulant property in relation to parasitic nutrition. One may imagine either that this was a gradual development or that such a property existed in certain forms in a state of pre-adaptation; it would then be the pre-adapted animals which would be particularly likely to become parasites. We have not the data to decide between the two hypotheses. The second ranks with those readily formulated in connection with numerous facts of evolution. The first seems to me infinitely preferable. It ties up with the production of anti-bodies and one may well suppose that the gradual establishment of an increasingly exclusive diet of blood has induced in the organism modifications of certain glandular secretions, which have resulted in an anti-coagulant character. In addition, the very general occurrence of anti-coagulant properties in blood-sucking parasites from widely divergent groups living under the most variable conditions appears to me forcibly to suggest that this physiological character is a direct consequence of conditions of nutrition. It seems to me that merely chance mutations are insufficient to account for the widespread appearance of this phenomenon amongst all blood-sucking parasites.

In addition to the hæmophilous glands of the cephalic region, *Ichthyotomus* possesses in each segment organs of the same structure and probably of the same significance although, in fact, they do not appear to be functional. Their presence is doubtless a demonstration of the way in which the different parts of the organism are correlated.

Eisig has shown still other effects of parasitism in this annelid. The general musculature of the parapodia is reduced. The eyes are small, lying beneath the skin, directly above the brain and in a state of regression. The pharynx differs from that of a normal syllid and corresponds to an embryonic state. The reproductive system is clearly hypertrophied. Thus the whole structure has been influenced by parasitism. But the animal still retains the characteristics of a free-living annelid and, moreover, it can change places on its host and attach itself afresh either on the same eel or upon another. Here we find a very interesting case of an animal which is still becoming modified. The detailed work

carried out by Eisig also shows how fruitful it is to combine morphological and physiological data. Even in a case as thoroughly investigated as this, the means by which the modifications have been brought about still remain obscure and even if certain characters, such as haemophily, seem clearly to be related to the functional activities of the animal, there are others, such as the differentiation of the stylets, which are much more perplexing unless they were the starting point from which others were derived.

MOLLUSCS

The molluscs, like the annelids, are a group in which parasitism is quite exceptional but which provides a series of graduated examples leading to a degree of extreme regression, a series which is the more significant since molluscs are animals showing a very high degree of organization. The range of examples allows us to imagine, by analogy, the origin of groups which have been wholly and profoundly modified by parasitism. It shows us, besides, that such a regression is not achieved by following along a single linear series but by a number of separate branches originating simultaneously, with many secondary variations, and comprising one of the most interesting fields of study in comparative anatomy. The behaviour of molluscs is extremely varied but they are essentially free-living animals. There are, however, some exceptions to this general rule amongst the bivalves and gastropods. We shall examine them in order.

I. LAMELLIBRANCHS

The facts to be observed in this group fall rather within the bounds of commensalism or inquilinism than those of true parasitism and do not involve profound changes in organization, although this is modified to some extent. The shell is reduced and often covered by the mantle. Hermaphroditism and incubation of the embryos have been found in most cases. The animals so modified belong more or less obviously to the Lucinidæ, characterized in particular by the presence of a single branchial lamella.

(a) *Entovalva*. These are species commensal on holothurians and especially on synaptids.

1. *Entovalva mirabilis*, internal parasite of a synaptid from Zanzibar, described by Veltzkov (1890).

2. *Entovalva perrieri* found on synaptids at Saint-Vaast-la-Hogue by Malard (1903) and studied later in the same locality by L. Anthony ³³⁰. This species is, as a rule, attached to the outside of the synaptid by a voluminous pedal papilla. If it is pulled off and put in a dish near the synaptid it very rapidly attempts to attach itself again. The foot is highly developed.

• On a synaptid at Cherbourg, Herpin ³⁴¹ found a small specimen (5 mm. long), which was perhaps a very young stage of *E. perrieri*; it possessed a long appendage (2 cm.), which is probably the foot.

3. *Entovalva semperi*, found in Japan by Oshima ³⁶¹, also on a synaptid, is perhaps the same species as one briefly noted by Semper (1868) in the Philippines.

4. *Entovalva major*, described by A. F. Brunn ³³⁴ from specimens collected by Mortensen at Ghardaqa (Red Sea) and found by him inside *Holothuria curiosa*.

These different examples show that *Entovalva* has a wide geographical distribution and represents a very stable type of a circumscribed association between bivalves and holothurians.

(b) *Montacuta*. The species *M. ferruginosa* is common on the French and English coasts, where it lives in the sand in direct contact with a spatangid sea urchin, *Echinocardium cordatum*. It is a well-established and regular association.

(c) *Scioberetia*. F. Bernard ³³² described under this name a bivalve nearly related to those above and living between the spines of a spatangid, *Tripylus*, at Cape Horn. It is hermaphrodite and incubates its eggs. The mantle covers the shell. The pedal and shell muscles and the foot itself are reduced.

(d) *Lepton*. This genus, observed by P. Fischer (1873) at Arcachon, was rediscovered there by Ch. Pérez on *Sipunculus nudus* and studied by Pelseneer. It is very close to *Montacuta*.

(e) *Ephippodonta*. The species *E. macdougalli*, described by Tate (1889), lives in the burrows of a crustacean, *Axiuss plectorhynchus*, on the southern coasts of Australia.

I shall not go into further detail here. The anatomy of these various types is, in short, not much modified, but their state of commensalism or inquilinism is undoubted and their geographical range shows that it is a firmly fixed type of behaviour.

II. GASTROPODS

The gastropods, among types that are very limited in comparison with the class as a whole, provide us with a series which is both much more varied and much more marked by profound morphological change due to true parasitism. We shall survey it briefly.

Amongst the Pyramidellidæ Pelseneer has made known many cases where the radula is reduced or absent, implying a radical change in feeding. He noted an *Odostomia* from China seas, which uses its proboscis to perforate the mantle of a *Tellina*; another species belonging to the same genus has an analogous relationship with the pearl oyster (*Pinctada margaritifera*). Finally, he has demonstrated that on French coasts species of *Odostomia* live under similar conditions: *O. rissoides* at the expense of the common mussel, and *O. pallida* on *Pecten*. They drive in their long proboscis when the valves are slightly open and suck at the mantle of these bivalves. The radula has disappeared; otherwise they are little modified.

But the most significant facts are those provided by a series of gastropods parasitizing echinoderms, which have often undergone considerable modification. They belong to the families Capulidæ, Eulimidæ, Entoconchidæ, and Pædophoropodidæ. Most of them are tropical species and comparatively rare. They are summed up in the table on the next page.

1. CAPULIDÆ. These are tænioglossid prosobranchs with a shell that is slightly coiled or in the form of a simple incurved cone. They are now represented by the genus *Thyca* that has been found on various starfish and they are relatively little modified. In Fig. 12B the drawing of *T. ectoconcha* gives an idea of organization in this genus. It shows that on the whole this gastropod is still normal in structure. The modifications affect the peribuccal region and the foot. The latter (*rp*) is reduced and no longer displays an operculum. The peribuccal region has developed as a large disc (*pseudo-foot df*), making a kind of sucker by which the animal adheres to the host. From its centre projects the proboscis which thrusts through the tegument of the starfish (*Linckia*). The proboscis, slightly developed in *T. ectoconcha*, is very long, three times the length of the body, in *T. crystallina*. The radula has completely disappeared, imply-

Family	Genus	No. of species	Host	Locality
Capulidæ	<i>Thyca</i>	5	Starfish (<i>Linckia</i>)	Indian Ocean, Malay Archipelago
	<i>Platyceras</i>	7	Fossils (Silurian-Triassic) on crinoids and starfish	
Eulimidæ	<i>Eulima*</i>		Crinoids, starfish	Indian Ocean Malay Archipelago and Indian Ocean
	<i>Robillardia</i>		Sea urchin	
	<i>Mucronalia</i>		Sea urchins, ophiuroids, starfish and holothurians	
	<i>Stylifert†</i>		Starfish, ophiuroids	Ceylon and Malay Archipelago
	<i>Megadenus</i>	4	Holothurians	Bahama, Zanzibar
	<i>Rosenia</i>	1	Sea urchin	North Sea
	<i>Pelseneeria</i>	1	Holothurians	Azores
Entoconchidæ	<i>Gasterosiphon</i>	3	Holothurians	Indian Ocean
	<i>Diacolax</i>	1	Holothurians	Falkland Isles
	<i>Enteroxenos</i>	1	Holothurians	Norway
	<i>Thyonicola</i>	1	Holothurians	Cape of Good Hope
	<i>Entocolax</i>	3	Holothurians	Bering Sea
Pædophoropodidae?	<i>Entoconcha</i>	2	Holothurians	Adriatic (Trieste), Philippines
	<i>Pædophoropus</i>	1	Holothurians	Sea of Japan
	<i>Asterosiphon</i>	1	Starfish	Japan
	<i>Ctenosculum</i>	1	Starfish	Hawaiian Isles

* A fair number of species of *Eulima* have been described by malacologists from empty shells found in isolation, which could have come from either free-living or parasitic forms.

† The remark on *Eulima* applies here too.

ing that the food is liquid and is sucked up. The species with a long proboscis have also enormous salivary glands, while the intestine and liver are reduced.

T. stellasteris (Fig. 12A), thoroughly investigated by Kœhler and Vaney, is the least modified species. The proboscis is rudimentary and the foot retains an operculum. The animal must move about on its host.

In these various species the sexes are separate; the male is clearly smaller than the female (Fig. 12A), and there is a certain amount of dimorphism in the shell, very marked in *T. cristallina*, where in the male it is turriculated and in the female simply cupular.

Adaptation of the Capulidæ to parasitism of echinoderms is very long-standing, since, from the Devonian to the Triassic, there are many forms comprising the genus *Platyceras*, with a shell recalling that of *Thyca*, attached to the anal region of crinoids. From 1888 onwards Keyes described a dozen species. Later (1920), A. O. Thomas³⁶⁹, when describing *P. inopinatum*, noted the perfect adaptation of the shell margin to irregularities on the surface of the crinoid. The occurrence of these very

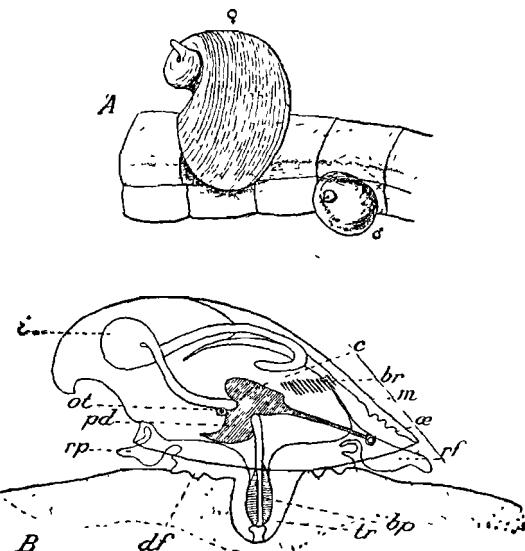


Figure 12. *Thyca stellasteris* and *T. ectoconcha*.

A, sexual dimorphism in *Thyca stellasteris* (after Kœhler and Vaney). *B*, anatomy of *Thyca ectoconcha* (after P. and F. Sarasin); *br*, gill; *c*, brain; *i*, intestine; *m*, mantle; α , eye; *ot*, otocyst; *pd*, pedal ganglion; *rp*, foot; *rf*, frontal fold; *df*, pseudo-foot; *bp*, pharynx; *tr*, proboscis.

ancient forms indicates that the parasitic capulids have passed through long geological periods of more recent date without showing any marked evolution.

2. EULIMIDÆ. This is a family allied to the Tænioglossa but lacking a radula (Aglossa). The shell is generally thin and translucent.

(a) *Eulima* is represented by a rather numerous assortment of small species whose turreted shells are common enough in the

littoral zone of our coasts. Certain *Eulima*, such as *E. polita*, still have a radula and are perhaps free-living. *E. distorta*, found on the coasts of Norway, is commensal or perhaps parasitic in a holothurian. Related species have been found in the alimentary canal of holothurians in Fiji and the Philippines where Semper has found them alive, creeping on the inner surface of the host's intestine. Three plainly parasitic species have been found: *E. ptilocrinicola* attached to an abyssal crinoid, *Ptilocrinus pinnatus*; *E. capillastericola* found at the base of an arm of *Capillaster multiradiata* at Singapore; and *E. equestris* on an arm of *Stellaster equestris*. This last species has been minutely studied by Kœhler and Vaney ³⁴⁸. It is a case of a true parasite which thrusts its long proboscis into the host, penetrating the general body cavity and acting as a sucking organ. Its anatomy is, on the whole, little modified; however, the foot is much reduced. The sexes are separate.

(b) *Pelseneeria* (a genus with which Vaney has fused the genus *Rosenia*) is comprised of species living on sea urchins and lacking a radula. One of these species, *P. stylifera*, has been found living on sea urchins in the North Sea. It moves about among the spines of its host but without leaving it to lay its eggs. Kœhler and Vaney have described three species, *P. profunda*, *P. media* and *P. minor*, from the dredge-hauls of the *Princesse Alice*. In these the proboscis is thrust through the test of the sea urchin. In *P. profunda* the mouth is surrounded by a large collar, with an irregular jagged border, partly covering the shell; we shall find this structure more or less developed in the following genera where it is known as the *pseudopallium*. It is a newly acquired adaptive structure, apparently derived from the epipodium. The foot is quite well developed but has no operculum. There is no radula. *Pelseneeria* species are hermaphrodite. With the exception of these characters their general anatomy is unmodified.

(c) *Megadenus* now includes four species: *M. holothuricola*, and *M. vältzkowi* living in the respiratory trees of holothurians; *M. cysticola*, found by Koehler and Vaney, producing thick-walled galls on the spines of a sea urchin, *Dorocidaris tiara*, in the Indian Ocean; and *M. arrhynchus*, found by A. V. Ivanov ³⁴⁵ on a starfish, *Anthenoides rugulosus*, in the Yellow Sea, where it, too, forms a kind of gall on the dorsal surface of the host. In the first two species there is a long proboscis, buried in the general

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body cavity of the host (*M. arrhynchus* lacks this, according to Ivanov). *M. cysticola* likewise has a proboscis. There is no operculum on the foot. A pseudopallium covers part of the shell round the mouth. The shell itself is turreted. Here, the sexes are separate and the animals are found in pairs, the male being the smaller (this is so in each gall containing *M. cysticola*), with the eggs nearby.

(d) *Mucronalia*. This genus includes rather a large number of species (in the single expedition of the *Siboga* six were collected) attached to sea urchins, ophiuroids, starfish and holothurians.

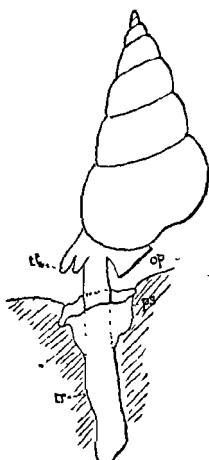


Figure 13. *Mucronalia palmipedis* (after Köehler and Vaney).
op, operculum; ps, pseudopallium; tt, tentacles; tr, proboscis.

The shell is well developed, as in the preceding genera, and terminates apically by several whorls which form a small cylindrical mucro. In this case, the operculum persists on the foot which itself is somewhat reduced. There is a long proboscis, without a radula, thrusting into the general body cavity of the host. On the other hand, the pseudopallium is very little differentiated. The sexes are separate. The anatomy remains clearly normal. It appears that these parasites always remain attached to one part of the host. Details of sexual phenomena have not been investigated up to the present.

M. variabilis, a parasite of *Synapta soplax* in Zanzibar, has

sometimes been found within the alimentary canal, sometimes on the external surface. It is a very variable species, primitive in some respects, modified in others. One aspect of modification which is of particular interest in connection with the following forms is the important regression shown by the alimentary canal. The proboscis pierces the intestinal wall of the synaptid and the parasite feeds by sucking up the host's cœlomic fluid. There is neither a radula nor salivary glands. One cannot find stomach or liver, and from the œsophagus there leads only a short canal ending blindly without an anus. The sensory organs remain; the eyes, which are very variable, tend to be buried under the skin. The animal is hermaphrodite. These different characters are very inconsistent, as is the behaviour of the animal.

In this genus, *Mucronalia*, the modifications undergone vary markedly from one species to another and these do not form a single plain series.

(e) *Stylifer*. This genus, too, contains a series of species some of which have been known for a long time. It is fairly closely allied to *Mucronalia*, but the foot, much reduced, has no operculum. The shell is thin and merely corneous. In certain species, *S. celebensis*, *S. linckiae*, the pseudopallium is very greatly developed (Fig. 14ps) and completely covers the shell; the animal is enveloped in it. A comparatively long proboscis, lacking a radula, penetrates into the cœlom of the host and sometimes spreads out into a large terminal swelling. The alimentary canal shows degeneration, notably in the liver which is rudimentary or completely absent. Four species of *Stylifer* are known. One, *S. sibogæ*, is hermaphrodite; in the others the sexes appear to be separate, and this is certainly so in *S. linckiae*. This genus is altogether interesting, particularly on account of the further development of the pseudopallium and the reduction of the foot. On the whole, anatomically, it does not diverge very far from the normal.

The various genera that we have just considered are fairly close to one another and represent multiple variations of the genus *Eulima*. They retain the fundamental anatomy of the prosobranchs.

(f) *Gasterosiphon*. The modifications due to parasitism become much more striking in this genus, of which two specimens

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have been found by Kœhler and Vaney³⁴⁸ in an abyssal holothurian, *Deima blakei*, in the Indian Ocean. They are of great interest as they clearly relate the Eulimidæ, which we have dealt with, to the Entoconchidæ which we shall come to later.

Gasterosiphon deimatis (Fig. 15) is an internal parasite remaining in contact with the outside world by means of a small opening passing through the skin of the holothurian. Examination of the general body cavity of the latter shows a slender duct

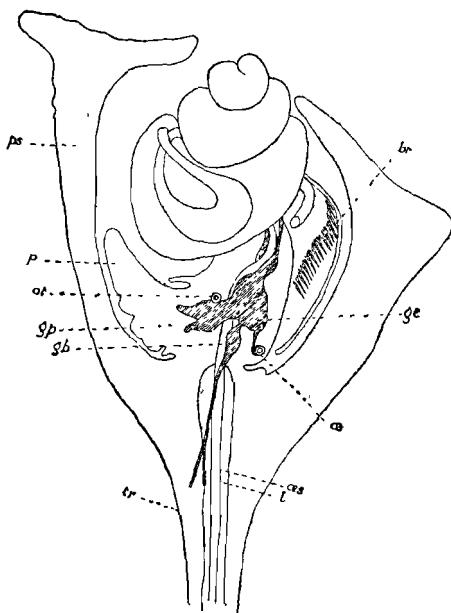


Figure 14. Anatomy of *Stylifer linckiae* (after P. and F. Sarasin).
br, gill; *gb*, buccal ganglion; *gc*, cerebral ganglion; *α*, eye; *ot*, otocyst;
as, oesophagus; *p*, foot; *ps*, pseudopallium; *tr*, proboscis.

leaving this opening; this is the siphon, *s*, which is about 10 mm. long and leads to an ovoid swelling of from 5 to 10 mm., from which there continues a second duct, also thin and very long (104 mm. long and 0·7 mm. in diameter); this second duct is attached distally to the marginal vessel on the intestine of the holothurian and is homologous with the proboscis of the preceding genera, but very highly developed. The parasite feeds by imbibing the blood of its host.

If one opens the swelling connecting the two tubes (siphon and proboscis) one finds (Fig. 15B) within it a clearly recognizable gastropod although manifestly degenerate. The shell has completely vanished but a visceral hump remains and there are vestiges of the foot, *p*. There is nothing to be seen of the cephalic tentacles, nor of the true mantle, the gills, kidney or heart. The central nervous system is, on the other hand, retained as a whole and condensed. The œsophagus leads into a gastric cavity, *st*, from which there ramify ducts constituting a hepato-pancreas.

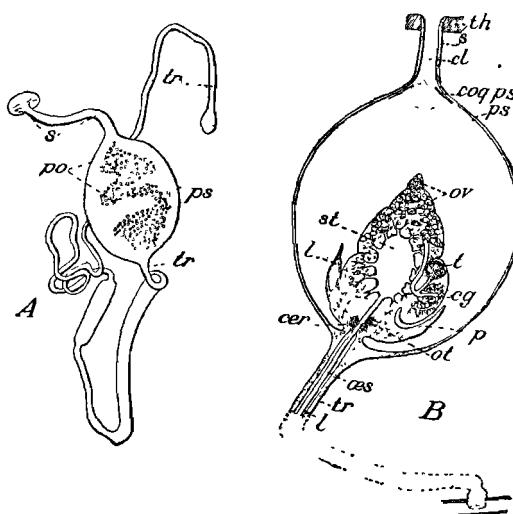


Figure 15. *Gasterosiphon deimatis* (after Kœhler and Vaney).

A, the whole parasite, *B*, its anatomy; *po*, egg masses; *ps*, pseudopallium; *s*, siphon; *tr*, proboscis; *œs*, œsophagus; *cer*, brain; *l*, blood lacuna; *ot*, otocyst; *p*, foot; *cg*, oviduct; *t*, testis; *ov*, ovary; *st*, stomach; *coq-ps*, pseudo-pallial shell calcification; *th*, body-wall of host.

There is neither intestine nor anus. The animal is hermaphrodite. Ovary, *ov*, and testes, *t*, are two distinct glands, but the ducts unite. Round the visceral mass the cavity of the swelling in which it is enclosed is filled with developing embryos. The outer wall of this swelling is none other than the pseudopallium enormously developed. In *Stylifer linckiae* it totally encloses the animal, which no longer communicates with the outside except by a narrow aperture. Here the pseudopallium has

developed further and is enclosed within the narrow duct which forms the siphon and maintains communication with the external environment. A slender peripheral calcareous ring ensures that the end of the siphon remains open.

In spite of the magnitude of the changes that have taken place *Gasterosiphon* is readily linked with *Stylifer* and to all the preceding examples.

(g) *Diacolax*. This genus was described in 1945 by Mandahl-Barth³⁵⁶ from a single specimen found on a holothurian, *Cucumaria mendax*, in the Falkland Islands. It is an external parasite. The pseudopallium completely covers the body, forming an ovoid mass terminating in a point, the siphon. The anterior extremity of the animal penetrates far into the general body cavity of the holothurian. The visceral mass (in the midst of the pseudo-pallium) consists only of the intestine surrounded by the ovary. There is no longer a shell. Within the cavity of the pseudopallium there are numerous groups of eggs in various stages of development. Segmentation is total and spiral. The veliger larva, resembling that of *Entocolax* and *Pædophoropus*, has a thin hyaline shell, slightly thickened at the peristome and with a greatly flattened apex.

Diacolax, according to Mandahl-Barth, would be the culmination of the Eulimidæ series (*Eulima-Mucronalia-Stylifer-Gasterosiphon-Diacolax*).

3. ENTOCONCHIDÆ. The genus *Gasterosiphon* is of particular interest in that it provides a solid basis for interpreting types that are much more degenerate than the Entoconchidæ. In fact, Schiemenz had, before the discovery of *Gasterosiphon*, interpreted these types fairly correctly although his grounds for doing so were purely conjectural. Knowledge of *Gasterosiphon* gave him a solid foundation of fact.

Anatomical degeneration in the Entoconchidæ is so considerable that it was the cause of a mistake in interpretation which remains historically significant. In Trieste, in 1851, Joh. Müller, studying the genital glands of a holothurian, *Synapta digitata*, found that in their vicinity there were in certain animals some long and unbranched ducts containing embryos and veliger larvæ of gastropods. He gave to these larvæ the name of *Entoconcha mirabilis*, but explained their presence by a most singular hypothesis, suggested by the idea, then becoming current, of

alternating generations. In fact, he believed that he had come across a case of this kind involving molluscs and holothurians, and that *Synapta* itself was producing the gastropod larvæ.* He missed the explanation, in reality so simple, of its being a case of parasitism; but it must be pointed out that there is no indication of molluscan structure in the ducts containing the veligers and, further, at that time none of the examples given above was known. It was Baur who, in 1861, on returning to the study of the holothurians of Trieste, showed that it was indeed a case of parasitism.

Since that time two genera analogous to *Entoconcha* have been discovered in holothurians: *Entocolax*, first met with in synaptids from the Bering Sea, and *Enteroxenos* in *Stichopus tremulus*, from the coasts of Norway. *Enteroxenos* has been thoroughly investigated, even cytologically. Degeneration in these three types (*Entoconcha*, *Entocolax* and *Enteroxenos*) is extreme. They are reduced to simple vermiform tubes where, practically speaking, there is no trace of molluscan structure; the larvæ alone allow of the identification of the group.

(a) *Entocolax* is now represented by three species which are internal parasites of holothurians: *E. ludwigii* in *Myriotrochus rinkii* (Bering Sea), *E. schiemensi* in *Chiridota pisanii* (Chile), and *E. trochodotæ* in *Trochodota purpurea*. We owe the correct interpretation of the anatomy of the genus to Schiemenz³⁶⁶.

One end of the animal is fixed to the skin of the host. An initial tubular section swells out into a vesicle from which is given off a long narrow duct floating freely in the general body cavity of the holothurian (Fig. 16A). This last duct is none other than the proboscis, with the oesophagus, *œs*, which at its proximal extremity enlarges to form a kind of blind stomach, *ih*, abutting against a mass of tissue within the base of the vesicle; within this mass, which juts out into the vesicular cavity, one can recognize ovary, oviduct and uterus. The eggs fall into the cavity and develop there. Now that we are familiar with *Gasterosiphon*, the vesicular swelling and the duct which attaches it to the skin of the host can be interpreted as a highly developed pseudopallium. But the visceral mass, which in *Gasterosiphon* still

* Haeckel made a similar mistake, though less extreme, in connection with certain medusæ, *Cunina*, which develop as parasites in other medusæ, but which he believed to be a stage in the life cycle of the latter.

contains the typical organs of a gastropod, is here reduced to the ovary.

Heding³³⁹, in 1935, made known a third species of *Entocolax*, *E. trochodotæ*, close to the preceding ones, and he recognized dwarf males (he found seven) attached to the inner surface of the pseudopallium within the vesicular cavity; similar males had been discovered earlier by Schwanzwitsch³⁶⁷ in *E. ludwigii*. The eggs develop freely in the cavity of the pseudopallium and

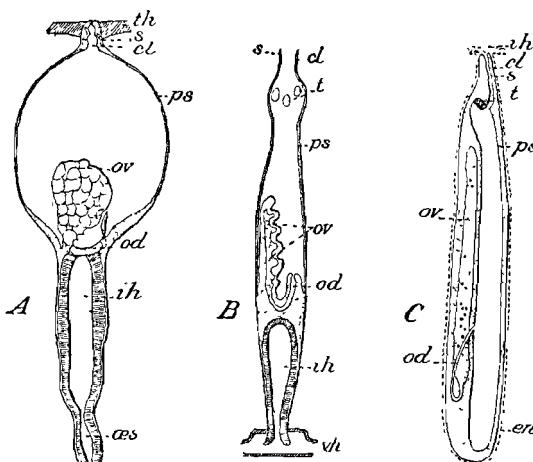


Figure 16. Structure of *Entocolax* (A), *Entoconcha* (B) and *Enteroxenos* (C) (after Vaney).

cl, ciliated canal; *ih*, hepatic intestine; *od*, oviduct; *as*, œsophagus; *ps*, pseudopallium; *s*, siphon; *t*, testis; *en*, sheath of the host's peritoneum (enveloping *Enteroxenos*); *vh*, ventral vessel of the host's intestine.

give rise to veliger larvae of typical gastropods, with shell, velum and foot.

It is clear that *Entocolax* shows marked regression in comparison with *Gasterosiphon*, and in particular with the other genera of Eulimidae that we have considered.

(b) *Entoconcha* provided J. Müller and Baur with relatively abundant material and it would be interesting to study this genus again, using modern techniques. We can still count on finding it in the Adriatic. *E. mirabilis* occurs (Fig. 17) in *Synapta*, in the shape of thin cylindrical tubes without any swelling and

attaining a length of up to 80 mm. They are attached by one end, the proboscis, to the ventral vessel of *Synapta*. From the point of attachment three successive regions can be distinguished: the first is the proboscis; the mouth (*b*) of the parasite is buried in the ventral vessel, *vv*, of the host; the digestive apparatus is reduced to a simple tube, the oesophagus, which extends for about a third of the total length and ends blindly. At the end of this section there is a partition enclosing the ovary and separating the oesophagus from another cavity which extends the whole length of the distal region and in which the embryos and

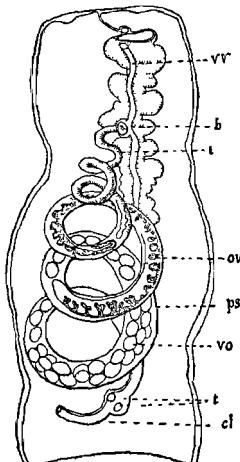


Figure 17. *Entoconcha mirabilis* (after Baur) and its relationships with the host.

b, mouth, fixed to the ventral vessel, *vv*, of the host's intestine; *i*, intestine; *ov*, ovary; *ps*, pseudopallium; *vo*, masses of developing eggs; *t*, testes; *cl*, ciliated canal.

larvae are found. It corresponds as a whole to the median swelling and siphon of *Gasterosiphon* and *Entocolax*. But here, at least as far as one can judge from the old descriptions, organic regression has gone even further. Of the viscera of the mollusc only the ovary remains. A group of small vesicles, varying in number and with a contractile wall, juts out into the siphon towards its distal extremity and is considered to be the testis. In the light of the more recent observations made by Heding³³⁹ on *Entocolax*, we may ask whether these so-called vesicles are not, in fact, dwarf males, attached at this point.

(c) *Enteroxenos*. The adults are tubular and 100 to 150 mm. in length, lying free in the general body-cavity of the holothurian, *Stichopus tremulus*. The young stages are attached to the outer surface of the anterior region of the intestine (Fig. 18). Younger stages have even been found completely enclosed within the wall of the oesophagus. It is the most degenerate of all the parasitic gastropods. The tube constituting it shows, indeed, only a single axial cavity extending along its whole length (Fig. 16C); it terminates blindly at its distal end and opens by a slender canal on the proximal side. The ovary lies in the wall of the central canal, the testis at one end. We can no longer distinguish either proboscis or a distinct alimentary canal, at

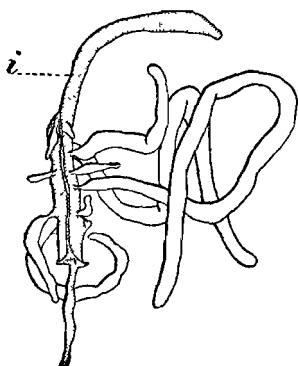


Figure 18. Part of the gut of *Stichopus* bearing individuals of *Enteroxenos* of various sizes (after Bonnevie).

any rate in the stages studied. The whole length of the animal seems to correspond to the pseudopallium. The parasite is thus reduced to a sac of embryos no longer showing any trace of the primitive structure of a mollusc.

On the other hand, the larvae of these degenerate types immediately reveal their nature. They are typical veligers, with a coiled shell, velum, visceral hump, foot, operculum, nervous system and otocysts (Fig. 19).

(d) *Thyonicola*. This genus was described in 1941 by Mandahl-Barth³⁵⁵ from a species *Thyonicola mortensenii*, found inside an abyssal holothurian, *Thyne secreta*, collected in the vicinity of the Cape of Good Hope. As many as 30 and 40 parasites (from

a few millimetres to 7-8 centimetres in length) were found in the same host. The large specimens formed compact tangled knots. They are tubular, long and narrow, and fixed by their anterior end to the intestine of the holothurian. There is no trace of intestine nor of other organs. At the anterior extremity there is a testis, at the posterior one an ovary. Within the tubes the eggs are incubated by thousands. The veliger larva possesses a tiny coiled shell and an operculum. Mandahl-Barth observes that in many ways this parasite resembles *Enteroxenos rentergios**. At present we know only six species and four genera of Entoconchidae. It is to be presumed that others exist. These four genera, *Entocolax*, *Entoconcha*, *Enteroxenos* and *Thyonicola*, while displaying great similarity in general, nevertheless differ much in their structure and their relations with the host. They

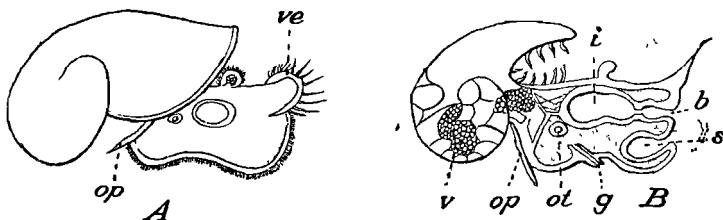


Figure 19. Veliger larva of *Entoconcha*. A, external aspect.
B, optical longitudinal section (after Baur).

b, mouth; g, pedal gland; i, gut; op, operculum; ot, otocyst; s, sac-like invagination; v, residual yolk; ve, velum.

cannot be regarded as being directly derived from one another. They belong rather to parallel series, having evolved independently, and the broadly similar conditions of parasitism have led to their general convergence. Knowledge of *Gasterosiphon* suggests that they may be derived from the Eulimidae, but, starting from types such as *Thyca*, other forms have been able to develop which are equally degenerate and more or less similar.

Here let us briefly consider two other types of gastropods which are also very degenerate and were discovered on echinoderms collected by the Albatross: one, *Ctenosculum hawaiiense*,

* On account of their being hermaphrodite, Mandahl-Barth puts forward the possibility of affinity between the Enteroxenidae and the Opistobranchia. I will confine myself here to drawing attention to this suggestion, which appears to me to be scarcely plausible.

described by Heath³³⁸ from a starfish, *Brisinga evermanni*, near the islands of Hawaii; the other by Heath and Randall³⁶² as *Asterophila japonica* from a *Pedicellaster* in the Sea of Japan. *Ctenosculum* produces on the arms of the starfish a type of gall provided with an external opening; *Asterophila* is entirely immersed in the cœlom of the arm and is attached to the wall of the latter by a filament; it has no means of communication with the exterior. These are highly modified forms but they are less degenerate than the preceding ones. The globular body is entirely surrounded by a pseudopallium. In both there are vestiges of typical molluscan organs (complete alimentary canal, radula, liver, foot). We may consider, without stressing it further here, that they belong to a series clearly distinct from those discussed above. *Ctenosculum* is hermaphrodite.

4. PÆDOPHOROPODIDÆ. Finally, there is another type of parasitic gastropod, *Pædophoropus dicælobius*, living within holothurians and quite distinct from the preceding molluscs. It is found either in the Polian vesicles or in the respiratory organ of *Eupyrgus pacificus* in the Sea of Japan, and has been thoroughly investigated by A. M. Ivanov³⁴⁶. He was able to examine a dozen specimens (7 females, 5 males). These parasites (Fig. 20) live in pairs, the male on the right side of the female. Both sexes possess a long proboscis which is applied to the alimentary canal of the host. The body itself forms a conical mass at the base of which the organs of the head may be seen. There is no trace of the shell. The male has a very large penis. Within the visceral mass are the principal systems of gastropod organs (digestive tube and related structures, nervous system, kidney, ovary or testis). There are, however, neither gills nor heart, and there is no structure to be seen that corresponds with the pseudopallium. The foot is produced into right and left lateral lobes; in the female these join along the middle line, forming an enormous spherical sac, opening ventrally, within which the embryos are incubated. The musculature of this foot is rudimentary. The larvæ have the typical and highly differentiated structure of a gastropod, with a dextral shell which is thin and transparent, an operculum, a voluminous foot with two large glands (anterior and posterior). *Pædophoropus* thus constitutes a type clearly distinct from the preceding ones and Ivanov has very properly created a new family for it, the Pædophoropodidæ.

LAMELLARIIDÆ. In conclusion we must mention a type of molluscan parasite, *Pseudosacculus okai*, described by Hirase from material collected by the Albatross and found in the depth of the test of some ascidians, *Ascidia prunum* and *Boltenia ovifera*, forming a type of gall open to the exterior. All things considered, the anatomy of these animals does not show any clear mark of parasitism. Hirase has been led to relate them to

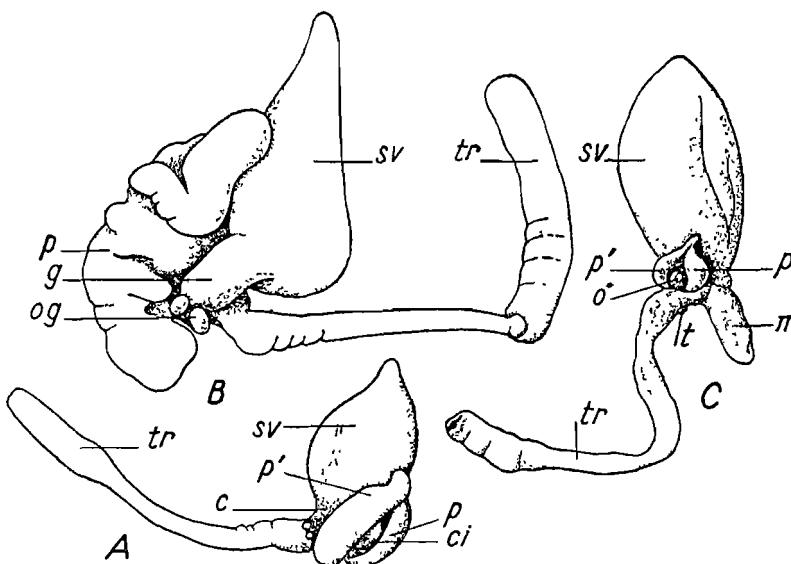


Figure 20. *Pædophoropus dicælobius* (after A. W. Ivanov).

A, young female (left side), *B*, adult female (right side), *C*, male (ventral surface); *c*, cephalic region; *ci*, brood pouch (early age); *g*, genital regions (♀); *o*, orifice of the pedal gland; *og*, region of the genital opening; *p*, *p'*, right and left lobes of the foot; π , penis; *sv*, visceral sac; *t*, tentacle (rudimentary); *tr*, proboscis.

the Lamellariidæ. If one considers that *Lamellaria* lays its eggs in batches in the depths of colonies of compound ascidians, where they appear as a kind of gall in which the embryos develop and from which they emerge as larvæ, and if, on the other hand, one remembers that *Pseudosacculus* has been found in groups of eleven and nineteen individuals in one gall, one is led to ask whether here we have simply a case of a gastropod close to *Lamellaria* laying its eggs in batches from which the

young escape in a very advanced stage, and whether it would have been these late larvæ, just about to escape, that the Japanese writer had before him.

I have thought it essential to examine in some detail these different cases of parasitism in molluscs, and especially in the gastropods, because they appear to me to demonstrate with particular significance the changes which may be determined by parasitism. In them the starting point may clearly be seen and from *Thyca* to *Stylifer* and in the Entoconchidæ we have been able to gauge the extent to which these modifications occur and the morphological degeneration that results from them. On the other hand, it is clear that in a given group parasitism is not a one-way track but that starting from the same general initial type it can lead to completely independent modifications, differing profoundly from one another. Particularly suggestive, to my mind, is the formation and progressive development of the pseudopallium in the Eulimidæ and the Entoconchidæ and its total absence in *Pædophoropus* where, on the other hand, we find the foot modified and hypertrophied to form a brood pouch.

As I have already said, it is probable that other types of gastropod parasites, whether members or not of the preceding series, still remain to be discovered. In this chapter I have left on one side the facts relating to temporary parasitism occurring amongst the bivalves belonging to the Unionidæ. They are of a special type and we shall return to them later.

CHAPTER V

ADAPTATION TO PARASITISM IN THE CRUSTACEA

IN the preceding chapter the molluscs have provided us with a graduated series of significant examples showing morphological degeneration under the influence of parasitism. We shall meet with the same kind of facts amongst the Crustacea, a group which, like the Mollusca, is essentially composed of free-living forms. But here, in the different orders and families, the cases of parasitism are much more numerous and extend to whole groups, families or collections of families, with varying degrees of adaptation. Considering the almost geometrical type of morphology amongst these animals, we shall find that the resulting malformations are highly significant and interesting to analyze. Let us first, from a general point of view, look at the way in which parasitism has extended into the different subdivisions of this class.

Among the *Entomostraca* there are several groups of parasites.

1. **CIRRIPEDIA**. Amongst these are the Rhizocephala parasitizing other Crustacea, and the Ascothoracica parasitizing coelenterates and echinoderms. These two groups are entirely composed of parasites and are both profoundly modified.

2. **COPEPODA**. This enormous order includes many families, consisting for the most part of free-living forms but with many members adapted to parasitism on a great variety of hosts and therefore more or less modified, sometimes very considerably.

The *Malacostraca* include the following:

3. **AMPHIPODA**. In this order there is only one isolated case of parasitism, that of *Cyamus*, the whale louse, which lives as a parasite but is little modified.

4. **ISOPODA**. This order provides us with examples of adaptations to parasitism that are varied and more or less profound in extent in the Gnathiidæ, which are parasitic in the larval stages

and free-living as adults; in the Cymothoidæ which, are external parasites of fish, and, above all, in the Epicaridæ, which parasitize other Crustacea; they particularly hold our attention on account of the diversity and extent of their modifications.

ISOPODA

GNATHIIDÆ. Amongst the Isopoda the Gnathiidæ comprise a sub-order of a highly specialized and homogeneous character, from the point of view of both morphology and behaviour. They have been the subject of exhaustive research by Monod²⁵⁵. During the course of development they are for a time parasitic on fish and suck their blood. At the end of this phase, that is when they are adult, they are free-living and show considerable sexual dimorphism, so much so that for a long time the males and females of a single species were placed in different genera: the males in *Anceus* Risso 1816 and the females and young of both sexes in *Praniza* Leach 1817. The adult female was first described as *Gnathia* by Leach (1813), a name which is still valid on account of the law of priority. It was E. Hesse²⁴⁶, who, in 1885, showed that *Praniza* was a young stage of *Anceus**. The generic name of *Gnathia* was restored to priority in 1880 by Harges.

The larva, as in all isopods, has all its segments differentiated when it hatches; it swims about, soon attaching itself to a fish and sucking its blood; this produces hypertrophy of the third, fourth and fifth thoracic segments and leads to the praniza form. The host species is very variable, and also the place of attachment. The skin of the fish is pierced by the first pair of maxillæ and the mandibles serve to fix the parasite in place. Monod calculates that the parasitic phase lasts for six months. Metamorphosis of the male into an *anceus* form, and of the female into a *gnathia*, occurs after the parasites have left the host; it is much more extensive in the male than in the female. The adults live in holes dug out in the mud of estuaries, or within hollows such as empty *Balanus* shells, where they form small

* "On 19th August, 1852, I collected from a *Trigla hirundo* a *Praniza* which, as usual, I was eager to paint in order to record its exact shape and colouring. As I was obliged to be away from home for a few days I kept it in seawater instead of putting it into alcohol as I always do. On my return my first thought was to visit my *Praniza*; but, what was my astonishment to find it replaced by an *Anceus*." (Hesse²⁴⁷, p. 235.)

communities usually consisting of one male and a series of females. The embryos develop within the body of the female, which gradually swells up. The blood ingested during the parasitic phase still fills the cæca of the intestine.

Parasitism is thus limited to the larval stages and so comes into the category of *protelean* parasitism which we shall consider later.

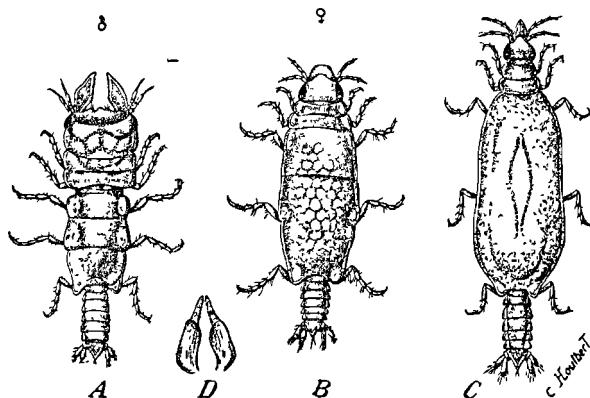


Figure 21. *Gnathia maxillaris*.

A, adult male (anceus form). *B*, adult female (praniza form). *C*, larva (praniza form). *D*, larval mandibles (after G. O. Sars).

CYMOTHOIDÆ. This group of Isopoda has been divided into some ten families of which two (*Ægidæ*, *Cymothoidæ*, *sensu stricta*) have some parasitic characters. The *Ægidæ* are commensals or inquilines rather than true parasites, e.g. *Æga spongiphila* in *Euplectella aspergillum*. However, many species live on the skin of fishes, where they attach themselves by means of the hooked terminal segments of their anterior limbs; the posterior limbs remain clearly ambulatory. The mouth-parts are modified for piercing, plainly an adaptation for parasitism.

The *Cymothoidæ* are much more obviously parasites. They are sedentary on the skin of fishes. One genus, *Ichthyoxenus*, of which four species are known, even lives in a special cavity, constructed so that it passes through the body wall of the host and bulges into the general body cavity. Inside this sac there are always two individuals, a male and a female, which must have made their way in while young and have completed their growth

there. Most of the Cymothoidæ change their sex, a peculiarity which is probably due to parasitism. On the whole, their structure is but little modified.

EPICARIDÆ. There is a very different state of affairs in the case of the Epicaridæ, which have a special interest for us on account of the often considerable extent and diversity of their modifications, resulting from adaptation to parasitism on various groups of other Crustacea. They have been the subject of a great deal of research, some of the most valuable being that of A. Giard and J. Bonnier, between 1880 and 1900. Facts established by them remain valid for us today; certain details have, however, been determined or corrected in more recent works.

One of the difficulties in studying the Epicaridæ is that very often the only available specimens are few in number and preserved in alcohol, since they come from museums or material collected by oceanographical expeditions. In many accessible localities they are usually rare animals, but this is not a case of absolute rarity, and a certain species which is extremely uncommon in some places is very abundant in others. I shall give two examples of this: *Hemioniscus balani*, a parasite of *Balanus balanoides* which in the English Channel covers the rocks in the upper part of the intertidal zone, and *Portunion mænadis*, an internal parasite of the common crab, *Carcinus mænas*. At Wimereux, Giard and Bonnier examined tens of thousands of these two hosts, but were only able to collect one or two *Hemioniscus* and a very occasional *Portunion*. But in the vicinity of the Cape de la Hague, F. Mesnil and myself ²²⁸ were able to collect large numbers of all stages of *Hemioniscus* without any difficulty, and recently Veillet ²⁷⁸ collected quantities of *Portunion*, also in all stages, near Sète, in the lagoon at Thau. It is only under such conditions that one can elucidate the details that are still obscure.

The Epicaridæ comprise well-defined types, very different from each other and profoundly modified, each type corresponding to a definite group of hosts. There has been special adaptation to each group. In the Epicaridæ this has resulted in a series of highly individualized families that we shall now review. But first we shall examine the fundamental unity of the sub-order which is clearly apparent from the strictly uniform

character of its larval types. Here we have a striking case of evolution brought about under the influence of parasitism.

There are three consecutive stages: *epicaridian*, *microniscan* and *cryptoniscan*. The eggs, as in all the isopods, are incubated by the female, either externally, beneath the thorax in a cavity bounded by the brood lamellæ which are the epipodites of the thoracic limbs, or (in the Cryptoniscidæ) in a special cavity, which develops at sexual maturity, within the body of the female. This double arrangement also occurs amongst the free-living Isopoda.

(a) *Epicaridian* phase. The larvæ hatch in the epicaridian stage (Fig. 22) and appear as typical small isopods like *Spha-*

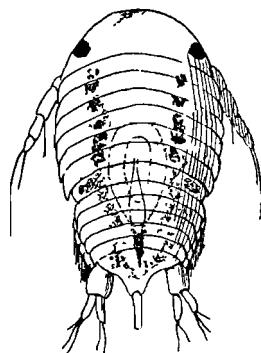


Figure 22. Epicarid larva of *Cancricepon elegans* (after Giard and Bonnier).

roma or *Cymothoa*, with all the thoracic and abdominal segments and appendages well defined, and apparently normal. Their parasitic nature is, however, shown by the hooked extremities of the thoracic limbs and more especially by the mouth-parts modified as stylets for piercing (Fig. 24C). This larval type is common to the whole family and is perfectly uniform. After hatching they swim actively and are part of the surface plankton.

(b) *Microniscan* phase. I was the first to have the opportunity of seeing, in living laboratory material²²⁵, how these epicarid larvæ, when placed in contact with other planktonic animals, rapidly attach themselves to copepods, as *Acartia*,

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Calanus, etc. (Fig. 23). It had already been observed that microniscan stages were present on copepods in plankton samples, but Giard and Bonnier, in particular, believed that these were autonomous Epicaridæ, localized on copepods. However, G. O. Sars had suggested that *Microniscus* was simply a stage in the development of various Epicaridæ.

Microniscan larvæ metamorphose on the copepod which carries them while they are undergoing their moults. Caroli²²³ was able to follow these in detail in an aquarium. The epicari-

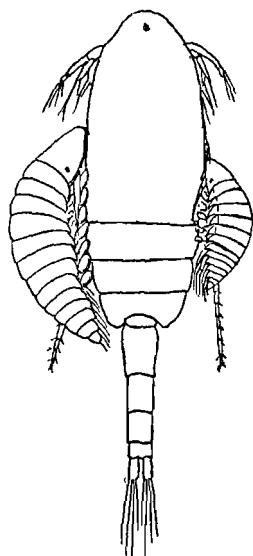


Figure 23. *Microniscus* stage, on *Calanus elongatus* (after G. O. Sars).

dian larvæ of *Ione thoracica*, a parasite of *Callianassa stebbingi*, were placed in contact with planktonic copepods to which they attached themselves, and Caroli was able to watch the changes by which in two successive moults and after six or seven days they achieved the larval form known as cryptoniscan; this larva leaves the copepod and is free swimming.

(c) *Cryptoniscan* phase. This third larval type (Fig. 24A) is much more slender than the epicarid and, like it, is very regular in character throughout the Epicaridæ. It, too, has the structure and appearance of a free-living isopod, swims actively, and is

frequently found in pelagic samples. All the thoracic and abdominal appendages are present and normal in structure; the mouth-parts retain their piercing and sucking character. It is this larva that seeks for and attaches itself to the final host, or the planktonic larvæ of the latter. This marks the onset of the

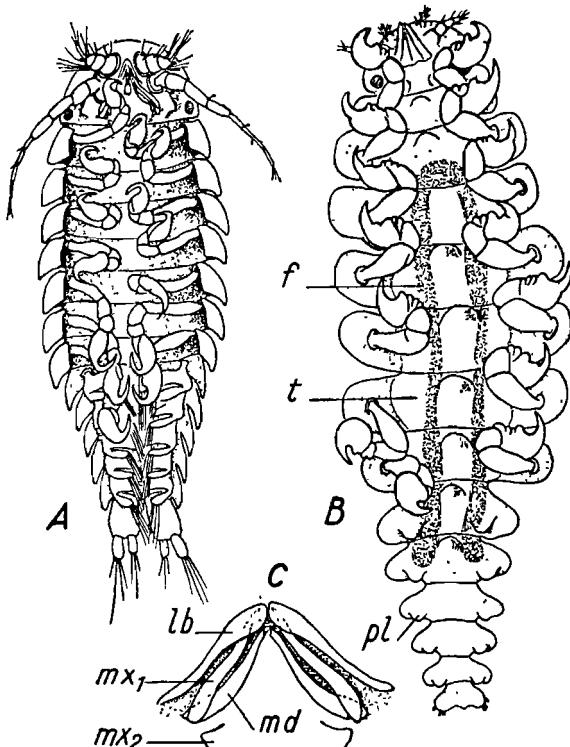


Figure 24. *Cepon elegans*.

A, cryptoniscan larva (ventral aspect). B, adult dwarf male (ventral surface): f, liver; pl, rudimentary pleopod; t, testis. C, rostrum of the epicarid larva with the mouth parts: md, mandible; mx₁, first maxilla; mx₂, second maxilla (after Giard and Bonnier).

truly parasitic phase. While up to now we have seen perfect regularity throughout the group, henceforth we shall witness profound divergences according to the different groups of hosts. We shall now indicate the principal types, constituting as many families.

FAMILIES OF EPICARIDÆ

1. **BOPYRIDÆ**, parasites in the branchial cavity of decapod Crustacea. They are subdivided into *Bopyrinæ*, parasitizing prawns and their allies, and *Ioninæ*, parasitizing Brachyura and Anomura. Principal genera : *Bopyrus*, *Cepon*, *Ione*, etc.

2. **PHRYXIDÆ**, found fixed to the abdomen of decapods (Macrura, Paguridæ), and generally very asymmetrical. Genera : *Phryxus*, *Athelges*, etc.

3. **ENTONISCIDÆ**, internal parasites of decapods, principally crabs, found among the viscera of the host and profoundly modified. Genera : *Entoniscus*, *Portunion*, *Priapion*, etc.

4. **DAJIDÆ**, external parasites of schizopods, attached to various parts of the host (thorax, abdomen, gills) and more or less modified. Genera : *Dajus*, *Notophryxus*, *Branchiophryxus*, etc.

Let us notice here and now a common characteristic of these four families: the sexes are strictly separate; the dwarf males, curiously modified, live regularly on the females, generally beneath the abdomen or in the brood pouch of the latter.

5. **CRYPTONISCIDÆ**, a very extensive group of varied aspect, found on different types of Crustacea (Entomostraca and Malacostraca), and profoundly modified. Amongst them one may distinguish a series of separate families, each corresponding to a given group of hosts. Let us now note that here, contrary to the preceding groups, there is sex reversal, with first a male phase in the free-living cryptoniscan larva, and secondly a female phase when the animal is attached to the host and becomes profoundly malformed. Here the brood pouch is internal.

Among the Cryptoniscidæ, the *Cabiropsidæ* live on isopods (some are hyperparasites attached to other Epicaridæ). The *Cyproniiscidæ* live on ostracods, the *Hemioniscidæ* on cirripedes (*Balanus*), the *Liriopsidæ* on Rhizocephala (and as a result some such as *Danalia* are secondarily carried on the crabs which are hosts of Rhizocephala), etc.

Altogether the Cryptoniscidæ vary in very different ways, according to the different types of host, but show a fundamental unity demonstrated by hermaphroditism and the conditions under which the embryos are incubated.

These few facts suffice to show the special interest of the Epicaridæ for the general study of parasitism. Let us now examine separately each one of these groups.

(1, 2) BOPYRIDÆ and PHRYXIDÆ. The Bopyridæ are, on the whole, the least modified of the Epicaridæ and form a natural group localized on decapods. *Bopyrus* and the Ioninæ live in the branchial cavity of their hosts and everyone has had occasion to notice the lateral swelling that a *Bopyrus* produces on the thorax of edible prawns (*Leander*). The Phryxidæ (*Phryxus*,

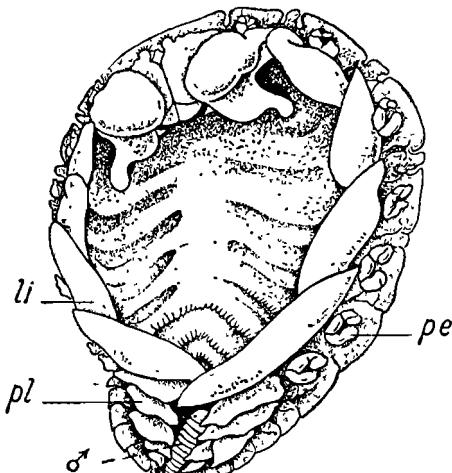


Figure 25. *Bopyrus fougerouxi*, a parasite of *Leander serratus*, from the ventral aspect.

li, brood lamellæ (oostegites); *pe*, thoracic limbs (pereiopods); *pl*, abdominal appendages (pleopods); ♂, dwarf male (after J. Bonnier).

Athelges) live on the abdomen of their hosts (Carididæ, Paguridæ) and have a rather different appearance though their structure is very similar.

In the female *Bopyrus* (Fig. 25) one may easily recognize the isopod type. It is enlarged but all the segments are easily made out and have retained their appendages: hooked pereiopods and lamellar pleopods with a respiratory function. These last appendages are highly developed in the Ioninæ (*Cepon*, Fig. 26), where they are pinnate and even branched. Between the pleopods there is always a male, dwarfed and slim, closely resembling the

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cryptoniscan larva but usually lacking its pleopods. In all the Bopyridæ there is marked asymmetry in connection with their lateral (right or left) attachment to the host. Among the Phryxidæ this asymmetry is very pronounced and leads to the disappearance of all the appendages on one side. This clearly shows how much the malformation of parasites depends on the conditions of parasitism. In the present case, is the development of asymmetry directly dependent on the site of attachment or does each

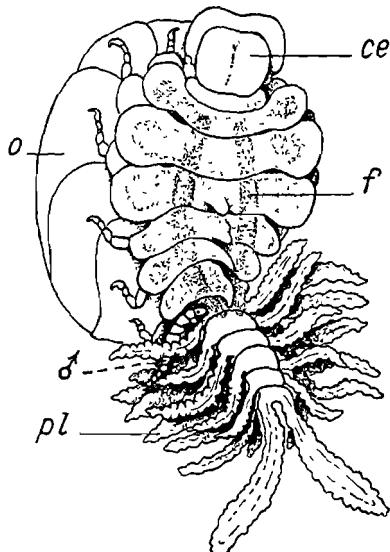


Figure 26. *Cepon elegans*, a parasite of *Pilumnus hirtellus* (after Giard and Bonnier).

Adult female (dorsal aspect) with dwarf male, ♂; ce, cephalogaster; f, liver; o, oostegites; pl, pleopods.

larva, in becoming attached, select one side for this on account of its appropriate constitution? Only precise experiments would allow us to decide this question and they are hardly possible in practice. For the sake of comparison, we may recall that among the gastropod molluscs which are also asymmetrical (dextral or sinistral), the direction of asymmetry is fixed in the egg and is expressed by the orientation of the spindle at the first division of cleavage.

Attachment of the parasite to the host generally takes place

when the latter is very young, either approaching the end of its larval life or immediately afterwards. I have myself had occasion to see this in *Bopyrus* parasitizing a prawn. The growth of the parasite parallels that of the host and Caroli³⁷⁶ was able to see that their moults occur simultaneously.

All these parasites, in order to feed, pierce the body wall of the host with their mouth-parts (mandibles and maxillæ) modified as stylets (actually in the epicardian stage) and ending in a small toothed blade. They suck the blood. On the dorsal part of the cephalic region there is a double hemispherical swelling forming the *cephalogaster* (Fig. 26 *ce*), especially developed in the Entoniscidæ, which must play an important part in the aspiration of the host's fluids. It is clearly an adaptive arrangement. The last part of the intestine is no longer functional; the imbibed fluids accumulate in the hepatic ducts, which become very large. There they are gradually dialyzed and altered so that finally they constitute reserves of fat within a special tissue or in the vitelline substance of the egg. Ventrally the thoracic segments bear the hooked pereiopods with epipodites constituting the brood lamellæ, *oostegites*, relatively little developed in *Bopyrus* (Fig. 25) but much more so in the Ioninæ (Fig. 26), and these lamellæ enclose the brood pouch where the embryos develop until they hatch as epicardian larvae.

The question of the conditions governing the determination and differentiation of sex in these parasites comes naturally to mind. An obvious conclusion is that sex results from the very conditions of parasitism; a cryptoniscan larva attaching itself directly to the host and therefore finding favourable conditions for feeding would develop as a female; on the other hand, a larva newly established on a young female would become a male. I myself have suggested²²⁷ that it could be thus, particularly among the Entoniscidæ where (see below), in the brood pouch of each female, one always finds rather large numbers of males and of cryptoniscan larvae which will develop as males. Recent observations (D. Atkins, Veillet) do not bear this out and tend to show that in the Entoniscidæ sex is already determined in the cryptoniscan larval stage where entry into the host occurs.

But my hypothesis is clearly established by some exact experiments carried out with one of the Ioninæ (*Ione thoracica*, a parasite in the branchial cavity of *Callianassa subterranea*) and in

addition with one of the Phryxidæ (*Stegophryxus hyptius*, a parasite on the abdomen of *Pagurus longicorpus*). Actually, Reverberi and Pitotti²⁷² took young males of *Ione thoracica* at the beginning of their metamorphosis on females and moved them into the branchial cavity of an unparasitized *Callianassa*; they quickly attached themselves, lived there and in most cases became females. Here we have an undeniable reversal of the sex which would normally have been realized. On the other hand, Reverberi²⁷¹ obtained in one case a contrary reversal, that of a young individual, already developing as a young female, into a male. He took an adult female and a very young female (at the beginning of the post-cryptoniscan metamorphosis) and placed them in a dish, putting the young female on the old one; the association persisted and the young one fed. When its nurse came to die Reverberi replaced her by another. This enabled him to extend the experiment over several months and in one case he finally obtained a typical male with testes and spermatozoa.

Quite recently, Reinhard²⁶⁹ carried out an analogous experiment with *Stegophryxus hyptius*. Some presumptive females, still very young but already attached to the abdomen of the pagurid, were taken off and transferred to older females. They changed into males. He was not successful in obtaining the reverse change (of a presumptive male into a female) as he was not able to bring about the attachment of young males to the pagurids.

The definitive sex in the Bopyridæ and Phryxidæ then seems to be labile and to result from the conditions, particularly as regards nutrition, in which the individual develops from the cryptoniscan stage onwards. This conclusion seems natural enough when one considers the normal change of sex in the Cryptoniscidæ (see below, p. 83).

(3) ENTONISCIDÆ. This group is perhaps the most specialized of the Epicaridæ, and the profound malformation of its members is obviously the result of parasitism. They live within the visceral cavity of the host (crabs, Porcellanidæ) and are enclosed within a membrane which in reality belongs to the host. When the parasite is mature, and just as the eggs are being laid, one end of this membrane becomes attached to the wall of the host's branchial cavity and forms an opening there by which

the epicarid larvæ can make their escape. On account of this arrangement, Giard and Bonnier supposed that the membrane enclosing the parasite was a diverticulum of the host's branchial cavity. According to them the parasite penetrated into the branchial cavity of the host, causing a hernia which projected into the visceral cavity but always remained in communication with the exterior; thus, they claimed, there must be a continuous flow of water round the parasite ensuring its respiration. Contrary to appearances, then, the Entoniscidæ would be ectoparasites.

This thesis prevailed generally until quite recently on account of the uncontested authority of Giard and Bonnier on this subject. I should say, however, that I found it difficult to accept, as I have many times found young Entoniscidæ (*Portunion koss-*

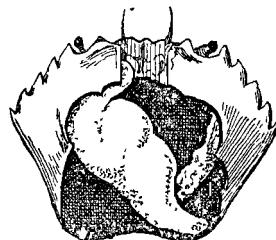


Figure 27. An adult entoniscid, *Portunion mænatis*, in its normal position inside the carapace of *Carcinus mænas* (after Giard).

manni in the crab *Platyonychus latipes*) in the midst of the host's viscera, far from its body wall and certainly without any external communication. But the truth of *endoparasitism* in the Entoniscidæ has recently been completely confirmed by the researches of P. Drach²³⁷ and in particular by those of A. Veillet²⁷⁸; indirectly also by the observations of D. Atkins²¹⁴. Drach puts crabs, *Carcinus mænas*, in sea water to which methylene blue has been added (1 part per 1,000). After a few hours their branchial cavity is deeply stained; on the contrary, young Entoniscidæ found in the visceral cavity show no trace of the colouring matter which they should do if the sheath enveloping them communicated with the branchial cavity of the host.

At Sète, where *Portunion mænatis* occurs very commonly in *Carcinus mænas*, Veillet was able to work with abundant material of every stage. Now, he was able to show clearly the way in which

the entoniscid, as a cryptoniscan larva, penetrates directly into the general body cavity of the crab. He found these typical larvæ, particularly beneath the hypodermis of the mouth-parts (Fig. 28A, B) or the apodemes, and watched their transformation into apodous larvæ while, at the same time, he recovered the empty cast of the cryptoniscan larva with the thoracic limbs still retaining their muscles. The young apodous female (Fig. 28C)

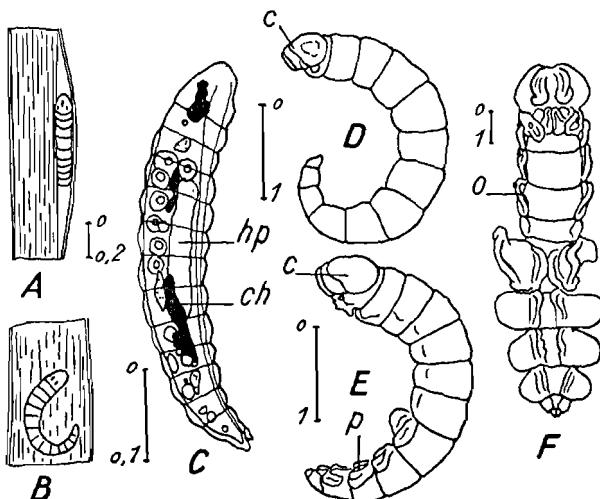


Figure 28. *Portunion mænадis*: stages of development in the crab *Carcinus mænas* (after Veillet).

A, B, penetration of the cryptoniscan larva under the cuticle of an apodeme (profile and surface view). C, young female after the moult in the cryptoniscan stage; ch, chromatophores; hp, hepatopancreas. D, female before the appendages have appeared (asticot stage). E, the stage when the pleopods begin to appear. F, a later stage (at the beginning of the formation of the oostegites, o). The scale is shown by the drawing of one millimetre beside the various sketches.

moves about between the hypodermis and the chitin and finally passes into the general body cavity of the crab. He was able to follow all the stages of the change into the typical entoniscid form (differentiation of the cephalogaster, appearance of the appendages), and to follow its growth and differentiation.

As for the enveloping sheath, Veillet's observations have shown that during growth it forms a complete sac, closely applied to the parasite, and that it is produced by an agglomera-

tion of the lymphocytes of the crab, just as during phagocytosis a sheath is formed round a foreign body; thus Kossmann's opinion, formulated in 1882, is confirmed. The mouth-parts of the entoniscid make a little opening in the sheath, enabling it to feed. Respiration takes place across the sheath. When the female is ripe and about to set the epicarid larvæ free, the sheath becomes fastened to the wall of the crab's branchial cavity and an opening is pierced in it so that there is a passage into the branchial cavity by which the larvæ will escape. But this passage is secondary and does not exist during the growth of the epicaridian. The entoniscid, in the crab, is a true endoparasite.

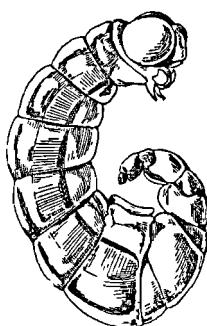


Figure 29. *Portunion mænatis*: very young female at the beginning of its metamorphosis (asticot stage, after Giard and Bonnier).

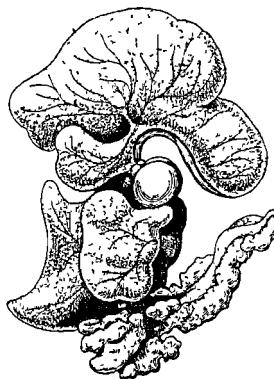


Figure 30. *Portunion kossmanni*: adult female with the brood pouch filled with embryos (after Giard and Bonnier).

In the adult stage, the entoniscid cannot be recognized as a typical isopod (Fig. 30). There is scarcely any metamorphosis, nor are appendages visible. The thoracic region is surrounded by enormous oostegites bounding the brood pouch and forming extremely extensive lobes. One recognizes the cephalic region in the cephalogaster. On the abdomen, the pleopods, serving as gills, are extensively scalloped and fringed. But it has, in fact, been possible to follow all the stages of differentiation in the animal from the moment when, still lacking oostegites, it resembles a worm (asticot stage, Fig. 29), and to see the gradual development of the oostegites and the pleopods. This has been

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done by Veillet with *Portunion mænadir* parasitizing *Carcinus mænas*, and by Giard and Bonnier, who worked on this species as well as on *Portunion kóssmanni* parasitizing *Platyonychus latipes*.

As for the male, it is a complete dwarf (scarcely 1 mm. long) and remains in the brood pouch of the female, in the centre of the egg mass. There are often several of them (Veillet has found up to thirty) and at the same time a certain number of cryptoniscan larvae that Giard and Bonnier thought were neotenic males. The males are much less malformed than the females and have retained a plainly isopod character (Fig. 31). They penetrate into the crab as the females do, in the cryptoniscan larval stage, and can develop as typical males without having any contact with

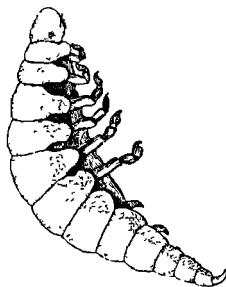


Figure 31. *Portunion kóssmanni*: adult male greatly enlarged
(after Giard and Bonnier).

the female, as Miss D. Atkins²¹⁴ has observed in *Pinnotherion vermiciforme*, a parasite of *Pinnotheres pisum*. It is quite easy to reconstruct the transformation of the cryptoniscan larva into the adult male. The last changes in the male have been carefully followed by H. Sansin.

In connection with sex determination in the males, Veillet, basing his ideas mainly on the observations made by D. Atkins, is inclined to consider it as already decided in the larval stage and not to result from contact with the female. The experiments described above, made by Reverberi and Reinhard, together with the fact that large numbers of cryptoniscan larvae and males are found in the brood pouch of the Entoniscidae, strengthen me in thinking that I was possibly right in the theory

I put forward in 1941; precise experiments with Entoniscidæ are clearly very difficult to make and I do not underrate the value of D. Atkins' observations.

What has just been said is sufficient to show the great interest of the Entoniscidæ for the study of parasitism, and the difficulty of the problems which face the worker, problems which can only be solved with abundant material. Recent researches, particularly those of Veillet, have, thanks to this, considerably modified the views which were previously held.

(4) DAJIDÆ. We shall deal much more briefly with this family, which consists of external parasites on schizopods. Their mode of malformation is very homogeneous. In them, as a general rule, the posterior segments of the thorax (two to four, according to the genus) hypertrophy but lose their pereiopods, the first segments retaining theirs which are grouped in the arc of a circle on the anterior ventral surface. The oostegites of these first thoracic segments remain rudimentary while, on the contrary, those behind them grow to a large size. The abdomen is much reduced and more or less completely devoid of pleopods. The lateral regions of the thorax develop to form two large sacs sheltering the embryos. The exact nature of this brood pouch has never yet been carefully studied. I should be inclined to think that it is really an internal structure in the Dajidæ and is produced by lateral invaginations such as we shall find in the Cryptoniscidæ. Plentiful material would be necessary for the solution of this problem.

(5) CRYPTONISCIDÆ. Although they form a very coherent group, the Cryptoniscidæ are divided into a series of sub-families each with its own special character and localized on the same group of hosts. On the whole, when adult, they display very considerable degeneration of all their organs. They are no more than sacs of embryos, dying when the brood emerges, which must be unique. They appear in the most disconcerting shapes, bearing no resemblance to an isopod, nor even to a crustacean. They show no trace of appendages nor of segmentation. The alimentary canal is only represented by mere vestiges ; the mouth has vanished. The nervous system itself is reduced to a very few ganglia. Nothing is more divergent than the series of different types of Cryptoniscidæ. It is not possible to study each one of them in detail here. We shall limit ourselves to a rather

rapid examination of a certain number, in order to gain some concrete idea of their diversity.

In *Hemioniscus*, which lives as an ectoparasite on *Balanus*, without physical continuity with its host, the head and first four thoracic segments retain the exact structure of the cryptoniscan

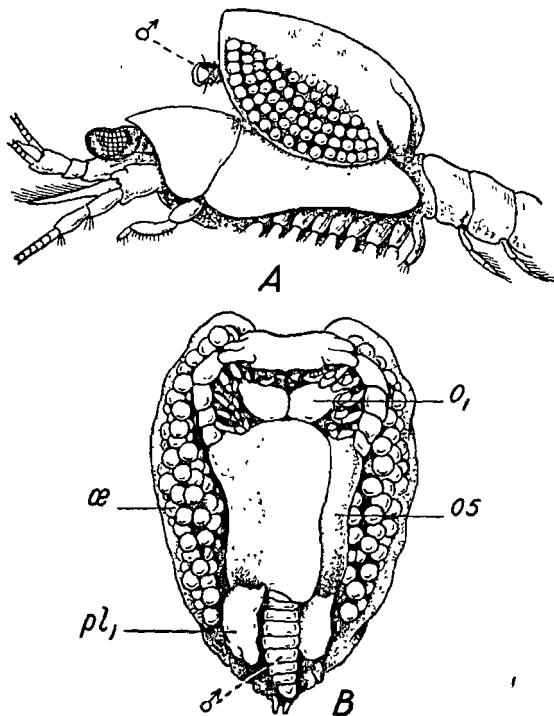


Figure 32. Epicarids of the family Dajidæ (after Giard and Bonnier).

A, *Aspidophryxus sarsi* on *Erythrops microphthalmia*. B, *Dajus mysidis* (ventral aspect); o_1 , o_5 , first and fifth oostegites; α , eggs after laying; pl_1 , first pleopod; δ , male.

larva, while behind them the whole of the rest of the body becomes a shapeless sac of considerable size, more or less lobed, without appendages or distinct segments. The name *Hemioniscus* gives a good idea of this dual aspect of the body. The posterior region finally becomes a sac full of embryos. The brood

pouch develops as an invagination of the ventral surface into the general body cavity.

The Asconiscidæ, parasites of schizopods, show the same type of degeneration, but our knowledge of them is limited to work on a few specimens, performed by G. O. Sars on a single species parasitizing a deep-water *Mysis*.

The Cyproniscidæ, parasitizing the ostracods, are scarcely better known. Up to the present time very few specimens of only two species have been studied. Scarcely more is known of the Podasconidæ, parasites of Amphipoda, and the Crinoniscidæ which are found on *Balanus*. We are better acquainted with the Cabriopsidæ on isopods, and the Liriopsidæ on Rhizocephala, since in these two cases abundant material of the different stages of certain species has been available for study.

Let us notice here that some of the Cryptoniscidæ are hyper-parasites, for instance *Danalia* (Liriopsidæ) on *Sacculina*, and *Liriopsis* on *Peltogaster*; certain Cabriopsidæ are parasites of Epicaridæ (*Gnomoniscus* on *Podascon*, *Cabriops* on *Bopyrus*). Recently, Carayon (1942) has studied another case of this hyper-parasitism, that of *Cabriops perezi* on one of the Bopyrinæ, *Pseudione fraissei*, itself a parasite in the branchial cavity of a pagurid (*Clibanarius misanthropus*).

I myself have had the good fortune to be able to work with ample material of all stages of several different types of Cryptoniscidæ: at Naples, with *Danalia* (on a crab) and *Liriopsis* (on *Peltogaster*); at the Cape de la Hague (with F. Mesnil) with *Hemioniscus balani* (on *Balanus balanoides*) and with one of the Cabriopsidæ, *Ancyroniscus bonnieri* (Fig. 33) on an isopod. It was thus possible to ascertain several important matters in connection with the biology of the group.

One of these matters was sex reversal, which is general throughout the group. All individuals first become functional males at the cryptoniscan larval stage, as well as growing to some extent. One finds these cryptoniscan males free-living and moving about on the surface of the females. They subsequently change into females, and one finds some individuals showing at the same time the remains of testes and rudiments of ovaries in various stages of development. It is then that they become attached to the host and undergo their metamorphosis. The sex life of the Cryptoniscidæ is then quite different from that of the other

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families (Bopyridæ, Entoniscidæ and Dajidæ). The young females attached to the host are fertilized at an early stage and the spermatozoa remain in the female genital tracts until the single batch of eggs is laid. The female phase thus includes a period of growth and youth, when the parasite nourishes itself at the expense of the host and undergoes its metamorphosis. At the same time reserve substances are accumulated in the large hepatic sacs and

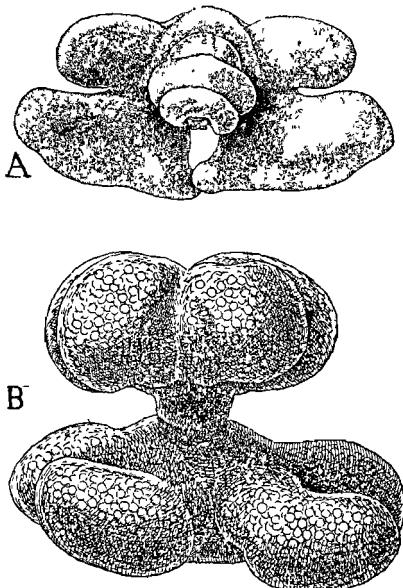


Figure 33. *Ancyroniscus bonnieri* (after Caullery and Mesnil).

A, sub-adult female (before egg deposition); the two pairs of lower lobes belonging to the abdomen are lodged in the visceral cavity of the host. B, adult female after laying, reduced to a lobed and closed sac filled with embryos.

these will later be utilized in the developing ovary. The eggs are deposited in the brood pouch, which in this case is inside the animal. We were able to follow its development very closely in *Hemioniscus balani* and found that it was very similar in *Ancyroniscus* and the Liriopsidae. It may be taken almost for granted that it is on the same lines throughout the Cryptoniscidæ. This brood pouch, which originates as a pair of ectodermal invaginations in the ventral region, spreads throughout the body and

compresses all the organs, which become vestigial and non-functional. As a rule, in the advanced stages of incubation the mother possesses neither mouth nor alimentary canal and only a few nerve ganglia remain ventrally. The animal, however, continues to contract regularly and rhythmically, thus ensuring the respiration of the developing embryos.*

As we have already been able to see, the Epicaridæ provide a highly significant example of the value of parasitism as a factor in evolution, which is the reason that I have lingered rather long over them. Starting from very similar types and being submitted to conditions of parasitism in different crustacean hosts they have developed into forms which are highly divergent when compared with each other. Each family of hosts has been the source of a particular evolution. Let us note that the initial character of these modifications is far from having persisted during development, as may be seen in the structure of the mouth-parts which, from the epicarid stage, have the definitive form corresponding to the parasitic life.

The progress that has recently been made in our knowledge of the Epicaridæ is due to their having been studied in suitable localities where there has been abundant material to work on, and where they have been observed in a living state and to some extent experimented on. Under such circumstances we may yet expect new facts and I draw the attention of research workers to this point.

RHIZOCEPHALA

Amongst the Crustacea the Rhizocephala provide another example of the intensity of changes brought about by parasitism. The most classical example in the order is that of the genus *Sacculina*, a parasite of crabs and Anomura. It appears as a fleshy sac (Fig. 34) attached transversely to the ventral surface of the abdomen and separating the latter from the ventral surface of the cephalothorax. At the free apex of the sac there is a median

* The dual conditions of incubation of the embryos in the Cryptóniscidæ and the other Epicaridæ cannot be considered to be the result of parasitism. Actually they are also found in the free-living Isopoda of the family Sphæromidæ where, in certain genera, such, for instance, as *Dynamene*, the eggs are incubated in an external cavity beneath the thorax, while in others, such as *Cymodoce*, there is an internal brood pouch. This suggests that within the Isopoda the Epicaridæ may have had a double origin, coming from two sources showing this difference in the methods of incubation.

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opening leading into a flattened cavity called the pallial cavity, which extends round a central, fleshy, visceral mass, and which, in the adult, is full of developing embryos. The visceral mass consists almost entirely of the paired ovary, besides which there is a pair of small testes and a nerve ganglion. This collection of organs outside the host does not constitute the whole *Sacculina*; there must be added to it an internal part consisting of a system of roots radiating and ramifying throughout the crab. It is by means of them that the *Sacculina*, like a plant, is able to assimilate its food at the expense of its host and to produce successive

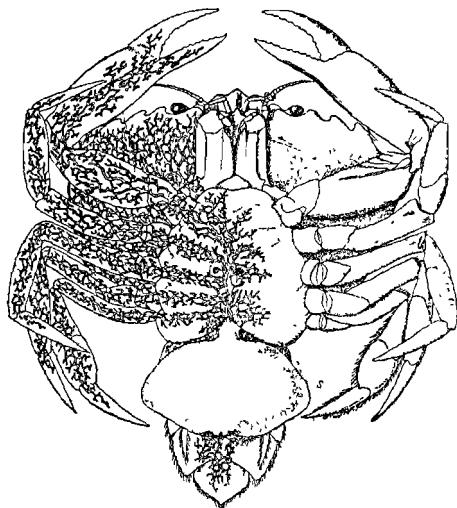


Figure 34. Crab carrying *Sacculina*, s; the system of roots is shown on the left side of the figure (after Boas).

batches of eggs. These few facts show how degenerate the *Sacculina* is, lacking appendages, alimentary canal, sense organs, etc. Even its relationship could not be ascertained from the adult.

Hermit crabs are parasitized by *Peltogaster*, which is close to *Sacculina*, and still other genera of Rhizocephala are known: *Parthenopea* on *Gebia* (= *Upogebia*); *Callianassa* and *Lernæodiscus* on *Galathea* and *Porcellana*; and *Thompsonia* (= *Thylacoplethus*) on crabs (*Melia* and *Thalamita*) and *Alpheus*.

Development reveals the affinities of the Rhizocephala which are Crustacea related to the Cirripedia, a group consisting of

fixed forms, *Balanus*, *Lepas*, etc. Indeed, the larvæ which leave the mantle of *Sacculina* are, at hatching, nauplii with lateral frontal horns like those of cirripedes (Fig. 35 I). Furthermore, after four successive moults in five days, the nauplius changes into a cypris larva (Fig. 35 II), equally characteristic of cirripedes. These two larval forms thus leave no doubt about the zoological position of the Rhizocephala. However, they differ in several ways from corresponding forms amongst the cirripedes: neither possesses an alimentary canal; interiorly there is a mass of tissue containing a great deal of fat, and no other differentiation of organs except for an eyespot; so here there is modification due to parasitism such as we have seen in the mouth-parts of epicarid larvæ of the Epicaridæ.

Cypris larvæ of cirripedes as a rule attach themselves by the antennule to the support where they will complete their development, and it is easy to watch the organs of the larva change into those of the adult. The larvæ of *Sacculina* similarly attach themselves to the crab and, by analogy, it was supposed from the very first that the system of rootlets derives from the anterior or cephalic region, hence the name of Rhizocephala for the group. It seemed evident, too, that the fixation of the cypris larva must take place where the adult parasite is found, that is, under the abdomen of the crab in the case of *Sacculina*; this must be the direct result of the metamorphosis *in situ* of the cypris. But one never finds sacculinas of a size comparable with that of a cypris larva (0·2 mm.); the smallest are from two to three millimetres, or ten times the length. In reality, between the larval cypris and the smallest sacculinas that may be seen attached to the abdomen of the crab, there is interposed a very unexpected and surprising series of stages whose discovery we owe to Y. Delage²³⁵ and which can only be the result of a long evolution under the influence of parasitism. Uncertainty remains only about the stages by which such an evolution has taken place and on the precise causes that determined it.

The cypris larva, after swimming about for a few hours, fixes itself by one of its antennules to a young crab (*Carcinus mænas*) of 4 to 7 mm.; this attachment only takes place during darkness, but it can be brought about during the day if a darkened vessel is used. But it never takes place, as one would naturally suppose, at the spot where the *Sacculina* will later be found. The cypris

settles anywhere on the surface of the crab, but it will only be successful in certain positions, in particular at the base of a seta on the carapace. As soon as it is fixed the larva begins to metamorphose (Fig. 35 III); its internal contents contract into rather a small, cellular, vesicular mass, and the carapace, with its larval limbs, becomes detached and is cast off; the internal mass, now

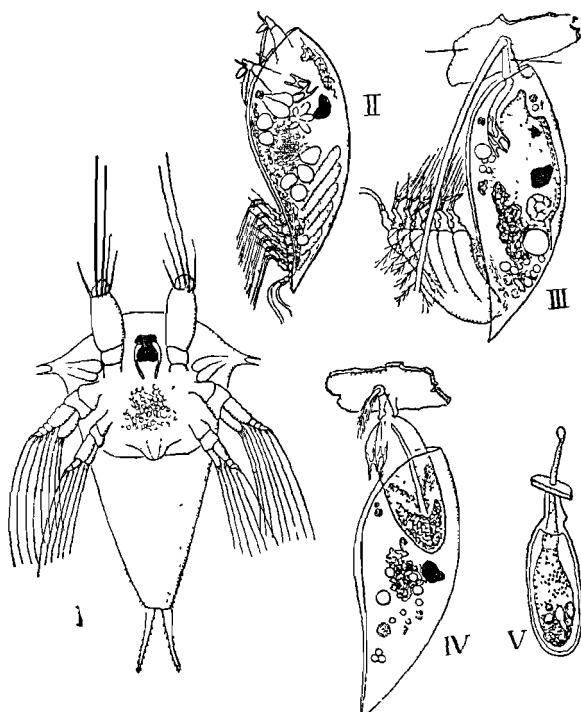


Figure 35. Larval development of *Sacculina* (after Y. Delage).

I, nauplius; II, free-living cypris; III, cypris attached to the base of a seta of the crab, having begun to degenerate; IV, end of regression in the cypris larva; V, kentrogon stage.

external (Fig. 35 IV), becomes covered over with a thin new layer of chitin. In the anterior part of this cellular mass, near the point of attachment, there differentiates a thin internal tube, chitinous and dart-shaped, which penetrates by means of the attaching antennule through the integument of the crab, which is thin here

on account of the articulation of the seta; by this kind of trocar (Fig. 35 V) the cypridian cellular mass is, so to speak, injected into the body cavity of the crab. Delage named this larval stage the kentrogon. The cypris larva is thus changed into a small cellular mass, naked and undifferentiated, and now within the body of the crab. There has taken place, then, a very great regression, beginning in the free-living stages and particularly from the ancestral cypris in which there were already the rudiments of all the essential organs of the adult cirripede. *Sacculina* will remain as an internal parasite of the crab for a very long time, according to Delage about twenty months, during which the crab completes its growth. Its history during this period was elucidated by G. Smith,* who confirmed²⁷⁴ and, in 1906, definitely placed beyond dispute the facts set out by Delage, which had been contested, particularly by Giard, on account of their peculiar nature.

The internal, undifferentiated *Sacculina* undertakes a regular migration within the crab, from the point of entry, which may be anywhere, to the position on the abdomen where the external *Sacculina* is regularly found. Using *Sacculina* in *Inachus mauritanicus* (= *I. scorpio*), Smith succeeded in finding the different stages of this migration which takes place along the length of the intestine, from the anterior region, where the paired cæca are given off, to almost opposite the unpaired abdominal cæcum, where it stops (Fig. 36). During this time the parasite is composed of a shapeless, lobed mass from which prolongations are pushed out, constituting the beginning of the radical system. At a certain moment, towards the end of migration, there becomes differentiated in the central part, from which the first roots are given off, a sort of tumour, or *nucleus*, which is the beginning of the actual *Sacculina*. The parasite, having arrived at the abdomen of the host, finally takes up its place on the ventral surface of the intestine, opposite the unpaired posterior cæcum. Within the nucleus there form, by a new differentiation, as Smith showed (and not, as Delage supposed, from rudiments present in the cypris stage), the definitive organs (pallial cavity, genital glands, nerve ganglia, etc.). Thus there is constituted the internal *Sacculina*. It presses against the ventral wall of the

* Geoffrey Smith, who was considered to be one of the best English biologists of his generation, was killed in 1917, at the battle of the Somme.

crab's abdomen and by its contact produces a necrosis of the parietal muscles and of the epidermis and then a softening of the chitin over a small disc of two to three millimetres. This disc gives way, or else the crab moults, and *Sacculina* is then *external*; it now grows rapidly.

A parallel type of evolution has been found in *Peltogaster* (Schimkewitch, Smith); in other much rarer genera it has not yet been studied.

The processes which constitute the development of the internal *Sacculina* (dedifferentiation and migration, then new differentiation) can only be the result of a progressive evolution (evidently

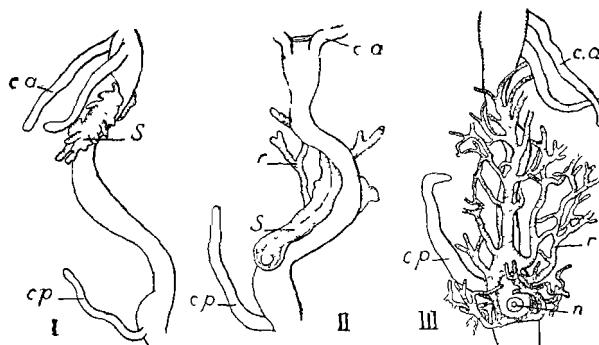


Figure 36. Internal stage of *Sacculina*.

S, in the course of its migration along the gut of the crab, with the differentiation of the root system, *r*; *ca*, anterior cæca, and *cp*, posterior cæcum of the crab's intestine; *n*, nucleus (future external *Sacculina*) (after Geoffrey Smith).

determined by the conditions of parasitism), of a more or less rapid type, with a succession of stages in the past which still remain entirely unknown to us. Perhaps the genera other than *Sacculina* and *Peltogaster*, whose development has not yet been studied, will throw light on these stages.*

* Smith observed that a cirripede, *Anelasma squalicola*, attached to the skin of a shark (*Spinax*) possesses rootlike prolongations buried in the integument of the host; but these are merely organs of attachment and the animal differs from the Rhizocephala in having a well-developed alimentary canal. It cannot possibly be considered to be one of the Rhizocephala. On the other hand, Smith considers that a parasite attached to the ventral surface of the isopod *Calathura branchiata* is probably a primitive member of the Rhizocephala, perhaps lacking roots. This animal, which was named *Duplorbis calathura*, is still very little known, and has unfortunately been found only once, in Greenland.

The external sac of the Rhizocephala seems clearly to constitute the differentiated part of the individual, the system of roots playing only a trophic role. It is interesting, in this connection, to quote here an observation of Ch. Pérez²⁶⁶ on *Peltogaster paguri*. On the root system he saw a recurrent branch slowly form, and after the descent of the *Peltogaster* (the roots were watched for several years) aneurisms were formed on these recurrent branches and in the aneurisms there developed ovaries whose oocytes matured but could not be shed. The question arises of knowing whether these late radical ovarian structures

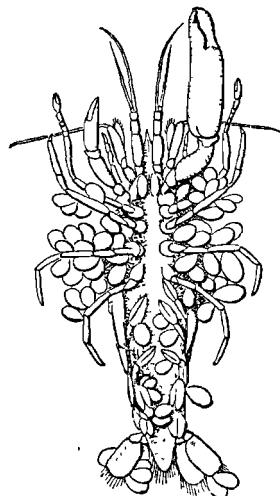


Figure 37. *Thompsonia* sp. on *Synalpheus brucei* (after F. A. Potts).

actually derive from the primordial genital cells of the individual or whether they are a straightforward new differentiation of root tissue, separate from the germ plasm.

Coutière²³⁴ thought that in a gregarious genus which he called *Thylacoplethus*, found by him on the Alpheidae, he had discovered a primitive form of Rhizocephala with direct development, not migrating into the interior of the host. Each individual, he thought, must have developed at the point where it was found, and the gregarious condition resulted from the attachment of a large number of cypris larvae to the same host. This genus is, in reality, identical with *Thompsonia* (Fig. 37)

mentioned earlier, and the researches of F. A. Potts²⁶⁷ have shown that it is, on the contrary, a type still more modified than the others, which under the influence of parasitism has acquired a new and particularly interesting habit, asexual reproduction.

Thompsonia is not the only gregarious member of the Rhizocephala. On the French coasts, particularly in the Mediterranean, the hermit crabs *Eupagurus prideauxi* and *E. meticulosus* sometimes carry a *Peltogaster* (= *Chlorogaster*) which is never solitary but always in groups of ten to twenty individuals, apparently of the same age, and therefore called *Peltogaster socialis*. Smith had already suggested that these multiple individuals could result from the budding of an undifferentiated internal stage but had not been able to demonstrate it, having always found that each individual was provided with its own system of roots, was independent of the others, and could therefore derive from a separate cypris larva.

In *Thompsonia* gregariousness is much more accentuated and often more than one hundred individuals are associated while there may even be two hundred (Fig. 37). These forms have until now only been found in the tropics, particularly in the Pacific, on crabs (*Melia*, *Thalamita*, *Pilumnus*, *Actaea*), on pagurids (*Diptychus*), and on Alpheidæ. They are attached to many different parts of the carapace and appendages. The anatomical study of these individuals reveals a much more simple organization than in *Sacculina*. Here all the individuals stand out from a single radical system which is common to all of them, suggesting that they arise by budding. Potts observed on an *Alpheus* that all these external individuals are cast off whenever the host moults, after having discharged their embryos (it seems that they lay only one batch of eggs), and that a fresh generation shoots out again from the system of roots within the host, as successive crops of cultivated mushrooms develop from the mycelium. Smith's suggestion is thus confirmed and it is very likely that it applies equally to *Peltogaster socialis*; but in this last case there must be either precocious and definitive fragmentation in the internal stage which succeeds the cypris or a budding resembling polyembryony. This type of sexual reproduction has been carefully studied by Ch. Pérez²³⁴, working on the social Peltogastridæ of the genus *Chlorogaster*, parasitizing pagurids. He showed that the individuals which emerge

successively from the abdomen of the host arise from buds formed on the system of roots that surrounds the mid-gut of the pagurid, and he has followed out their differentiation. All the members of one branch develop at the same time. In other respects this reproductive cycle displays a certain amount of plasticity.

Thus, in the Rhizocephala, parasitism, after leading to the intercalation of an internal phase characterized by an absence of cellular differentiation and by the radical nutrition that we have seen in *Sacculina*, has also resulted, thanks to this lack of differentiation, in a process of asexual reproduction that is altogether surprising in a group such as the Crustacea. These animals, which, as far as individuality and organic functioning are concerned, are amongst the most highly differentiated in the animal kingdom, have been led by parasitism to a way of life and reproduction akin to the lowest of the Metazoa—the coelenterates and even the sponges—and recalling plants to an even greater extent.

ASCOThorACICA

I shall now devote some pages to the group of Ascothoracica, which are close to the ostracods and the cirripedes; our knowledge of them has recently made important advances. They, also, are a striking example of the different degrees to which parasitism affects the modifications of a single group, and thus of a true secondary evolution developing from a known point of departure. First of all, for the sake of clarity, a list of the forms so far studied is given in the table on the next page; a complete bibliography is provided by Yo K. Okada²⁶⁰.

It is to Lacaze-Duthiers²⁵⁰ that we owe our first knowledge of this group. He gave an excellent and detailed anatomical description of *Laura gerardiae* which he found at La Calle (Algeria) on *Gerardia*, one of the Antipatharia. We may note that his hostility to, and his lack of understanding of, the theory of evolution prevented him from arranging his description in a clearly comparative way. The best comparative study of the group is that of Yo K. Okada²⁶⁰, who, as well as studying different species *in vivo*, has also carefully worked over the material collected by Norman and Fowler, which is in the British Museum.

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Species	Hosts	Position in host	Localities	Authors
Fam. I <i>Synagogidae</i>				
<i>Synagoga mira</i>	<i>Antipathes larix</i> (Cœl.)	Ecto-parasite do.	Naples Japan	Norman 1887, 1913 Okada 1926, 1939
<i>S. metacrinicola</i>	<i>Metacrinus rotundus</i> (Echin.)	do.	Iceland, etc.	Diakonow 1914 Stephensen 1935
<i>Ascothorax ophiocenesis</i>	<i>Ophiocten sericeum</i> (Echin.)	do.		
Fam. II <i>Petrarcidae</i>				
<i>Petrarca bathyactidis</i>	<i>Bathyactis symmetrica</i> (Cœl.)		Pacific (abyssal)	Fowler 1889
Fam. III <i>Lauridae</i>				
<i>Laura gerardiae</i>	<i>Gerardia</i> (Cœl.)	Ecto-parasite do.	Mediterranean	Lacaze-Duthiers 1883
<i>Baccalaureus japonicus</i>	<i>Antipatharia</i> (Cœl.)	do.	Pacific	Broch 1929
<i>B. maldivensis</i>	do.	do.	Maldives	Yosii 1931
<i>B. argalicornis</i>	do.	do.	Madagascar	Pyefinch 1935 Brattström 1936
Fam. IV <i>Dendrogastridae</i>				
<i>Ulophysema oresundense</i>	<i>Echinocardium cordatum</i>	Endo-parasite do.	Norway	Brattström 1936
<i>U. pourtalesiae</i>	<i>Poutalesia jeffreysi</i> (Echin.)	do.	Greenland	Brattström 1937
<i>Dendrogaster astericola</i>	<i>Echinaster</i> , <i>Solaster</i> (Echin.)	do.	White Sea, Pacific	Knipowitsch 1892 W. K. Fisher 19—
<i>D. murmanensis</i>	<i>Solaster</i> , <i>Crossaster</i> (Echin.)	do.	Murman coast	Kluge, Korschelt 1933
<i>Myriocladus arborescens</i>	<i>Dipsacaster studeni</i> (Echin.)	do.	The Cape	O. Le Roi 1905 Okada 1926
<i>M. ludwigii</i>	<i>Echinaster fallax</i> , <i>Certonardoa semiregularis</i> (Echin.)	do.	Pacific, Japan	O. Le Roi 1907
<i>M. astropectinis</i>	<i>Astropecten multicantheis</i> (Echin.)	do.	Japan	Yosii 1931
<i>M. okadai</i>	<i>Asterias calamaria</i> (Echin.)	do.	Japan	Yosii 1931

The fundamental feature in the organization of the Ascothoracica is that the actual body of the animal is enveloped in a kind of sheath formed by a bivalved carapace, often of great size in comparison with the animal itself. It is within the mantle cavity that the eggs develop until the hatching of the larvae. First of all, it must be said that this carapace is nothing but the bivalved shell of the cypris larva, the existence of which shows

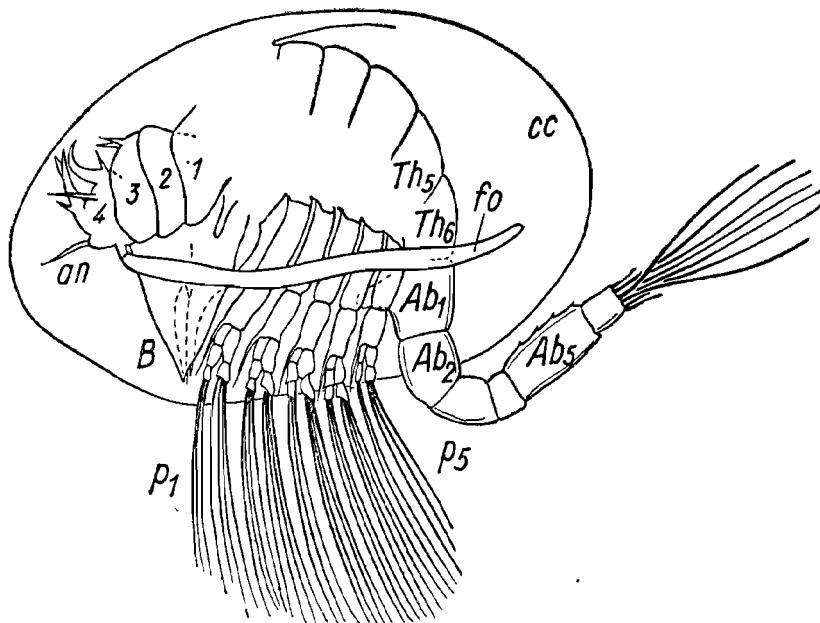


Figure 38. Cypris larva of *Myriocladus* (after Yo K. Okada).

an, antenna; *Ab₁*–*Ab₅*, abdominal segments; *B*, buccal cone; *cc*, cavity of the right valve; *fo*, olfactory filament; *p₁*–*p₅*, thoracic limbs; *Th₅*–*Th₆*, fourth and fifth thoracic segments.

clearly that the Ascothoracica belong to the cirripedes, as Lacaze-Duthiers recognized from other characters. We must note, however, that the nauplius larva of the Ascothoracica lacks the anterior lateral horns that characterize the cirripedes, and their absence serves to mark the autonomy of the group. In some forms, principally the polar species, hatching does not take place until the cypris stage.

The cypris larva (Fig. 38) will provide us, in other respects,

with a general landmark for interpreting the group. The different parts of the body may be recognized without difficulty. The buccal cone, *B*, encloses the mandibles and maxillæ, which are modified for piercing and sucking, a sign of adaptation to parasitism. Let us now see the different ways in which this prototype becomes modified.

SYNAGOGIDÆ. *Synagoga*. Only two species of this genus are so far known, *S. mira*, found on *Antipathes larix* at Naples by Norman, and *S. metacrinicola*, found on a crinoid, *Metacrinus rotundus*, in Japan by Okada. Only a few specimens of each of

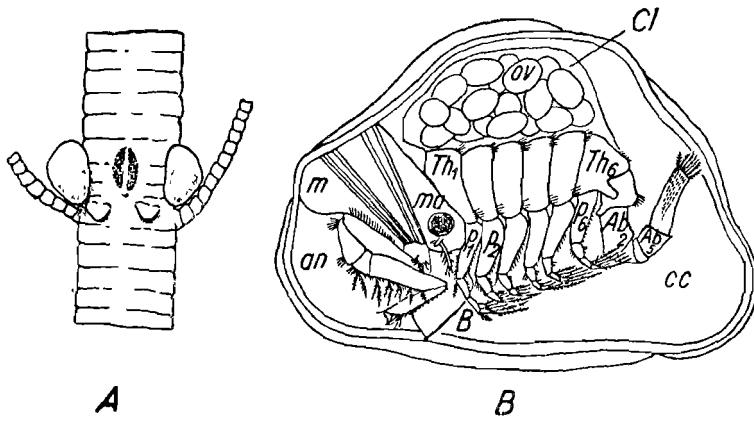


Figure 39. *A*, fragment of the stem of *Metacrinus rotundus* bearing two females of *Synagoga metacrinicola*; between them are the marks of a third individual which has fallen off. *B*, female of *Synagoga metacrinicola* (left half of the carapace removed).
an, antenna; *cc*, cavity of carapace; *ci*, cavity of brood pouch; *m*, muscle;
ma, the adductor muscle of the valves in section; *p₁-p₆*, thoracic
limbs; *Th₁-Th₆*, thoracic segments (after Yo K. Okada).

these species have been studied. They are external parasites (Fig. 39*A*) appearing as somewhat globular masses, attached to the surface of the host and limited by a bivalved carapace, the edges of which are more or less joined. Within the carapace is the animal itself (Fig. 39*B*), which closely resembles the larval form described above. In it we recognize the typical structure of a crustacean, with head, thorax and abdomen clearly segmented; the thoracic segments bearing biramous pereiopods. In the buccal cone the mouth-parts are modified for piercing (as in

the larva). The first abdominal segment in the female bears a chitinous process which corresponds to the penis, very much more developed in the male. The internal organization scarcely departs from the normal except that both the alimentary canal, on leaving the stomach, and the genital glands send into the two valves of the carapace a pair of diverticula which ramify there. This is one of the chief characteristics of the group.

The sexes are separate. The male is smaller than the female (1 mm. instead of 2·5 mm.) and is flatter. In shape and structure they are visibly similar. Okada, after studying Norman's specimens of *S. mira* at the British Museum, came to the conclusion that they were all males.

Ascothorax. The species *A. ophiocrenis* is a parasite living in the branchial sacs of the ophiuroid, *Ophiocren sericeum*. First described by Diakonow²³⁶ it has been further studied by Stephensen²⁷⁵ from fresh material collected by the *Ingolf* expedition. The two sexes are usually found beside each other, the male being smaller than the female. We may still consider this as a case of external parasitism, the branchial sacs of the ophiuroid being, in short, part of the external environment. The organization of *Ascothorax* agrees for the most part with that of *Synagoga*, but there is already a clear reduction of the thoracic appendages, particularly in the male; the pereiopods especially have lost the long terminal setæ that they possess in *Synagoga*.

PETRARCIDÆ. To this family belongs *Petrarca bathyactidis*, which has been found on only one specimen of an abyssal anemone, *Bathyactis symmetrica*, dredged by the *Challenger* at a depth of 3,000 fathoms. Only three specimens of the parasite are known; they were studied in 1889 by Fowler, and re-examined later in the British Museum by Okada. They live in the digestive cavity of the anemone, which communicates with the exterior, so that, properly speaking, they are not internal parasites.

Their morphology recalls that of *Synagoga*, a more or less spherical structure within a bivalved carapace. The cephalic region bears antennules with many segments. The pereiopods are reduced to foliaceous, unjointed protuberances; the abdomen has only three segments. The digestive tube gives off two diverticula which ramify in the carapace; the ovaries and testes do likewise. *Petrarca* is hermaphrodite, the only such case we have so far seen.

LAURIDÆ. This consists of the two genera *Laura* and *Baccalureus*. *Laura gerardiae* was discovered and studied by Lacaze-Duthiers. The animal is attached to a branch of the host, *Gerardia* (Antipatharia) (Fig. 40A). The two valves of the flattened carapace are enormous in comparison with the animal itself, and their edges are joined except at one point in the

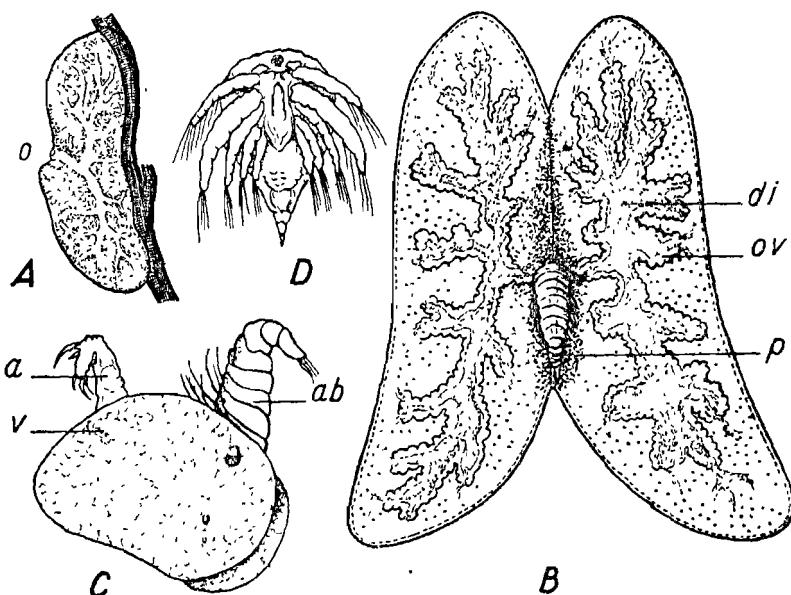


Figure 40. *Laura gerardiae*.

A, the female attached to a stem of *Gerardia* (the polyps covering it have been removed); o, orifices of the valves. B, valves opened along the line of insertion on the stem of *Gerardia* and pressed back; in the axis the body of *Laura* (p, posterior extremity); in the wall of the valves are the ramifications of the intestinal diverticula, di, covered externally by the ovary, ov. C, the male within the valves, v; ab, abdomen; a, antenna. D, nauplius stage (after Lacaze-Duthiers).

vicinity of the mouth. In the natural state the carapace is covered by the polyps of the cœlenterate. But it is still, in reality, an external parasite. The animal itself, which is very small (Fig. 40B), is to be seen inside the carapace, opposite its free surface and in the immediate vicinity of the external opening. Its structure is allied to that of *Synagoga*, showing the same regions of the body (head, thorax and abdomen) and a regression of the setigerous

armature of the pereiopods. From the stomach is given off a pair of diverticula, *di*, which ramify in the two valves of the carapace, these ramifications being accompanied by those of the

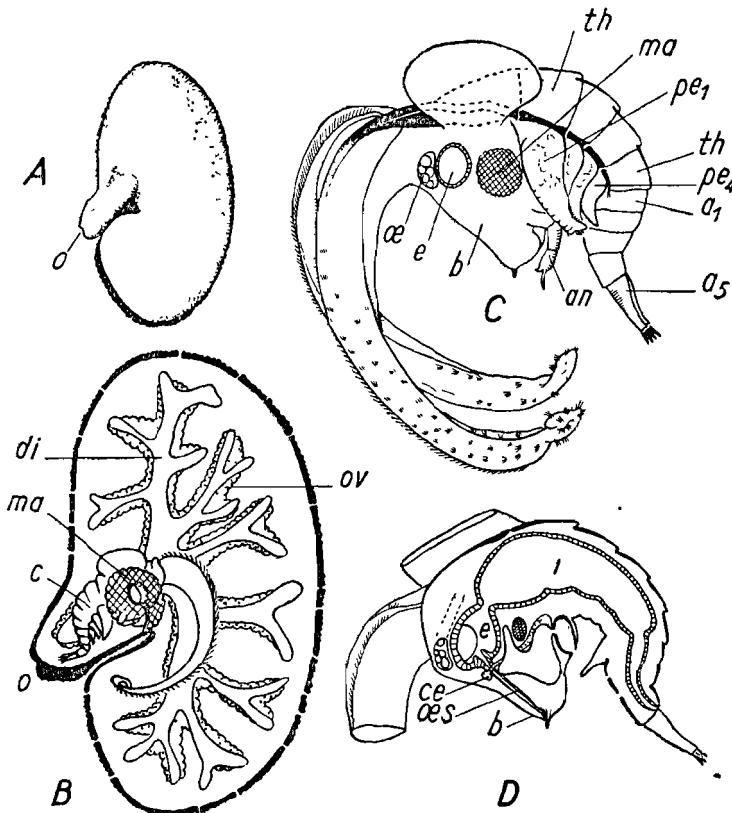


Figure 41. *Baccalaureus japonicus* ♀ (after Yosii).

A, in the carapace. *B*, external aspect, right valve removed. *C*, the actual body isolated (left aspect). *D*, internal anatomy: *a₁-a₅*, abdominal segments; *th*, thoracic segment; *an*, antenna; *b*, buccal cone; *c*, body of the animal; *ce*, cerebral ganglia; *di*, intestinal diverticula ramifying through each valve; *e*, stomach; *ma*, adductor muscles; *o*, orifice of the carapace; *ae*, laid eggs; *œs*, œsophagus; *ov*, ovary (forming an external sheath to the intestinal diverticula); *pe₁-pe₄*, pereiopods.

ovary, *ov*, which they mask. The dwarf male (Fig. 40C) within the valves was drawn by Lacaze-Duthiers²⁵⁰ (pl. VIII, Fig. 102), but not recognized as such by him. He referred to it as "un

animal indéterminé représentant peut-être la forme cypridienne", but he states that when he compressed it there escaped from within it some corpuscles filled with motionless filaments, which are perhaps spermatozoa. Giard (1891) recognized that it was a male and Okada²⁶⁰ gave the same interpretation, independently.

In the genus *Baccalaureus*, first described by Broch²²⁰, there are now three species known (*japonicus*, *maldiviensis* and *argaliicornis*), all parasites of Antipatharia. They are close to *Laura* but

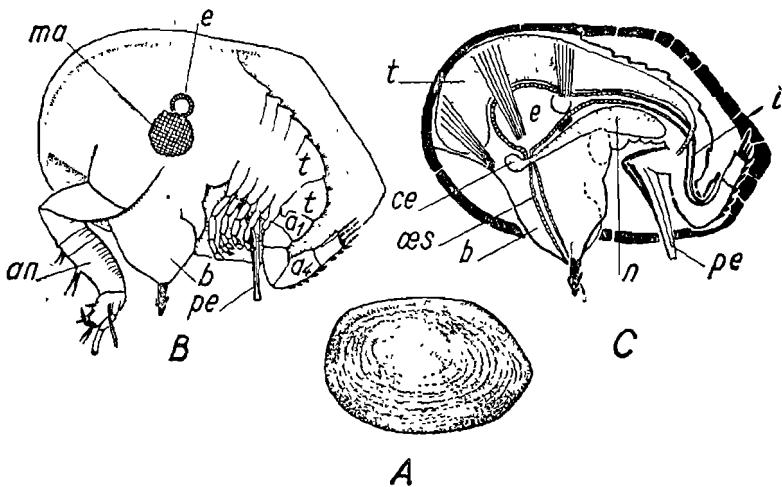


Figure 42. *Baccalaureus japonicus* ♂ (after Yosii).

A, external aspect of the carapace. B, external structure (left valve removed). C, internal anatomy: a_1-a_5 , abdominal segments; an, antenna; b, buccal cone; ce, cerebral ganglia; e, stomach; i, intestine; ma, adductor muscles; aes, oesophagus; pe, pereiopods; n, nervous system; pe, penis; t, testis.

reach a new stage in the regression of the thoracic appendages which are no longer clearly articulated. On the other hand, in the anterior region there is a pair of very large appendages, probably the first pair of pereiopods, whose function is doubtless the moving about of the eggs in the brood pouch; these are not nearly so well developed in *Laura*. The dwarfing of the male is very pronounced (0.6 mm. in length as against 8 mm. in the female). The anatomy of both sexes has been thoroughly studied by Yosii²⁸⁰. Again, there are always two diverticula from the

stomach, ramifying with the ovary or testis in the valves of the carapace (Fig. 42).

DENDROGASTRIDÆ. All the known members of this family are *internal parasites* of echinoderms: *Ulophysema* occurs in sea urchins (Spatangidæ); *Dendrogaster* and *Myriocladus* in starfish. In this family we see a profound modification of the bivalved carapace which changes into a double arborescence of branching diverticula corresponding to the ramifications of the alimentary canal and ovary. The body proper, enveloped here by a sheath which is closely applied to it and is only a vestige of the bivalved carapace of the preceding forms, is no more than a small tubercle in the centre of the arborization.

Ulophysema. This genus, set up by Brattström²¹⁸, now comprises two species: *U. öresundense*, a parasite of *Echinocardium cordatum* in Norwegian waters, where it has been found in abundance, and *U. pourtalesiae*, a parasite of another spatangid, *Pourtalesia jeffreyi*, in Greenland waters. These parasites live within the general body cavity of these sea urchins; *U. öresundense* is found near the gonads of *Echinocardium*. The young stages are free-living, the older individuals are attached to the test of the urchin and at that point there is a small hole, formed by the parasite, through which the larvæ escape. *Ulophysema* attains a length of 30 mm. and looks like a simple unbranched sac with a small median conical protuberance in which there is a slit-like opening leading into the mantle. This last structure is formed by the two valves of the cypris larva, which have become joined together. As in the preceding types, its wall contains the ramified branches of the paired diverticula from the stomach and the ovary. The tips of these branches bulge at the surface like a kind of excrescence. The body proper, which is very small, lies in the conical protuberance of the pallial sac noticed above. In it are the structures that characterized the preceding types: a buccal cone with antennules, an unsegmented thorax with almost rudimentary pereiopods and four pairs of lateral prominences, and a segmented abdomen. To sum up, there is the same general structure but reduced differentiation in some regions. The eggs ripen in the branches of the ovarian diverticula and fall into the mantle cavity where they develop, giving rise to a nauplius which changes to a perfectly regular cypris with biramous pereiopods. Brattström did not find any males and wondered

whether *Ulophysema* might not be hermaphrodite. He placed this genus in the Dendrogastridae, of which it is in any case only one representative and rather a primitive one.

Dendrogaster and *Myriocladus*. The genus *Dendrogaster* was created by Knipowitsch²⁴⁸ for *D. astericola*. Of the other species described by O. Le Roi²⁵¹⁻², *D. arborescens* and

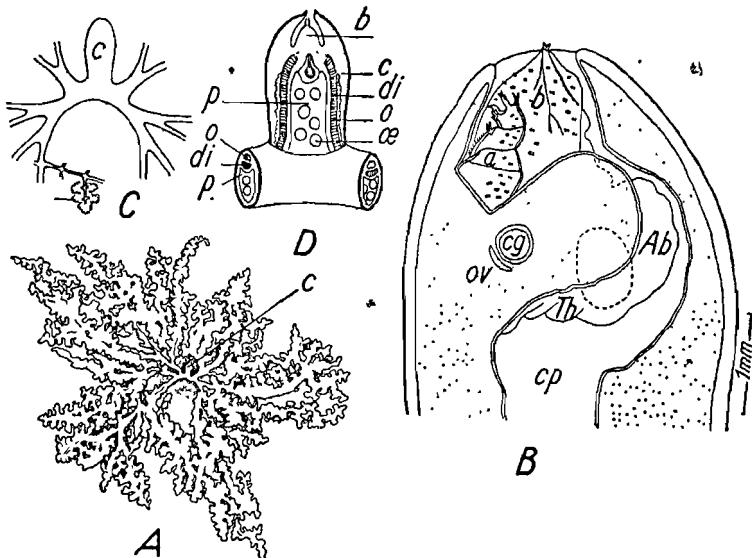


Figure 43. *Myriocladus okadai*.

A, female (note the minute size of the actual body, c, in comparison with the ramifications). B, optical section of the central part of the body of the young female; a, antenna, Ab, abdomen; b, buccal cone; cp, pallial cavity; cg, lumen of stomach; ov, ovary; Th, thorax (after Yo K. Okada). C, central region of the body with the base of the lateral branching diverticula. D, diagram of the structure of the central region of the body showing the base of the two lateral diverticula in section: c, central region; b, buccal cone; di, intestinal diverticula; o, ovary; α , deposited eggs; p, pallial cavity (after Yosii).

D. ludwigii were finally placed by Okada in a distinct genus, *Myriocladus*, which now contains two other species, *M. okadai* and *M. astropectinis*, described by Yosii²⁸⁰. These types appear to be particularly common in the Sea of Japan. They are internal parasites of starfish.

Dendrogaster and *Myriocladus* are characterized by a general regression of the mantle, which is reduced to a sort of small

cylindrical tubercle (Fig. 43A, c) covering the body proper. From the base of the tubercle are given off two tubes containing the gastric diverticula, and branching more or less freely. The two valves have thus become an arborization (Fig. 43A) with branches enclosing the diverticula of the mantle cavity, the gastric and ovarian cæca. Thus here again we find the primitive type but with prodigious malformation. It is highly probable that nutrition takes place, at least to some extent, by diffusion across the walls of the branching diverticula which are bathed in the coelomic fluid of the host. At all events, we are witnessing a profound modification of the morphology of the animal as a result of parasitism.

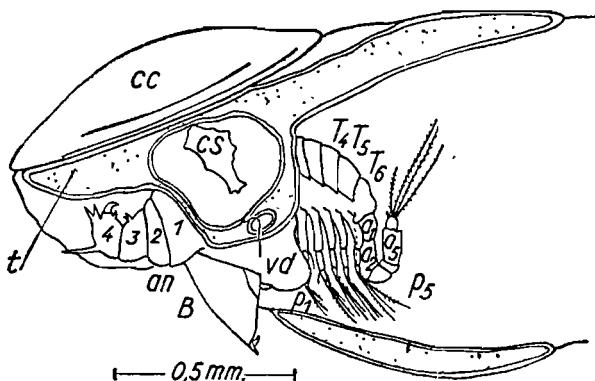


Figure 44. Male of *Myriocladus okadai* (after Yo K. Okada); the left valve has been removed to show the animal's body.

a₁-a₅, abdominal rings; *an*, antenna; *B*, buccal cone; *cc*, cavity of the right valve; *cs*, gastric cæcum; *p₁-p₅*, pereiopods; *T₄-T₆*, fourth to sixth thoracic segments; *t*, testis; *vd*, vas deferens.

The genus *Dendrogaster sensu stricto* at present contains two species (*astericola* and *murmanensis*) with less developed ramifications. The two primary arms each divide into five branches, which are lobed but not arborescent.

There is a different state of affairs in the genus *Myriocladus* (created by Okada for *Dendrogaster arborescens*); here the two initial arms divide into secondary arms, which themselves give off lateral branches. This arborization attains its maximum in *M. okadai* (Fig. 43A). In the female, the animal proper, greatly reduced, lies in the central tubercle near the opening of the

mantle. In it one finds the buccal cone with its antennule (Fig. 43B); and an undifferentiated mass representing both thorax and abdomen which lack distinct segments. The male, on the other hand, has retained the cypris structure with all its appendages (Fig. 44).

We see what a range of regressive and, at the same time, adaptive changes in the mantle have resulted from parasitism in the Ascothoracica. There obviously remain many points to be decided, either by knowledge of new forms or by the careful investigation of species now known, using plenty of material in good condition. But, all things considered, we have here a multiple series of modifications of a very definite type, induced by parasitism.

COPEPODA

To the preceding data we shall add some facts relating to the copepods. Amongst the Crustacea this order is the one containing the most extensive and varied types of parasitism. There are copepods parasitizing almost every group of marine animals (Alcyonaria, anemones, annelids, Crustacea, molluscs, tunicates, fish, cetaceans, etc.) as well as freshwater fishes; they display all kinds of parasitism: external, intestinal, even cœlomic, and all degrees of adaptation from considerable reduction of the appendages to their complete disappearance, the body being reduced to a sac, more or less bizarre in form. Usually there is very pronounced sexual dimorphism as in the Bopyridæ; the male remains free-living or partly so, while the female is obviously parasitic; he is a dwarf in comparison with her; in many species he comes to live on her. The female is hypertrophied and produces several batches of eggs. As in the Epi-caridæ, nutrition takes place by the sucking up or aspiration of the host's fluids (blood, or cœlomic lymph) into the gut. The number of genera and species known is very large. It is not possible to consider them all here. I shall restrict myself to summarizing the life history of an exceptionally degraded type which, on account of its anatomical relationships with the host, has undergone modifications of the same degree of importance as those of *Sacculina*; I refer to *Xenocæloma*²³⁰, a parasite of the annelid *Polycirrus*; it is perhaps connected with the Herpyll-

biidæ, which are parasites of annelids and include some highly modified types.*

At first sight *Xenocœloma* is simply an external parasite forming a cylindrical sac on the side of its host, without any appendages, cephalic or otherwise, and recognizable as a copepod by its ovigerous sacs and its nauplius larva. Under the microscope one can see that the sac unites with the body wall of the annelid without any discontinuity of the tissues. The histological examination of serial sections, both longitudinal and transverse, immediately reveal that in reality *Xenocœloma* is not an external parasite but is entirely covered by the epidermis of *Polycirrus* and communicates with the exterior only by the terminal opening from which emerge the two strings of eggs: in short, it is lodged in a hernia of the host's skin. But its structure is paradoxical in that it is the epidermis of the host that serves as the external body wall of the parasite, the integument of the latter having disappeared. On the other hand, the parietal striated muscle has been retained and is, moreover, strongly developed as a network which is inserted under the annelid epithelium. There is union and complete interdependence of the tissues of both annelid and crustacean.

There is no trace of either cephalic region or nervous system in the copepod. Its axis, for about two-thirds of the length, is occupied by a cavity which opens directly into the general body cavity of the annelid and is lined by the peritoneal endothelium of the latter; it is then in reality a diverticulum of the host's cœlom (hence the name *Xenocœloma*): this endothelium is applied to a wall belonging to the crustacean and constituting the proper wall of the axial cavity and perhaps representing the digestive tube. One sees to how great an extent there is reciprocal penetration between parasite and host; part of the tissues of the second being radically incorporated into the first, both morphologically and functionally. It is an example which is so far unique, and indicates extreme adaptation. One may consider from one point of view that this arrangement is the opposite of that shown by *Sacculina*. In the latter, indeed, it is the parasite that penetrates into the host by means of its roots, but with

* The polychætes also harbour other particularly degenerate copepods, such as *Flabellicolæ*, found by Gravier on *Siphonostoma diplochaitos*, and different types (*Saccopsis*, *Cryptidomus*, etc.) from Greenland, which are still almost unknown.

Xenocæloma it is the host that covers the parasite with its epidermis and penetrates into it by means of its peritoneal endothelium and its cœlom. Of the copepod organism, which is of some size (5-6 mm. long), there remains, in short, only the genital apparatus which is, as it were, grafted on to the annelid. The ovary continuously produces eggs which ripen in the oviducts; filling almost the whole mass of the parasite and finally passing out into an atrial cavity, which opens by the terminal aperture of the sac mentioned above. In other respects the ovaries and

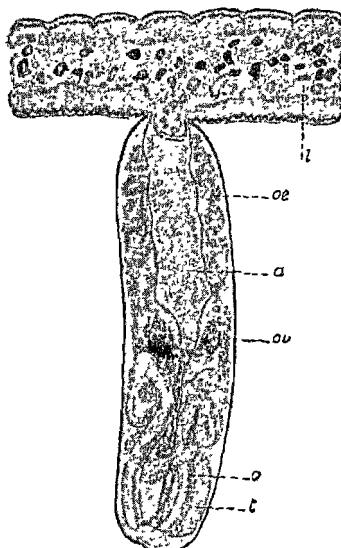


Figure 45. *Xenocæloma brumpti* attached to *Polycirrus arenivorus*.
i, gut of host filled with sand; *a*, axial cavity of the copepod; *o*, oviduct;
ov, ovary; α , oocytes undergoing maturation; *t*, testes (after Caullery
and Mesnil).

oviducts are similar to those found in less degenerate copepods. But *Xenocæloma* presents a further paradox, differing from all other known copepods, in being hermaphrodite; the end of the body is occupied by two large testes which produce giant spermatozoa (1.5 mm. long) and open into a median seminal vesicle from which the spermatozoa pass out by spermiducts opening at the distal extremity of the oviducts; there is self-fertilization; the males seem to have completely disappeared.

The developing eggs give rise to a typical nauplius larva,

which, however, *completely lacks a digestive tube*. It has not so far been possible to follow larval development between hatching and attachment to the host. It is probable that fixation takes place, as in other copepods, only after a free-living period and some moults. The youngest stages found on *Polycirrus*, which are scarcely larger than the nauplius and cannot have been attached for long, already show rudiments of the organs of the adult, and in particular that of the ovary. The testes do not develop until much later.*

At this time the sub-epidermal parasitic tumour is completely closed. Its structure is already very complex and it is impossible to find in it the organization of other copepods. There are grounds for thinking that, as in the case of *Sacculina*, it results from a new differentiation, due to the special adaptation of this type and largely independent of the organization of the free-living larva.

Under the influence of this tumour the parietal musculature of the annelid, to which the lower side of the tumour is applied, gives way and is resorbed; the tumour then comes into contact with the peritoneal endothelium and breaks down, so that the endothelium comes to spread into its interior. Thus are achieved the specialized relationships that we have seen in the adult. The rest is no more than a matter of growth.

We see that this parasite, differing completely from *Sacculina*, shows changes which are no less remarkable both from the importance of the regressions sustained and from the establishment of particularly intimate connections with the host. One may say here that the parasite is indeed incorporated into the host, certain organs becoming truly common, both in structure and function.

We shall note, at the same time, in this case and in that of *Sacculina*, that if there is extreme degeneration it is accompanied by the development of the most perfect adaptive modifications ensuring nutrition and the functioning of the parasite on the host, so that on the whole it is better to regard the changes brought about in these organisms by the influence of parasitism as a specialization rather than a simple degeneration.

* This is an important fact, for it proves clearly that the spermatozoa found in the adult could not come from a male which might have copulated with the female during a free-living phase before she settles; we actually have such a case as this in *Lernaea*.

/ CHAPTER VI

TEMPORARY PARASITISM

IN the examples that we have just considered, which are representative of the general state of affairs, the parasitic life begins after an initial free-living phase and is final. After having reached the host the organism undergoes adaptive modifications or permanent regressions. There are, however, exceptional cases, which have been augmented in number by recent research, where, on the contrary, parasitism is only a temporary youthful phase and leads to a free-living adult with normal structure. The young animal may sometimes undergo very profound modifications, but they are only transitory adaptations and their echoes in the final structure are very faint or non-existent. It is a remarkable and paradoxical state of affairs which goes to prove how complex the effects of parasitism are; it may be called *provisional parasitism* or one may use a special term, *protelean parasitism* (*προ* before, *τελεῖος* adult). We shall devote the present chapter to its study.

MONSTRILLIDÆ

Our first example, a striking one, is taken from the copepods of the family Monstrillidæ. In the adult state they are highly adapted for pelagic life and are rapid swimmers (Fig. 47, I): they have a nauplius eye, as bright as a jewel, and robust appendages for swimming; they show marked sexual dimorphism; the male is much smaller than the female. The alimentary canal is atrophied and reduced to a thin non-functional filament, and there are no longer buccal or thoracic appendages. The animal does not feed: in short, the case is similar to the state of affairs in praniza forms which are perfect examples of protelean parasites; but this atrophy of the alimentary canal, and cessation of feeding, may also occur quite independently of parasitism in the adults of certain types, as in some Sphæromidæ (*Dynamene*

bidentata), in some annelids (i.e., epitokal forms, as *Dodecaceria concharum*, cf. Caullery and Mesnil ⁵⁹²), and in some insects. The adult, or imago, is only a means of disseminating the ripe genital products; it no longer needs to assimilate. Such is the case in the Monstrillidæ.

Young Monstrillidæ are never found in pelagic samples; there are only adults, as perfect as the imagos of holometabolous insects. The reason for this is that they are parasites during the

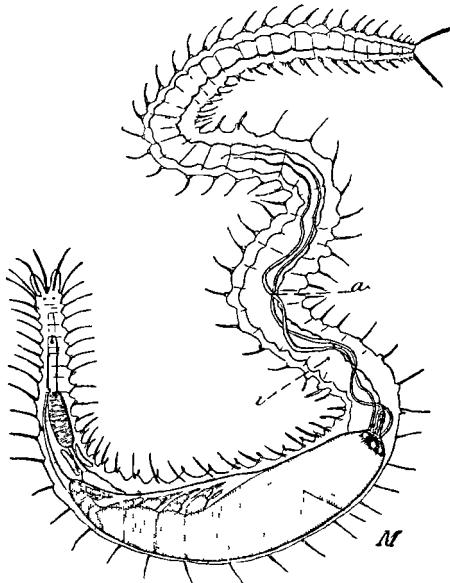


Figure 46. Monstrillid parasite, *M*, in the dorsal vessel of *Syllis gracilis*.

Note the considerable length of the absorbing appendages, *a*; *i*, intestine of the annelid (after Caullery and Mesnil ²²⁹).

whole period of growth, just as Giard observed in 1896 ²⁴⁰ in material collected by F. Mesnil; he was dealing with *Thaumaleus* which was, indeed, a parasite in an annelid, *Polydora giardi*. The parasite was inside a sheath which Giard compared with the enveloping membrane in the Entoniscidæ, believing that here endoparasitism was only apparent and that in reality the monstrillid caused a hernia within the host, and remained in communication with the external world. Since then other

monstrillids have been found parasitizing Syllidae* (Fig. 46), and *Salmacina*†. In reality, as Malaquin recognized²⁵³, these are true internal parasites, lodged in the vascular system of the host, lacking communication with the outside, and only emerging when they are fully adult. That is why the young are never found in pelagic samples.

Here is a summary of their development, which was thoroughly worked out by Malaquin²⁵³ in *Hæmocera danæ*, a parasite of *Salmacina*. The egg develops as far as the nauplius stage within an ovigerous sac carried posteriorly by the free-living female (Fig. 47, I). The nauplius (Fig. 47, II) lacks a digestive tube and the third pair of appendages is reduced to a pair of hooks. It swims actively, then makes its way through the integument of *Salmacina*; here, it moults, casting off both body wall and appendages and becoming reduced, like *Sacculina*, to an undifferentiated cellular mass (Fig. 47, III). In this form it makes its way, doubtless by amoeboid movement, into the longitudinal vessel of the annelid. There it surrounds itself with a chitinous cuticle, a proceeding equivalent to a moult. At the anterior extremity there develop two unsegmented lobes (Fig. 47, IV), which elongate as two long intravascular appendages; they function as organs of absorption, like the roots of *Sacculina*. In the species parasitizing *Polydora* and *Syllis* there is only one pair of appendages; in *Monstrilla danæ*, found in *Salmacina*, there are two (Fig. 47, V); in *Monstrilla helgolandica*, a parasite of *Odos-tomia rissoides*, discovered and studied by Pelseneer²⁶⁴, there are three pairs. The morphological significance of these appendages is an interesting problem: are they entirely new adaptive structures, or are they metanaupliar appendages (mandibles and maxillæ which no longer exist in the adult) changed into organs of absorption?

The first chitinous cuticle formed around the parasite is cast off and replaced by another which will form an expanding envelope persisting throughout the rest of development; it is ornamented posteriorly with rows of little spines and constitutes the

* Besides the species shown in Fig. 31, I had the opportunity, in Naples in 1906, of finding another case (in connection with a species that was certainly different) in another syllid, but I was unable to pursue this observation further; I mention it here in order to record it.

† Pelseneer even found a species of monstrillid parasitizing a mollusc, *Odos-tomia rissoides*²⁶⁴.

sheath, incorrectly interpreted by Giard, which does indeed belong to the parasite and has probably the morphological value of a moult.

Within this sheath, and feeding by absorption through the appendages just described, the adult monstrillid progressively differentiates with all its organs and appendages (Fig. 47, VI),

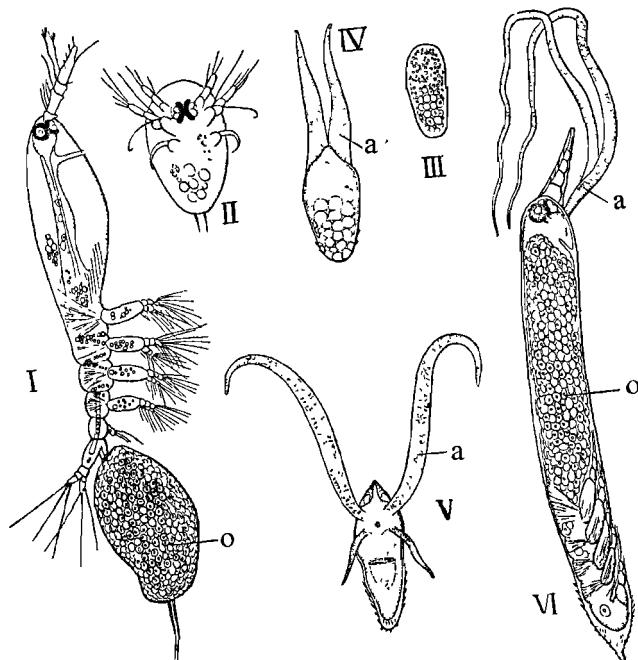


Figure 47. Development of some Monstrillidæ (after Malaquin).

I, *Hæmocera danæ*, adult female carrying an egg mass, *o*; II, free-swimming nauplius; III, the stage at which the animal is an undifferentiated cellular mass in the vessel of the host; IV, development of the absorbing appendages, *a*; V, larva with two pairs of absorbing appendages; VI, stage towards the end of the parasitic period; the monstrillid is completely differentiated within the larval sheath.

and its gonads. When development is complete it emerges from the sheath and its host in the perfect state, as a butterfly leaves the chrysalis. Its pelagic life begins, during which the animal does not feed; the sexes meet, the female lays her eggs and carries them in the ovigerous sacs until the nauplii hatch.

Such is the development of an individual monstrillid. It shows us the greatest possible degree of endoparasitism, starting off by complete regression, continuing by a method of nutrition depending on diffusion through roots, and therefore doubly reminiscent of *Sacculina*. Here again we know of no other stage in the achievement of so specialized an adaptation; it must nevertheless result from a long evolutionary process. Only, far from there being a final regression, as in the Rhizocephala and *Xenocaloma*, here there is only temporary degeneration, which is not reflected in the adult, except for the complete atrophy of the alimentary canal, the buccal and thoracic appendages. One could object that the adult ancestors of *Sacculina* were very different from the pelagic copepods ancestral to the Monstrillidæ, and that this difference is sufficient to explain the different condition of the two actual parasites. But *Xenocaloma* is a copepod like the Monstrillidæ, whose ancestors were free-living in the adult state, and the objection is not valid here. In any case, the Monstrillidæ are by no means an isolated example.

In reality, the evolution of a parasite depends in the first place on the connections which are established between its host and itself. We may imagine that the unmodified adult has persisted in the Monstrillidæ because in this family adaptation to parasitism has been in special temporary structures, the organs of absorption, and the organization of the adult has remained independent of these structures; or else, if, as I believe, these are modified metanaupliar appendages, the result of this adaptation has been the loss of these appendages in the adult, and that has doubtless involved the atrophy of the mouth and the alimentary canal. But, this sacrifice once made, so to speak, the rest of the final organization is built up more or less sheltered from parasitism and independently of it, while in *Xenocaloma* the whole of the young organism is adapted to parasitism and ultimately it degenerates.

PARASITIC PLACENTATION. Giard has very suggestively, and to my mind very rightly, compared this kind of parasitism to placentation such as we find in mammals, salps and other animals: the comparison applies, moreover, to several of the examples which follow. *Parasitic placentation* differs from normal embryonic placentation in that the latter is a graft on an individual of the same species instead of on an alien one. Physio-

logically, the organs of absorption in a monstrillid are equivalent to the villi in the placenta of mammals whose embryos feed by means of this placenta and are truly parasitic on their mother; this does not prevent them from reaching a final state which reflects nothing of this temporary parasitism. But, here again, this parasitism is operated by a subsidiary organ, while the embryo itself, in every part of its structure, is organized for an independent life. One can complete this comparison by contrasting the case of *Xenocæloma* with it. This animal, too, achieves placentation on its host. Nothing could be better compared with a placenta than its axial cavity where there is the most intimate union, as in a mass of maternal and placentary villi, of the peritoneal endothelium of the annelid and the tissue of the crustacean. But here placentation, instead of being achieved by means of an accessory structure, is established at the expense of the essential organs of the individual, which are thus irremediably utilized. There is no more material available for constructing the normal adult. It is clear, therefore, that there is no irreducible contradiction between the two cases but that they may be connected by transitional stages. In many of the cases of protelean parasitism that we are going to review, the animal emerges more or less in the condition of the perfect imago* with its sexual organs completely mature, and has nothing further to do but immediately to dispose of the eggs without having to elaborate anything.

In the Crustacea we have another example which can be related to that of the Monstrillidæ, in that it is limited to the growing period: this is the case of *Gnathia* with which we were concerned earlier (pp. 66-7). It is, in other respects, less accentuated and only reflected in the mouth-parts and the digestive apparatus. It may be noted that the mouth-parts, which have undergone adaptive modifications in the parasitic phase, disappear in the adult.

ORTHONECTIDÆ

We may consider the Orthonectidæ as an example of protelean parasitism. Let us begin with the cycle of *Rhopalura*

* We may repeat that types such as the Monstrillidæ behave like holometabolous insects. Parasitism goes no further than the larval organs, leaving the permanent organs to develop as if from imaginal discs.

ophiocomæ, which is the most completely known, starting off with the larva. These ciliated larvæ, which escape from the free-living female, penetrate into the genital openings of *Amphiura squamata* and give rise in various tissues of the ophiuroid to plasmodia in which the germ cells differentiate and develop

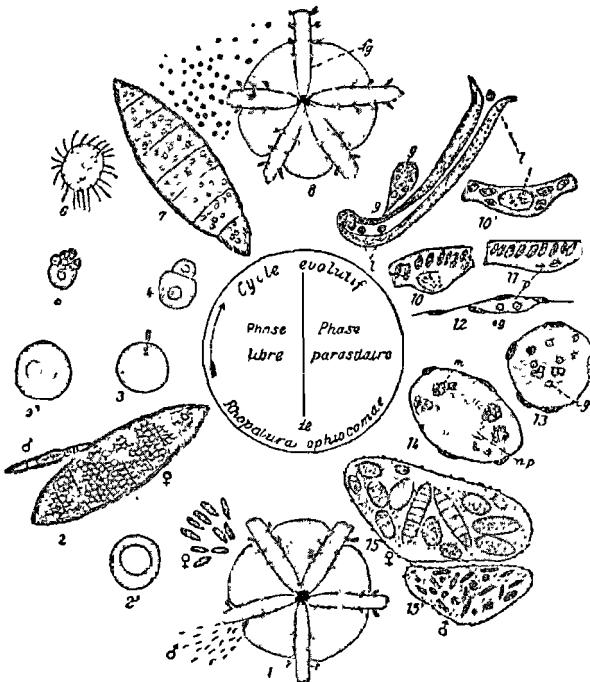


Figure 48. Developmental cycle of *Rhopalura ophiocomæ*.

- 1, emission of male and female adults from the host, *Amphiura squamata*;
- 2, fertilization; 2', ripe oocyte; 3, emission of polar bodies; 3, fertilization (stage of vesiculate pronuclei); 4, 5, segmentation; 6, ciliated larva; 7, emission of ciliated larvæ; 8, 9, their penetration into the ophiuroid; 10-14, initial stages of the plasmodia and differentiation of the germ cells; 15, male and female plasmodia.

into the males and females of *Rhopalura*. These, in fact, constitute a new generation for which the plasmodium acts as a placenta. They emerge, like the Monstrillidæ, in the adult state to lead an independent life, for which they are obviously constructed. The adult orthonectid has much more the appearance of a free-living animal than of a parasite. Its powerful

cilia allow it to swim rapidly in the surrounding water. A more careful histological study than any so far made will probably disclose a nerve ring. What is lacking is the digestive apparatus, as in the Monstrillidæ, and this is almost certainly because the life of the adult is here even more ephemeral, and entirely devoted to the production and dissemination of larvæ. Indeed, both sexes are perfectly ripe on leaving the host; after a few moments, and while they are swimming rapidly about, pairing takes place (Caullery and Lavallée¹³⁴⁾ and the fertilized eggs immediately begin to develop. After about twenty-four hours the ciliated larvæ hatch and proceed to complete the cycle by infecting another ophiuroid. We may suppose that the absence of a gut in the Orthonectidæ has not been determined simply by degeneration brought about by parasitism, but also, perhaps altogether, because the animal does not need to feed during its very short adult life. Of the two generations which alternate regularly in this cycle, it is the asexual generation, formed by the plasmodia, which is really parasitic. The sexual generation may be considered as developing with the assistance of a type of placentation, its own independent life being essentially ephemeral.

EUNICIDÆ

A certain number of Eunicidæ develop up to the adult stage as internal parasites of annelids or other invertebrates, without, however, showing any sign of regression except for some simplification of the jaws. Here are the cases now known to us:

Oligognathus bonelliæ (Spengel¹⁸⁴⁾ developing in *Bonellia* and attaining a length of 10 cm. with more than 200 segments (Naples).

Hæmatocleptes terebellidis (Wiren, 1886) in the longitudinal vessel (cf. the Monstrillidæ) of *Terebellides stræmi* (Greenland).

Labrorostratus parasiticus (de Saint-Joseph¹⁸³) in various syllids, particularly *Odontosyllis ctenostoma* (English Channel).

Oligognathus parasiticus (Cerruti, 1909), in *Spió mecznikovianus* (Naples).

Labidognathus parasiticus (Caullery¹⁷⁹) in a terebellid from the *Siboga* expedition (Malay Archipelago).

It seems that another species was collected under the same conditions in *Marpysa* by Koch (1847).

It is, then, a type of development which is widespread in the Eunicidæ. The parasite often comes to be as long as the host in which it lives. In spite of the intensity of such parasitism the annelid remains normal and must leave its host when it is ready to reproduce. It certainly enters at an early stage (one *Labro-rostratus* observed by de Saint-Joseph possessed only nine segments with neither parapodia nor chætæ); it then accomplishes the whole of its growth as a parasite, without undergoing any regression.

UNIONIDÆ

The bivalves of this family, the freshwater mussels, *Unio*, *Anodonta*, *Margaritana*, pass through an equally intense phase of protean parasitism which leaves no trace in the adult. The

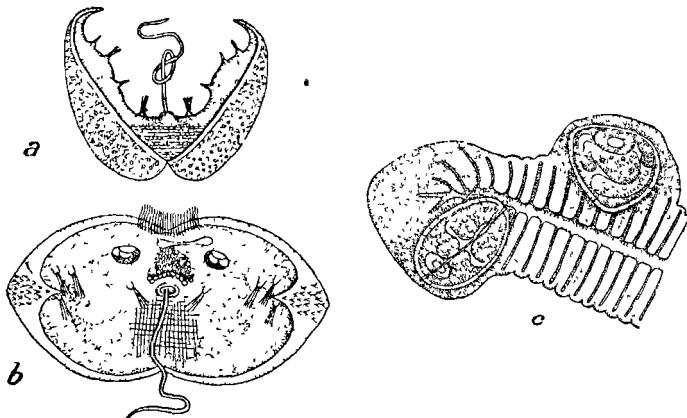


Figure 49. Glochidium larva.

a and *b*, free-living stage in optical section, from the internal aspect (after Flemming); *c*, two glochidia encysted in a branchial lamella of *Cyprina* (after Harms).

eggs are incubated amongst the branchial lamellæ of the mother and give rise to a larva known as the *glochidium*, of a very special character. It has a bivalved shell with a pair of long teeth in the plane of symmetry, and accessory spines laterally

(Fig. 49 *a–b*). The mantle is covered by a special kind of epithelium with tufts of sensitive hairs. The visceral mass is quite rudimentary; *there is no digestive tube*. In the centre there rises up a long slender mobile tentacle that can be seen moving between the valves. At this stage the glochidia are discharged and float about. Leydig, in 1866, discovered that they become parasites of fishes (Cyprinidæ). When a glochidium comes into contact with a cyprinid (often through being drawn in with the respiratory current), then as a result of a tactile reflex in the tentacle described above, the valves tend to close and their teeth penetrate the tissues of the fish, particularly on the branchial lamellæ (Fig. 49*c*). They are easily found at the right season and it is very simple to produce experimental infection of cyprinids and amphibia. The host rapidly reacts to the presence of the parasite (we shall return later to this phenomenon) and envelops it in a thick vascular cyst. The mantle cells of the glochidium, as Faussek has shown, although epidermal in character, behave as active phagocytes, digesting, on contact, the tissues of the host and so ensuring the nutrition of the young parasite, which has no alimentary canal. The vascular tissue of the cyst formed by the host may be compared with a placenta. Under these conditions of nutrition the definitive organs (digestive tube and mouth, foot, kidney, etc.) of the young *Unio* gradually develop, and the definitive shell slowly forms around that of the larva. After a delay, depending on the temperature (80 days at 8°-10°, 21 days at 16°-18°, 12 days at 20°, according to Harms³³⁷), the young mollusc abandons the cyst, which it ruptures with its foot, leaves the fish and falls to the bottom, where it will complete its growth.

Here again we have a case of parasitism that is intense and temporary, anticipated by a preliminary adaptation which allows of the differentiation of special organs, simultaneously with the regression of normal organs. The relationship with the host, during the period of parasitism, suggests a striking physiological analogy with a placenta, and nutrition is carried on by the metabolic activities of accessory organs (larval mantle). The definitive organs (digestive tube, etc.) are unaffected by parasitism; one may therefore consider them to be formed in the normal way. Contrary to the state of affairs in the Monstrillidæ, the digestive tube here persists, evidently because parasitism

comes to an end at a very early stage and the whole of the animal's growth is accomplished in the free-living state.*

GORDIAN WORMS

The gordians, a group related to the nematodes, complete the whole of their growth as internal parasites of terrestrial arthropods (insects and myriapods). When adult they escape from the host by breaking out of it under the influence of humidity, and reproduce outside it, in the free-living state. They resemble long thin twists of twine that have been compared to the strings of a violin; the females are several decimetres long, sometimes more than a metre; the males are usually smaller. These strings undulate and move about in the water. The digestive tube is completely atrophied.

Their development and biology were thoroughly studied by Dorier¹⁸⁹ in 1930. Their escape from the host takes place as a rule when the latter is in water (generally by accident). Once free they usually form clusters containing males and females, and pairing takes place. These adults, unable to feed, cannot live long in a free state. The eggs are laid immediately after pairing and the larvæ hatch out. They are free-living for a time and then either encyst or are swallowed by an aquatic animal (insect larva, mollusc, etc.) in which, however, they soon encyst again. For the completion of development it is necessary that the intermediate host, and with it the cysts, should be swallowed by a suitable final host, which is always terrestrial. The gordians are thus essentially internal parasites, but they have an adult free-living phase during which reproduction takes place. They may therefore be classified amongst the protean parasites.

Completely analogous conditions are to be found in species of *Nectonema*, which may be regarded as the marine representatives of the gordians. They, too, look like long thin strings, white and opaque, and are found from time to time in the surface plankton, where they were first pointed out by Verrill (1879). Externally they possess two brushes of long swimming chætae,

* One of the marine Aviculidæ, *Philobrya*, has a larva analogous to a glochidium, but its development is not known. The larva of South American Unionidæ, called a *lasidium*, is rather different from the glochidium; it is not known for certain whether it has a parasitic stage in fishes.

arranged longitudinally. Since then they have been seen sporadically as internal parasites in various decapod Crustacea: *Palæmonetes* (Ward, 1892), *Pontophilus* (Brinkmann¹⁸⁷); Ch. Pérez (199) found them at Roscoff in Paguridæ (12 individuals from 239 specimens of *Anapagurus hyndmanni*) and once saw a *Nectonema* emerging from one of the pagurids in an aquarium; under the uniform cuticle the chætal brushes were visible: evidently the newly freed animal was going to moult. In 1930 Brinkmann¹⁸⁷ was able to make more complete observations, finding that, in Norwegian waters, the galatheid *Munida tenatmana* is the regular host of *Nectonema munidæ*. Out of 776 specimens of *Munida* examined, 61 were parasitized; the parasites were in clusters in lacunæ in the cephalothorax. The males, completely devoid of pigment, were from 90 to 155 mm. long, the females from 170 to 845 mm.; six of them exceeded one metre. The chætae attained a length of 300 μ . *Nectonema* is clearly a marine gordian, and, like *Gordius*, is an example of protelean parasitism.

ENTOMOPHAGOUS INSECTS

The most considerable example of protelean parasitism is provided for us by the entomophagous insects, in the first place by Hymenoptera and secondarily by Diptera. Far from consisting, like the preceding cases, of curious and specialized exceptions, it is here a very general phenomenon and of fundamental importance for the equilibrium of species in nature. Starting either from the egg, or from a more or less precocious larval stage, they develop as parasites in, or on, other insects and emerge as free-living imagos in no way modified by this preliminary parasitism. Here again the imago is usually short-lived, entirely engaged in disseminating the eggs, and in many cases it takes no food; the alimentary canal is often so constructed that it is impossible for the animal to feed.

The importance of this type of parasitism is seen from the number of species of Hymenoptera alone that exist: there are 200,000 of them, perhaps more, according to Sharp, and they are distributed amongst ten families.* The parasitic Diptera, which

* The Cynipidæ, Proctotrypidæ, Chalcididæ, Ichneumonidæ and Braconidæ are the most important.

are less numerous and are not limited to insect hosts, are also legion; they belong to the Calyptera.* Of the story of this parasitism we still know only vague scraps, pointing to many important aspects and processes of fundamental interest for biology. Each species has for its victim a more or less strictly specific host, and all these victims perish without reproducing. The part played by a phenomenon of this magnitude is at once apparent. As soon as one of these entomophagous Hymenoptera begins to multiply—and the hundreds of eggs laid by these minute insects allow of very rapid multiplication under favourable circumstances—the parasitized species is decimated. On the other hand, if the latter becomes exceptionally abundant it immediately supplies numerous victims to the parasite and so favours its reproduction. The entomophagous insects are thus by far the most efficient natural agency checking the multiplication of a very large number of insects, above all, the Lepidoptera and also the Coleoptera. In particular they are a factor of the first importance in the control of harmful insects; indeed, they are the most powerful barrier to their excessive propagation.

In addition, there is a matter worth mentioning here, although, strictly speaking, it does not come into the scope of this work: attempts are now made to utilize insects from this point of view, both experimentally and directly. The entomological service in the United States has regularly made use of these data. Under natural conditions a comparatively stable equilibrium is automatically established amongst the species composing a fauna, and it is both difficult and dangerous to upset it. But in our time the intensive development of communications and trade between countries and continents far removed from one another constantly introduces grave disturbances into natural states of equilibrium. The accidental introduction of a new insect into a fauna where it did not previously exist may have serious consequences, even when in the country of its origin it was relatively inoffensive. *Phylloxera* on vines, introduced from America into Europe, is a terrible example of this. There is another more recent one in the Colorado potato beetle, *Leptinotarsa decemlineata*. It was possible to check the first invasions into Germany in the second part of the 19th century. A second invasion, in the Bordeaux region of France, during

* Anthomyidæ, Tachinidæ, Dexiidae, Sarcophagidæ, Estridæ, Muscidæ.

the 1914-1918 war, was not dealt with in time and now the beetle has become established in France, and every year, in spite of the war waged against it, it causes considerable damage. Conversely, very many Asiatic and European insects introduced into the United States have found suitable conditions for breeding there, and have thus changed into formidable pests.*

Such was the case with two of the Bombycidæ, which caused minor damage in Europe, but in the United States rapidly became terribly destructive: *Lymantria dispar* (Gipsy Moth) and *Euproctis chrysorrhœa* (Brown Tail). The gipsy moth invasion of America was started by the escape of a few caterpillars that were bred by the entomologist Trouvelot at Medford, near Boston, about 1868. He had sent for this species from Europe in order to study hybrids between it and the American forms. In a few years *Lymantria dispar* had multiplied to the extent of destroying whole forests, and also the trees of towns in Massachusetts and the neighbouring states. The fight against insects there is carried out by an annual expenditure of several millions of dollars, and it is now based primarily on the exploitation of parasitism by the entomophagous insects. As early as 1886 Riley had triumphed over an exotic scale insect, *Icerya purchasi*, which was devastating the citrus orchards of California, by introducing and naturalizing an Australian coccinellid, *Novius cardinalis*, which was, moreover, not a parasite but a predator of the scale insect; the same experiment has been repeated in other countries with constant success. Riley applied the same principle against the white cabbage butterfly, *Pieris brassicæ*, using an entomophagous hymenopteron, *Apanteles glomeratus*, and against the olive scale, *Lecanium oleæ*, using a chalcid, *Scutellista cyanea*, a parasite from the Cape.

One of the principal reasons for the enormous increase in numbers of an insect newly introduced into a country like the United States is that it arrives there without being accompanied by the many parasites which, in its native country, check its multiplication. In the experimental introduction of these parasites equilibrium must be re-established. Working from this principle, the naturalists of the Bureau of Entomology

* We know, moreover, how similar introductions of European plants and animals into Australia and New Zealand have had disastrous consequences for numerous elements of the indigenous fauna and flora of these isolated regions where independent states of equilibrium had been reached.

in Washington attempted to control the Gipsy and Brown Tail Moths by coming to Europe to make a thorough investigation into all the parasites of these two species; then hundreds of thousands of caterpillars and pupæ of both moths were taken from Europe and Japan to America so that the parasites could be collected, bred in numbers in special laboratories, and finally acclimatized under natural conditions^{297, 305}. In Europe, no less than 27 species of Hymenoptera, and 25 species of Diptera are known to attack the caterpillars of *Lymantria dispar*. The caterpillar of a geometrid, *Cheimatobia brunnea*, is parasitized in Europe by 63 Hymenoptera.

But a war of this nature leads to many surprises. Together with the parasites that destroy a harmful species in conformity with the intentions of the experimenter, there are the parasites, or *hyperparasites*, of these useful parasites, which, by attacking the latter, reduce their numbers and thus indirectly favour the propagation of the enemy. The parasites are auxiliaries, the hyperparasites adversaries, and they are introduced simultaneously. The balance of the operation will then depend on the predominance of the one over the other, once acclimatization has been achieved. Sometimes, too, under new conditions, a parasite changes into a hyperparasite. Thus, a chalcid, *Pteromalus egregius*, a European parasite of *Euproctis chrysorrhæa*, also lays its eggs in the larvæ of a braconid, *Apanteles lacticolor*, which itself is a parasite of *Lymantria*. It also happens that American species, parasites of indigenous caterpillars, have changed, after the introduction of the European Hymenoptera, into hyperparasites of these Hymenoptera, thus becoming harmful themselves. *Apanteles fulvipes*, a braconid introduced from Europe as a useful parasite, was attacked in the United States by 16 American species, which became hyperparasitic on it and thus checked its expected increase. One sees how complex and important a part is played by the entomophagous insects in the balance of species and on what a vast scale this factor works; and, as a result, how interesting this class of parasite is, both for general and applied biology. In the United States, the war waged under the direction of the Bureau of Entomology against the Gipsy Moth has supplied biology with data of paramount importance which it was only possible to assemble thanks to enormous resources of material, equipment and staff.

But let us return to the investigation of parasitism itself amongst the entomophagous insects. It is clear that a phenomenon of this magnitude admits of a considerable number of categories which cannot here be reviewed in detail. They fall into the following major classes:

1. The eggs of the parasite are laid in the external environment, and the larva, after hatching, searches actively for its victim on which it lives as an external parasite.
2. The eggs being laid under the same conditions, the larva penetrates into its host where it completes its development as an internal parasite.
3. The parasite inserts its eggs directly within the host where they will complete their entire development; in this case the eggs are either placed in larvæ of various instars, or they may be inserted in an egg which has not yet developed.

The development of entomophagous insects, although it has been the subject of a large number of researches, is still very incompletely known to us. The imagos are discovered more easily since very often the rearing of a larva, e.g., a caterpillar, brings about not the emergence of the awaited butterfly but, in its stead, and at the expense of the chrysalis, either hymenopterous or dipterous parasites. But there are few species in which the whole of the development is known, and we must still expect many interesting facts from these studies.

The circumstances in which the eggs are laid, which are often difficult to observe, set us problems of very great general importance. How does the parasite recognize the presence of the larva or egg on which it will deposit its eggs and where its progeny will find favourable conditions for development? What factor, for example, reveals to the Ichneumonidæ or Braconidæ the presence of a wood-eating larva under the bark of a branch or trunk? And nevertheless the hymenopteron knows how to find the exact point where, by drilling with its ovipositor, it will deposit its egg, just touching the larva that it cannot see but wishes to parasitize. Thus *Thalessa lunator* reaches the larva of *Sirex gigas*, deep in wood. And so, as Picard and Lichtenstein³⁰¹ have shown us precisely, does the braconid *Sycosoter lavagnei* drill through a branch of the fig tree to lay its egg on the larva of a scolytid, *Hypoborus ficus*, which lives in the wood. From the egg thus deposited there hatches a larva which remains

motionless on the host without penetrating into it: with its sharp-edged mandibles it pierces the skin of the *Hypoborus* larva and sucks up from the general body-cavity the fluid on which it lives, slowly emptying its victim which nevertheless continues to feed. It is true that this instinct is far from being infallible and many insects sometimes make regular mistakes to the detriment of their progeny. Thus *Pteromalus egregius*, which lays its eggs in the caterpillars of *Euproctis chrysorrhæa*, frequently places its eggs on the cast skins of the caterpillars where they are lost. And so, quite generally, many larvæ are lost through the mistakes made by the females when laying their eggs.*

The larval forms of entomophagous insects are often most unexpected and most difficult to explain. Such are those of *Platygaster*, a genus of Proctotrypidæ, which lays eggs in the larvæ of the Cecidomyidæ, and whose development was first studied by Ganin, and later by Marchal³⁰³. The first-stage larva is quite different from the vermiform larvæ commonly found in the Hymenoptera. It is strongly chitinized with a huge and distinct cephalic region and a small abdomen. It recalls a copepod and hence has been called a *cyclopoid larva*. The mandibles are enormous. Its affinities will probably be clearer when we are better acquainted with the development of species where the larva is free-living to begin with and only penetrates into the host at a rather later stage. Such is, for instance, the *planidium* larva, discovered by Wheeler³⁹⁸, belonging to the chalcids *Orasema* and *Perilampus*, which penetrates into tachinid larvæ, sometimes themselves the internal parasites of caterpillars. It is very different in structure from the usual vermiform larva. The first stage larvæ of parasitic Hymenoptera must, besides, be very variable. Some of them are illustrated here (Fig. 50), amongst them that of *Eucoilä keilini*, discovered by Keilin³⁰⁰ in a larva of *Pegomyia* (Diptera).

* The development of the larvæ of entomophagous insects in other insects makes it necessary for the former to leave the body of the latter before the emergence of the imago and this is sometimes achieved by arrangements which appear as very precise adaptations. In this connection Kunckel d'Herculais observed that a dipterous fly, *Systropus conopoides*, one of the Bombyliidæ, which develops in the caterpillar of *Sibine bonaeensis* and becomes enclosed in the pupal cocoon, leaves it by the same means as the pupa itself; with the help of a sharp point on the head and a gyratory movement it cuts a ring in the cocoon. Thus the parasite has acquired an organ similar to that of the host. Kunckel gives this parallelism the name of *homœopraxy* (*ὅμοιος*, similar, *πρᾶξις*, action).

The difficulty of understanding these larval forms applies particularly to those that are not manifestly adjusted to the conditions existing where they are found. And yet the egg from which they come is adapted to these conditions both in its structure and in its early development. It is very poor in yolk and segmentation is total, which is related to the fact that the larva will immediately find beside it the wherewithal for nourishment. Doubtless, an ancestral larval form has been retained here by hatching at a very precocious stage, in the same way that the free-living imago is retained at the end of the larval period.

Usually these entomophagous larvæ live in or on their hosts without destroying their essential organs, or even without

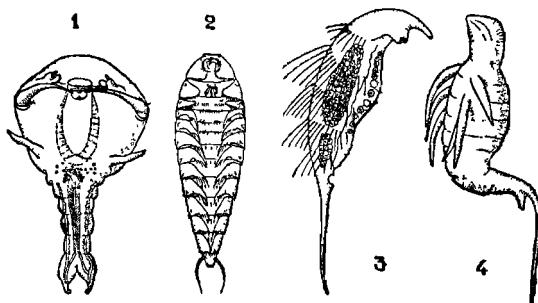


Figure 50. Primary larvæ of various entomophagous Hymenoptera.

- 1, *Platygaster (Trichacis remulus)* (after Marchal); 2, planidium of *Perilampus* (after H. S. Smith); 3, *Teleas* (after Ayers); 4, *Eucoila keilini* (after Keilin).

devouring the fat body, as has sometimes been believed. At the beginning of development, and until the emergence of the larva, they are frequently surrounded by an epithelium originating from the host and isolating them from it. Within this envelope the egg segments and right from the start the actual embryo is separated from the easily stained vegetative masses which fragment and evidently play an important part in nutrition. Here again, then, at least at the beginning of development, there is an arrangement for nutrition recalling placentation. This must play an important part in the retention of the initial larval forms with which we are concerned. When these larvæ have hatched and are mobile within the host, they suck up the fluid of the general body cavity which contains substances extracted from

the plant food of the host and elaborated by it. Their development would doubtless be checked if the host only ceased to feed. Thus the latter may be considered as a mere intermediary for transforming nutritive substances during larval growth and, as the imaginal organs are for the most part new structures which among the holometabolous insects play no part in the functional life of the larva, so it is clear that in any causative sense the parasitism of the larva may not affect them and may lead to an imago similar to that of insects with free-living larvæ. In this sense the present example is connected with some preceding ones, such as that of the Monstrillidæ. One may explain, too, that in families like the Cynipidæ there are, in addition to the entomophagous forms, other closely related types that are gall-forming. Under conditions that we shall come to later, they induce in plants, particularly oaks, the formation of galls where the plant accumulates reserve materials and juices on which the parasitic larvæ feed. Thus they take directly from the plants what entomophagous forms absorb indirectly, and in an already elaborated state, in the body of a host. It is clear that different species of the same type have been able to adapt themselves to either regime, much less different in reality than in appearance. But still this is only a vague analogy and it is obvious that the precise physiological investigation of nutrition in both the parasitic forms as well as the gall-producing ones will be of very great interest.

In the whole of this discussion we have so far only considered entomophagous insects, but a certain number of forms develop in an analogous fashion as plant parasites, and in animals other than insects. One finds parasitic dipterous larvæ in widely different groups. When Keilin was studying the development of *Pollenia rudis*, a very common fly whose larvæ he found in the seminal vesicles of an earthworm, *Allolobophora chlorotica*, he reviewed the general features of parasitism in the larvæ of the Cyclorrhapha. A certain number of these Diptera are of special interest as parasites of vertebrates, particularly of mammals and man. The phenomenon of *myiasis* is interesting on account of the variety of conditions it reveals in this type of parasitism. These somewhat cursory indications allow us to perceive the enormous extent and practical interest of this subject of the entomophagous insects.

CHAPTER VII

PARASITES WHICH CHANGE THEIR HOST

THE preceding chapters have shown us clearly enough that the major event in the life of a parasite is the meeting with the host. Failure to find, at the right moment, a suitable host—and this is usually strictly specific—results in the death of the young parasite, embryo or larva. An enormous number of individuals fails to make this propitious meeting and is thus lost; we shall see how this immense loss of individuals is compensated. But there are some parasites for which the cycle of development is even more complicated and full of risk; they are those that can only complete it by passing through two successive hosts: the first, a temporary one called the *provisional* or *intermediate host*, in which the immature parasite lives, and the second, called the *final* or *definitive host*, in which the adult stage is reached. There are even some parasites that must pass through three successive hosts. These changes of host are termed *migrations* and the parasites in which they occur are said to be *heteroxenous*.

The existence of migrations complicates the study of parasites, for it is extremely difficult, in general, to identify them in their successive phases or, on finding them in one of two hosts, to determine what the other one is. On this account the story of the migrations of parasites is of special interest and we shall review the different cases known to us, passing rapidly over the classical examples and laying more stress on others discovered later.

CESTODA

The first case of parasitic migration to be discovered was that of the cestodes. It was elucidated about the middle of the 19th century. Until then they were considered to be two distinct zoological types, one the ribbon-like *Tænia* dwelling in the vertebrate intestine, the other the vesicular worm cysts, which we

know today as the *cysticercus* stage, situated in the deeper organs such as the peritoneum, the muscles, the liver and brain.

Küchenmeister and P. J. Van Beneden were the first to show experimentally that the cysticercus was simply a stage in the development of the tapeworm, and that the change of one into the other was conditional on the change of host. The cysticercus dwells in an intermediate host and becomes a tapeworm when it is ingested, with all or part of this temporary host, by the definitive host. Without this necessary step, it remains indefinitely in the cysticercus stage and finally degenerates.

Today the developmental cycle of the cestodes is classical and has actually been followed out in a considerable number of species. Let us summarize the case of *Tænia solium*. The egg develops in the uterus of the segment or *proglottis* of the *tænia*, where it originated, and gives rise to an embryo provided with six hooks, arranged in three pairs; this is called the *hexacanth embryo* or the *oncosphere*. Together with the proglottis, it is evacuated from the host. If it is then swallowed by a mammal—the pig is the typical host but other species may serve—the egg shell is broken down by the action of the gastric juices and the oncosphere is set free. With the help of the hooks it passes through the intestinal wall, makes its way into the blood vessels and lymphatics and is drawn into the general circulation. Finally, in the capillary network, it attaches itself to the connective tissue of the muscles, swells up into a vesicle and so becomes a cysticercus, the so-called *Cysticercus cellulosæ*. At the end of some weeks an invagination develops in the vesicle and in it there differentiates a scolex, a structure which may conveniently be termed the head of the future *Tænia*. But, at this point, development is arrested and the cysticercus may remain in this state for months or even years. This cysticercus infestation of the muscles of the pig produces the condition known as "measly" pork. If such meat is eaten by an appropriate mammal such as man, the cysticercus is set free, the scolex evaginates, attaches itself to the mucous membrane of the intestine, elongates and strobilates into the adult *Tænia*.

One finds in textbooks of zoology and parasitology the description of the life history of many species. I shall confine myself here to giving a table in which some of them are summarized.

Species	Definitive host	Cysticercus	Usual provisional host	Situation in the provisional host
<i>Tenia solium</i>	Man, pig	Cysticercus cellulose	Pig	Muscles (measly pork)
<i>Tenia saginata</i>	Man	Cysticercus bovis	Cattle	Peritoneum, muscles (measly beef)
<i>Tenia serrata</i> -	Dog	Cysticercus pisiformis	Rabbit	Peritoneum, liver, etc.
<i>Tenia cænurus</i>	Dog	Cænurus cerebralis	Sheep	Brain
<i>Tenia echinococcus</i>	Dog	Echinococcus	Various mammals	Liver (hydatid cyst)
<i>Dipylidium caninum</i>	Cat, dog	Cercocystis	<i>Trichodectes canis</i> <i>Pulex serraiipes</i>	
<i>Davainea tetragona</i>	Fowls	Monocercus	<i>Helix carthasianella</i>	
<i>Davainea friedbergeri</i>	Pheasant		<i>Formica rufa</i>	
<i>Hymenolepis diminuta</i>	Rat, mouse	Cercocystis	Insects (the beetles <i>Akis</i> , <i>Sciarus</i> , etc.)	
<i>Hymenolepis brachycephala</i>	Disputed		<i>Cyclops</i> and <i>Cypris</i>	
<i>Hymenolepis uncinata</i>	Shrew	Cercocystis	<i>Silpha laevigata</i>	

Each one of these cycles has its own particular characteristics. The intermediate hosts are very varied, a circumstance which has led to surprises and mistakes. P. J. Van Beneden carried out experiments before a commission in Paris in order to prove the specific identity of *Cysticercus pisiformis* and *Tænia serrata*. Young dogs fed exclusively on milk were made to swallow cysticerci from rabbits. At the autopsy he was surprised to see that, in addition to *Tænia serrata*, the dogs contained *Dipylidium caninum*. Today this is easily explained because although the

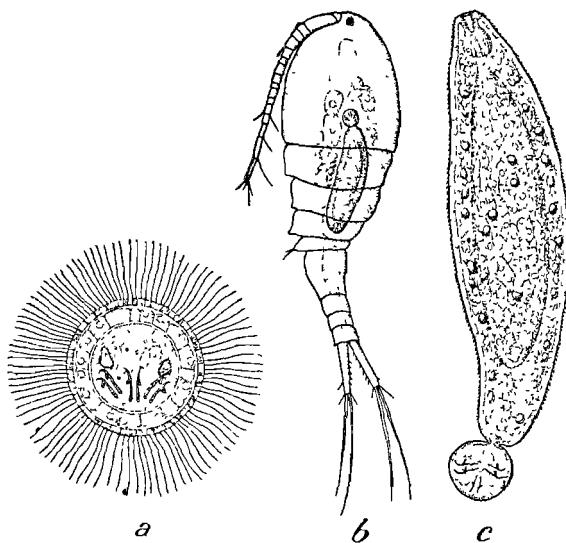


Figure 51. Larval forms of *Bothriocephalus latus* (after Rosen).
a, free-living larva (coracid); b, Cyclops infested by a procercoid larva, c.

dogs were fed entirely on milk they were nevertheless infested with the other species through their fleas and lice, about which no precautions had been taken.

The cycle is sometimes complicated by there being two intermediate hosts instead of only one. Such is the case with *Bothriocephalus*, whose complete life cycle was worked out by F. Rosen¹⁷². It has been long known that a *Bothriocephalus* larva infests man. It is an elongated whitish worm, called a *plerocercoid* larva, which lives in the viscera and muscles of different fishes (Salmonidae, pike), and man becomes infected

through eating undercooked fish* and, in particular, their roes (caviar). But the stages between the egg and this larva were unknown. The eggs of *Bothriocephalus* only develop when they have passed outside the host and then very slowly, taking several months; in running water they develop in 10-15 days at 30-35°. The hexacanth embryo is here covered with a coat of long cilia; it hatches and lives in water as a free-swimming larva or *coracid* (Fig. 51a). The researches of Rosen have shown that this coracid must be ingested by the first intermediate host, which is a copepod (*Cyclops strenuus* or *Diaptomus gracilis*). It passes into the general body cavity of the host† and there develops into a larval form called the *procercoid* larva (Fig. 51b, c). On swallowing copepods infested with these larvæ, fish such as salmonids and pike become infested in their turn with the *plerocercoid* larvæ previously known. Thus here there are two intermediate hosts—copepod and fish—preceding the definitive host where the actual *Bothriocephalus* develops.‡ Under these circumstances it is not surprising that *Bothriocephalus* must produce immense numbers of eggs; it is frequently eight metres long and may be fifteen, with several thousand proglottids.

CESTODARIA

The best established facts and the conclusions to be drawn from them can scarcely ever be generally applied without reservations and exceptions, and the cycle in the Bothriocephalidæ, as it has just been set out, provides us with an interesting example throwing light on this. The cycle is repeated with minor variations in numerous genera and species, but the increase in our knowledge shows that it allows of exceptionally interesting variations. These concern the cestodes that are classified as

* For this reason, *Bothriocephalus* is found particularly in the lake districts of Switzerland and Italy, and in Finland.

† Development is not successful except in certain species of copepods; in others, such as *Cyclops viridis*, the coracids are digested.

‡ Rosen has shown experimentally that the same type of development occurs in *Triænophorus nodulosus*, one of the Bothriocephalidæ which, when adult, lives in the pike (intermediate hosts: *Cyclops*, perch); also in *Abothrium infundibuliforme*, a parasite of trout (*Trutta lacustris*) with a coracid devoid of cilia (intermediate hosts: *Cyclops*, perch); and, finally, in *Ligula simplicissima* which, when adult, lives in the intestine of water birds (*Colymbus*, *Mergus*, *Anas*). The eggs of *Ligula* pass out with the faeces of the bird host and fall into water. The larva passes through a ciliated coracid stage, infests a *Cyclops* and later a fish (gudgeon, bream or roach).

Cestodaria: *Amphilina*, *Gyrocotyle*, *Caryophyllæus*, and *Archigetes*, the first three parasitizing fish, the last occurring in the cœlom of earthworms. In these, the body of the adult, at the time when the genital products are being formed, is no longer segmented into proglottids. The careful examination of these types has recently resulted in their being regarded as more or less closely related to the Bothriocephalidæ, but as reproducing at the stage which in the latter family is larval. This is a case of neoteny.

Amphilina is a parasite in the intestine of sturgeons; investigation into the cycle of development has shown that there is an intermediate host, a copepod, in which there becomes differentiated a tailed larva corresponding to the procercoid larva of *Bothriocephalus*. The sturgeon ingests the copepod together with this larva which, in the fish's gut, develops into the sexually mature *Amphilina*, corresponding to the plerocercoid stage of *Bothriocephalus*. Thus sexual maturity is achieved in a larval stage; that is to say, it is a case of neoteny.

Gyrocotyle is a parasite in the intestine of *Chimæra*, a selachian of the high seas, on which it is almost impossible to experiment; thus the development of these Cestodaria remains unknown but from their structure they appear to correspond closely to the plerocercoid stage.

Caryophyllæus is a parasite of the Cyprinidæ and accordingly more accessible to embryological research. The structure of the adult relates them rather closely to the plerocercoid stages of *Bothriocephalus*. Now, they pass through a procercoid stage, found in the cœlom of earthworms; they then have a long tail and the gonads are already beginning to differentiate. Development is completed when the earthworm is swallowed by a carp and the *Caryophyllæus* becomes sexually mature in this phase which corresponds to the plerocercoid. Here again, it is a case of neoteny.

There remains *Archigetes*. This animal is also found in the cœlom of earthworms and resembles a stage of a procercoid larva; it has a tail bearing at its tip the hooks of the first larval form. But here sexual maturity is attained at this stage. It is thus a much more pronounced case of neoteny than the preceding examples; nothing is known suggesting that *Archigetes* might achieve further development in a second host.

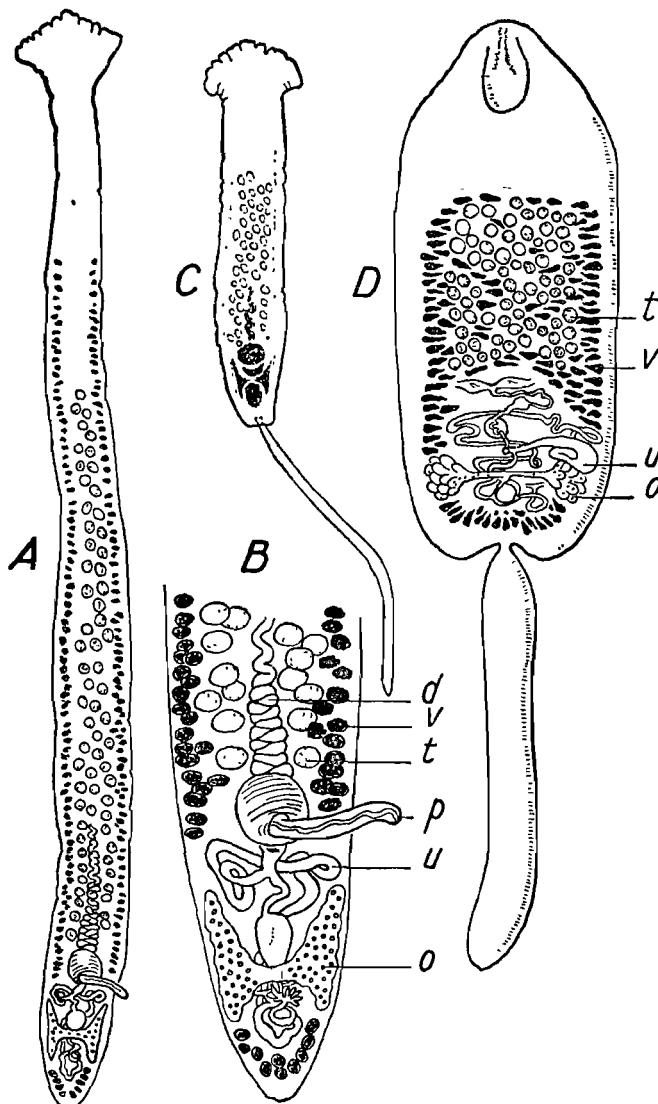


Figure 52. *A-C*, *Caryophyllaeus laticeps*, a parasite in the gut of the carp (after Fuhrmann).

A, adult (4 cm. long); *B*, posterior extremity further enlarged; *C*, plerocercoid larva, parasite in the general body cavity of *Tubifex tubifex* (rudimentary genital organs at the posterior end of the body); *D*, *Archigetes appendiculatus*, parasite in the general body cavity of *Tubifex tubifex* (after Mrazek): *d*, vas deferens; *o*, ovary; *p*, penis; *t*, testis; *u*, uterus; *v*, yolk glands.

A question presents itself in connection with these various Cestodaria: is their development, which we have just summarized, a matter of secondary regression through the loss of the cestode adult, or does it, in the general development of the group, represent a primitive stage, antecedent to the differentiation of the typical forms of true cestodes? It is impossible to reply categorically to this question. It is nevertheless probable that at least in *Archigetes* we are witnessing a secondary state resulting from the loss of development of more advanced stages and the neotenic acquisition of sexual maturity in the first intermediate host.

I have briefly given these details here to show the diversity of facts in a given group and the general interest of the problems raised. As well as in the Bothrioccephalidæ, one may see in other typical cestodes modifications of the usual conditions of development, consisting of the suppression, by secondary adaptation, of the intermediate host, and direct development in the definitive host. This was established by Grassi and Rovelli¹⁵³ for a tapeworm (*Hymenolepis fraterna* = *H. murina*) in rodents; and by Calandruccio for *Hymenolepis nana* in man. The hexacanth embryos change within the lumen of the intestine into cysticercoids which do not acquire the vesicular structure of a cysticercus but attach themselves to the intestinal wall and develop directly into adult tapeworms.

The experimental study of the developmental cycle of cestodes still suggests great numbers of special problems that need elucidation. We have precise knowledge of only a relatively small proportion of existing species. It is a vast chapter of zoology which cannot here be dealt with in detail but only in its general aspects.

TREMATODA

We find, in general, two distinct categories in the developmental cycle of trematodes. Those that are *ectoparasites* complete their whole development on a single host; they are termed *monogenetic*. On the other hand, those that are *endoparasites* undertake, in the course of development, migrations to two or even three successive hosts, these migrations being accompanied by reproductive processes; they are termed *digenetic*. Since the present chapter is devoted to heteroxenous parasites

it must be restricted to the second category. Nevertheless, I shall first mention, by way of parenthesis, the very interesting particulars of development in *Polystomum integerrimum*, a monogenetic trematode parasitic in the bladder of frogs. It is possible that analogous cases will be found later.

MONOGENETIC TREMATODES. The case of *Polystomum integerrimum*. The monogenetic trematodes constitute an extensive group comprising numerous forms that are parasites on the external surface of aquatic animals of different groups, either on the skin or on the gills. They only reproduce sexually. In the family Polystomidae, certain species, amongst them *Polystomum integerrimum*, are parasites in the bladder of amphibia or reptiles. In *P. integerrimum*, Zeller^{177, 178} showed that there is developmental dimorphism. He observed that as a rule the larvæ attach themselves to the gills of frog tadpoles, leaving them at the metamorphosis of the host, and migrating via the gut to the bladder. In this their development parallels that of the frog, sexual maturity being achieved only after a period of three years. But, on the other hand, certain larvæ grow very rapidly on the gills of the tadpole, their rudimentary gonads develop, eggs are laid and a new generation of larvæ is produced. This is a case of neoteny.

This cycle of development has been methodically and precisely re-investigated by Gallien¹⁵⁰. I shall restrict myself here to recalling the essential results of his experiments. He showed that the two types of development depended on the age of the tadpoles carrying the larvæ. On tadpoles less than eight days old and still provided with external gills, they all developed rapidly as neotenic individuals which laid eggs after thirty days. If attachment occurred on tadpoles between eight and thirteen days old both types of development resulted, that is, neotenic and normal, the latter with migration into the bladder and sexual maturity only in the third year. On tadpoles more than thirteen days old there was only retarded development with migration to the bladder and reproduction at three years. The fate of a larva, then, depends essentially on the type of nutrition in the tadpole, and on the effect of hormones, with a threshold of change existing between the eighth and thirteenth day of the tadpole's life. Experiments have clearly shown that the particular constitution of the different larvæ does not intervene, but

that the result depends exclusively on the age of the tadpole. From *Polystomum* eggs of the same batch one can produce either type of development at will. On the other hand, *Polystomum* larvae produced by the neotenic generation, even when fixed on tadpoles less than eight days old, always undergo the retarded type of development. Neoteny cannot be repeated in successive generations. Here is a fact of great interest for general biology. Perhaps it will be found with other variations in related types parasitizing other amphibia and reptiles. Perhaps also processes of this kind are involved in naturally neotenic forms like *Archigetes*.

DIGENETIC TREMATODES. Although the cycle in trematodes has been the subject of very numerous researches, it is only well known in a limited number of species. Broadly speaking, it follows fairly regular lines, and I shall briefly review its essential aspects. The larva, on leaving the egg, first of all penetrates into an intermediate host, a mollusc, in which the animal passes through the stages of sporocyst, redia and cercaria. The classical case and the first to be elucidated is that of *Distomum* (= *Fasciola*) *hepticum*, the large liver-fluke of sheep; the numerous eggs are evacuated with the faeces of the sheep and develop slowly (in two to three weeks at 25°, and very much more slowly at low temperatures), giving rise to a ciliated larva, the *miracidium*, which emerges in water and swims about freely for a time until it meets a small pulmonate snail, *Limnæa truncatula*. It is only within this species, at least in Europe, that its further development can be completed; in *Limnæa stagnalis* it begins but does not go far.* The miracidium settles in the pulmonary sac of the snail and there metamorphoses into a sporocyst, in the interior of which rediae are formed. These migrate to the liver and immediately give rise either to cercariae or to a fresh generation of rediae. The ripe cercariae leave the snail, swim about for a few hours and then settle on a blade of grass where they encyst. When the cyst is swallowed by a herbivore such as a sheep, it breaks down in the

* Quite recently, S. B. Kendall (*Nature*, 163, 1949, p. 880) succeeded in infesting newly hatched *Limnæa stagnalis* with miracidia of *D. hepticum* (13 *Limnæa* were infested out of 101 that were used in the experiment), but he was unsuccessful in infesting adult *Limnæa*. This result is not, however, of importance from a practical veterinary point of view, on account of the entirely aquatic habitat of *Limnæa stagnalis*.

stomach and the young *Distomum*, set at liberty, gains the bile ducts where it reaches maturity. These data are classical and text-books of zoology and parasitology should be referred to for details.*

Cycles of this kind involve the loss of a considerable number of organisms, a loss compensated by extreme fecundity. Here is a typical example:

E. Meyerhof and M. Rothschild¹⁶⁶ report an individual *Littorina littorea* infested with *Cryptocotyle lingua*, and kept in captivity in the laboratory for five years; it emitted about 1,300,000 cercariæ per annum. Now, in certain localities it has been found that the proportional parasitism of gastropods was as much as 40 per cent. One sees what an enormous number of cercariæ is implied.

The complete life cycle is known for only a limited number

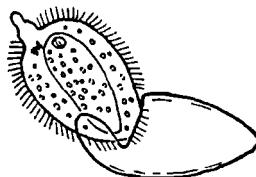


Figure 53. Miracidium of *Parorchis avitus* (parasite of the gull *Larus argentatus*) on hatching, with a young redia (after Linton).

of species. Some of them are summarized for the sake of reference in a table (p. 138). In some very common forms, such as *Distomum lanceolatum* (the small liver-fluke of sheep), the intermediate host has not yet been determined. Likewise many sporocysts and cercariæ are known, but not their adult forms.

The redia stage is sometimes suppressed. This happens in *Distomum macrostomum*, a parasite of birds (woodpeckers, etc.), whose very remarkable sporocyst, the so-called *Leucochloridium paradoxum*, lives in *Succinea putris*. It branches into ducts, one of which distends the tentacles of the mollusc and there hypertrophies into a large tube that pulses in sunlight and is brightly

* Another distome, living in the bile ducts of various mammals, both wild and domesticated, and commonly in man in the Far East, is *Clonorchis sinensis*. The miracidium develops in different species of *Bithynia* and *Melania*. The second intermediate host is a cyprinid fish, particularly the common goldfish, *Carassius auratus*.

Species	Final or definitive host	First intermediate host	Second intermediate host (Encysted metacercaria)
<i>Distomum hepaticum</i>	-	- Sheep, cattle, man	<i>Limnea truncatula</i> -
<i>D. ascidia</i>	-	- Bats	<i>Limnea stagnalis</i> , <i>Planorbis corneus</i>
<i>D. leptosomum</i>	-	- Hedgehog	<i>Helix hortensis</i> , <i>H. nemoralis</i>
<i>D. spinulosum</i>	-	- do.	do.
<i>D. macrostomum</i>	-	- Various birds (woodpeckers etc.)	<i>Succinea putris</i> (sporocyst = <i>Leucocochlidium paradoxum</i>)
<i>D. echinatum</i>	-	- Swans, geese, ducks	Species of <i>Limnea</i> -
<i>D. cygnoides</i>	-	- Frog	<i>Pisidium</i> , <i>Cyclas</i> -
<i>D. nodulosum</i>	-	- Perch	<i>Bithynia tentaculata</i> -
<i>Streiga tarda</i>	-	- Anatidae	<i>Limnea stagnalis</i> -
<i>Hypodereum conoidatum</i>	-	- Anatidae, Gallinaceæ	<i>Limnea stagnalis</i> , <i>L. limosa</i>
<i>Psirolrema spiculigera</i>	-	- Birds, mice	<i>Bithynia tentaculata</i> -
<i>Schistosoma (= Bilharzia) haematobium</i>	-	- Man	<i>Planorbis</i> , <i>Physa</i> -
<i>Amphistomum subclavatum</i>	-	- Frog, toad, newt	<i>Planorbis</i> -
<i>Gasterostomum fimbriatum</i>	-	- Perch, pike	<i>Unio</i> , <i>Anodonta</i> -
<i>Paragonimus westermani</i>	-	- Man	<i>Melania libertina</i> -
			Aquatic insect larvæ
			<i>Leuciscus erythrophthalmus</i> -
			Freshwater crabs (<i>Potamon</i> , <i>Sesarma</i> , etc.) -

coloured. This peculiarity attracts the attention of birds, which go for the parasitized *Succinea*, devour them and become infested. In these sporocysts there is direct development of cercariae.

Many species of cercariae, instead of encysting externally as in *Distomum hepaticum*, penetrate into a second intermediate host where they encyst in the general body cavity and wait there until this host is ingested by the definitive one. The animal at this stage of the cycle is termed a *metacercaria*: metacercariae are very widely distributed, particularly in the polychaetes; the lugworm, *Arenicola*, for instance, very commonly contains one belonging to the genus *Echinostomum* (characterized by a series of hooks arranged like a cape) and these cysts in their turn are covered by a thick mantle of phagocytes from the annelid. Many of these metacercariae are doomed individuals which will never reach maturity for lack of being swallowed by the final host.

In an account by P. Mathias¹⁶⁵ there is a good experimental study of this cycle in three species of trematodes which are parasites of birds (especially of ducks): *Strigea tarda* (fam. Holostomidae), *Hypoderæum conoideum* (fam. Echinostomidae) and *Psilotrema spiculigera* (fam. Psilostomidae).

It is only in comparatively recent decades that we have understood the cycle of two trematodes that cause severe illness in man; these cycles are interesting on account of the way in which they differ from the general run of such life histories.

One of these distomes causes a disease, bilharziosis, that is widespread in warmer countries. It was Dr. Bilharz, in Egypt, who recognized that it is due to a trematode (*Schistosoma* (= *Bilharzia*) *haematobium*) living in the venous system. The Schistosomidae have the curious characteristic, found nowhere else in the trematodes, of being unisexual, the male regularly carrying the young female in a ventral groove. The way in which infestation with this parasite occurs long remained unknown. It was noticed that infection was most common in men working in water, such as the workers in rice fields. Looss, guided by his researches on *Ancylostomum*, concluded that the miracidium penetrated directly into the skin when in water. In 1913, in Japan, Miyairi and Susuki¹⁶⁷ discovered the life history of these trematodes; it is in reality closely parallel to that of

Distomum hepaticum. The results of the Japanese authors were rapidly confirmed by Leiper¹⁶¹ in Egypt, by Iturbe and Gonzalez¹⁵⁷ in Venezuela, and by Lutz¹⁶⁴ in Brazil.

The eggs that pass out with either the urine or faeces (depending on the species) contain a ciliated miracidium which hatches when the egg reaches pure water. It then penetrates into an intermediate host, *Planorbis*, *Bullinus* or *Physa*: the favourite place of entry is through the tentacles of the mollusc. The miracidium develops into a sporocyst within the tentacle which swells up.

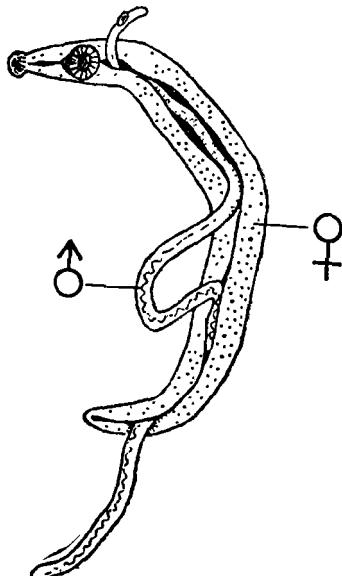


Figure 54. *Schistosoma haematobium* (after Looss).

After about twenty days the primary sporocysts, now mature, burst *in situ*, emitting numerous undifferentiated cellular masses, which will, in the different viscera (liver, gonads) of the water snail, develop into secondary sporocysts where there will differentiate very large numbers of cercariae with forked tails. Under the influence of warmth and bright sunlight these cercariae leave the snail. They come to the surface of the water and float there, hanging by the tail. Man becomes infested either by their coming into contact with his skin when he is bathing, or when he drinks contaminated water. The cercariae

accordingly penetrate either the skin, or the mucous membrane of the mouth or oesophagus. Penetration takes place rapidly, in a matter of some twelve minutes. Experimental infection has been achieved with rodents. We now know a whole series of Schistosomidae which cause serious infection in man or domestic mammals. Let us quote only the following:

Schistosoma haematobium, causative agent of vesical bilharziosis, characterized by haematuria, very common in hot countries (particularly Egypt). The intermediate molluscan host is *Bullinus*;

Schistosoma mansoni, causing intestinal bilharziosis (South

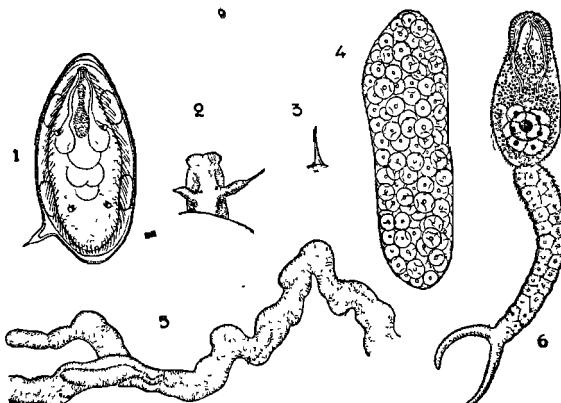


Figure 55. Development of *Schistosoma* (=*Bilharzia*) *mansoni* (after Lutz).

- 1, normal egg containing the ciliated embryo; 2, infested tentacle (swollen) of *Planorbis olivaceus*; 3, normal tentacle; 4, secondary sporocyst; 5, the same at a later stage of development; 6, cercaria with forked tail.

America, Antilles, Africa) and also splenomegaly (particularly in Egypt); the intermediate hosts are species of *Planorbis*;

Schistosoma japonicus, the subject of the researches carried out by the Japanese workers Miyairi and Susuki¹⁶⁷, who thereby established a method for the experimental study of bilharzia diseases. The worm infests various domestic and wild animals. The host in which the cercaria develops is *Oncocotylus nosophora*. The disease it causes is termed arterio-venous bilharziosis, which is common in China and Japan;

Schistosoma bovis, a parasite of cattle and various mammals in the eastern Mediterranean region; the intermediate host is *Bullinus*.

The other parasite of man to be mentioned here passes through a metacercarial phase in a second intermediate host; it is *Paragonimus westermani* which, in the Far East, causes a serious illness, pulmonary distomatosis. The adult trematode, localized in the lungs, causes severe haemoptysis. The miracidium develops in several species of *Melania*. The cercariæ penetrate various freshwater crabs and encyst there; man becomes infested by swallowing the encysted metacercariæ which are found in these crabs (*Potamon obtusipes*, *Sesarma de haani*, *Eriocheir japonicus*), one hundred per cent. of them sometimes being infected. The crabs are the second intermediate host of the trematode, the first being *Melania*.

NEMATODA

A certain number of the parasites in this group are also heteroxenous. *Spiroptera obtusa* of the mouse begins its development in the larvæ of the flour beetle, *Tenebrio molitor*. The Acuariidæ are, as a rule, first parasites of coprophagous insects, and secondly of mammals. *Spirocerca sanguinolenta* and *Physoccephalus sexalatus* thus have as successive hosts *Ateuchus sacer* and the dog or jackal.

Ollulanus of the cat lives as a larva in the mouse; *Cucullanus elegans*, of the perch has for the first host either *Cyclops* or a larva of *Agrion*; an *Ichthyonema* of *Uranoscopus* is, in the first place, a parasite of *Sagitta*.

Trichina (= *Trichinella*) *spiralis* encysts in the muscles of mammals (pig, wild boar, rat, etc.) and can remain alive without developing for several years. When the infected meat is eaten by man or other mammal the trichinas are set free in the stomach, become mature, copulate in the small intestine, and lay their eggs there. Their larvæ break through the intestinal wall and are then carried in the circulation; finally they encyst in the muscles of the new host.

Filarial worms perform complicated migrations which are only partly known. The guinea worm, *Filaria medinensis*, which lives in the subcutaneous tissues of man and may be up to a

metre in length, with a diameter of one to two millimetres, has for its intermediate host a copepod, *Cyclops coronatus*, discovered by Fedzchenko. It enters by the mouth and alimentary canal and from there passes into the general body cavity (Roubaud 202). Man becomes infected through swallowing these crustaceans, but it is necessary for the worm to have undergone rather a long process of development in them. Experimental infection of monkeys has been obtained.

A whole series of filarial worms which, as adults, live in the deeper organs, particularly the lymphatic vessels, and whose embryos (microfilaria) enclosed in a sheath circulate in the blood, have an analogous cycle. Such are *Filaria bancrofti* (= *nocturna*) with larvae that circulate during the night and cause serious illnesses, *F. loa* (= *diurna*), *F. pertans*, *F. volvulus*, etc. Of the filarial worms in man, the only one with a completely known life history is *F. bancrofti*, discovered in 1877 by P. Manson.* The intermediate host is a mosquito, *Culex fatigans*, that swallows the microfilaria in the blood. In the stomach of the mosquito these microfilaria divest themselves of their sheath, pass into the general body cavity and to the muscles and there undergo a phase of development lasting about a fortnight, by which time their organs have developed.† They then migrate into different parts of the mosquito's body and come to accumulate in the labium. At the moment when the mosquito bites they are deposited on the skin, through which they quickly pass without having to make use of the bite, since they can penetrate healthy skin.‡

Today we know a certain number of parasitic nematodes, belonging to the family Filariidæ, which cause more or less serious illnesses in man and are transmitted in similar ways. Here I shall cite only the following: *Onchocerca volvulus*, transmitted by the bite of simuliids, and *Filaria loa* (loa-loa), transmitted by a tabanid, *Chrysops*.

* This discovery, apart from its own particular interest, has that of having been the point of departure for the researches which ultimately led to our knowledge of the cycle of the malaria parasite. Historically, it is the origin of the whole fruitful series of researches into the illnesses caused by parasites in the blood.

† *Culex fatigans* is practically the most important vector of *Filaria bancrofti*, but many other species are capable of carrying it. Brumpt (2, 5th ed. p. 967), in this connection gives a table containing 30 different species.

‡ *Filaria bancrofti* is the cause of many serious pathological conditions in man, especially elephantiasis.

Filaria immitis in the heart of the dog is also transmitted by culicids; the mechanism is the same as with *F. bancrofti*, except that the young worms complete their development in the malpighian tubes of the mosquito. *F. grassi*, also in the dog, is transmitted by a tick, *Rhipicephalus*. Other examples could be added to these.

GORDIAN WORMS. These aberrant nematodes also undertake complex migrations, involving as a rule two successive hosts. We have already had occasion to summarize the essentials of their life history in connection with the facts of protelean parasitism.

ACANTHOCEPHALA

These, when adult, are parasites in the intestine of vertebrates, to which they are fastened by a proboscis provided with numerous rows of hooks. There is no trace of an alimentary canal. The larval stage is passed in an intermediate host which varies according to the species: either a crustacean (*Asellus*, *Gamma-rus*, etc.), an insect (*Blaps*, *Cetonia*), or a fish.

Such a cycle with an intermediate invertebrate host occurs in Acanthocephala parasitizing fish or amphibia. But with those that in the adult state infest birds or terrestrial and aquatic (Pinnipedia and Cetacea) mammals, one must allow that there are in fact two successive intermediate hosts, the first being, as usual, an arthropod and the second a fish, an amphibian or even a reptile (snake), which is finally eaten by birds or mammals. I restrict myself to this general statement without entering into details of particular cases.

PENTASTOMIDA

These vermiform animals (also known as Linguatulida or Porocephala) live as parasites in the respiratory passages of mammals (particularly carnivores) and snakes. Thus *Linguatula serrata* is found in the nasal fossæ of the dog, and *Porocephalus armillatus* in the tracheal artery and lung of large snakes. The affinities of this group are very obscure. For a long time they were associated with the arachnids. Heymons, after extensive investigation,* contented himself with assigning to them a place

* In Kükenthal-Krumbach, *Handbuch der Zoologie*, III, I, 1927, p. 128.

between the annelids and the arthropods, in the vicinity of groups such as the tardigrades and the Onychophora.

They are heteroxenous parasites. The eggs, which are very numerous, make their exit with the nasal secretions of the host and contamination takes place on the soil where the eggs are lying. This is how the many animals are infected that constitute the intermediate hosts: rabbits, hares, rats, cattle, etc., and also man (particularly in Africa, with the eggs of *Porocephalus armillatus*). The ingested larvæ pass from the gut of that host into other organs and finally encyst. The parasite becomes adult when the intermediate host is eaten, either by a carnivorous mammal (in the case of *Linguatula serrata*) or by a snake (in the case of *Porocephalus*). There it passes via the gut to the respiratory tracts, where growth is completed.

PROTOZOA

Migration with a passage through an intermediate host is no less widespread in the parasitic Protozoa than in the Metazoa, particularly in the Sporozoa and Flagellata.

In the gregarines, Léger and Duboscq¹⁰³ have shown conclusively that the cœlomic gregarines of Crustacea, forming the genus *Aggregata*, are no other than the schizogonic members of a cycle in which sporogony takes place in cephalopods, there developing into the forms known as *Klossia* or *Eucoccidium*, hitherto considered as Coccidia. In causing the ingestion by *Portunus* or *Inachus* of the sporozoites of *Eucoccidium eberthi* from the cuttlefish they induced an intense infestation of *Aggregata* in the crabs, and were able to follow out all the stages.

The same applies to the intestinal gregarines known as *Porospora* in decapod Crustacea (lobsters and crabs); their sporozoites are naked and represent only an asexual part of the cycle, the sexual stages occurring in bivalve molluscs (*Tapes*, *Solen*, *Tellina*, *Mytilus*, *Cardium* and *Donax*), where the gregarines live as parasites described under the name of *Nematopsis*. In bringing about the ingestion of *Nematopsis* by *Portunus*, Léger and Duboscq^{104, 105} obtained the whole development of *Porospora* (cf. Fig. 56).

These researches of Léger and Duboscq have been extended by those of P. Hatt⁹² on the cycles of *Porospora gigantea* in

the lobster, and of a corresponding gregarine occurring in a crab, *Eriphia spinifrons*, and in various molluscs. Hatt was able to bring about the infection of *Trochocochlea mutabilis* with gymnospores of *Porospora* from the lobster, and that of the mussel, *Mytilus edulis*, with *Porospora* (formerly known as *Nematopsis legeri* at this stage) from *Eriphia*; he then traced the steps of development in this second host. He described in detail the penetration of the gymnospores into the gill lamellæ of the mollusc and followed their changes through to the nematopsis

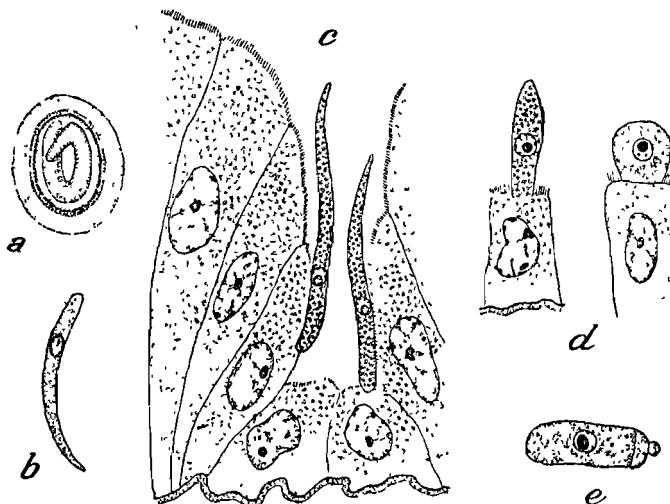


Figure 56. Cycle of *Porospora portunidarum* (after Léger and Duboscq).

a, nematopsis stage (in the gills of *Cardium edule*); *b*, sporozoite from a nematopsis just after hatching in the alimentary canal of *Portunus depurator*; *c-e*, sporozoites attached to the intestinal cells and developing into sporadins.

stages, and finally succeeded in infecting Crustacea (lobsters or crabs). This cycle, at the beginning of parasitic life in the mollusc, includes a phase in which the elements of the gymnospores appear in the shape of pairs of minute spheres that Hatt interprets, not without some reserve, as the pairing of two bodies equivalent to gametes. The resulting zygotes are said to become the sporozoites which produce infestation in Crustacea.

It is particularly in the Hæmosporidia and the Hæmoflagellata that migrations assume paramount importance on account

of the pathogenic role of many of these parasites. The study of these migrations was one of the principal subjects of zoological research at the beginning of the twentieth century. In general, amongst the vertebrates, the Hæmosporidia multiply asexually (schizogony) and differentiate into sexual elements (gametocytes) but without the formation of true gametes being achieved. Such a development only occurs when the gametocytes leave the blood vessel of the vertebrate. On microscopic examination of the blood of infected birds or mammals, one sees, after a few moments, male gametocytes rapidly emitting some long filaments, which are none other than the microgametes; for a long time these were taken to be degenerating forms. It was at Constantine (Algeria) that A. Laveran first watched under the microscope the formation of these filaments in the blood of a malarial sufferer, and he saw that the parasite caused the illness. It was only in 1897 that McCallum¹⁰⁶, working with *Hæmoproteus columbae* from the pigeon, saw under the microscope these filaments fertilizing the female gametes. Under natural conditions this development of the gametes and their pairing is only accomplished in the stomach of a biting insect—mosquito, leech, tick, etc. In this new host the second part of the cycle is achieved, leading to great numbers of organisms which are inoculated into vertebrates when they are bitten by the invertebrate host.

Ronald Ross¹¹⁵, in 1898, first made known all the components of this cycle; he was working with *Proteosoma*, a bird parasite, with gamogony in *Culex*. Shortly afterwards the researches of Grassi⁹¹ and his pupils exactly reconstituted it for the closely related parasite, *Plasmodium*, which causes human malaria; here the second host is another culicid genus, *Anopheles*.

Let us rapidly recapitulate the facts concerning *Plasmodium*, which today are classical. The parasites multiply by schizogony in the red blood corpuscles of man (rosette forms) and there elaborate "melanin" pigment. After a certain number of generations of this kind they produce elements of a special nature (crescents), which are the gametocytes and do not develop further in the human blood stream; if, however, they are ingested by an *Anopheles* sucking blood, they no sooner reach the stomach of the mosquito than the female gametocytes, or macrogametes,

round up; and the male gametocytes give rise to the filaments or microgametes (seen by Laveran), which will fertilize the macrogametes. The resulting zygote (*ookinete*) is vermiform and mobile; it breaks through the stomach wall of the mosquito and encysts (*oocyst*), causing a hernia on the external wall of the stomach, which juts into the general body cavity. Within these oocysts there differentiate immense numbers of filiform mobile sporozoites, which spread throughout the body of the mosquito and invade the salivary glands. They will be inoculated into man when the mosquito bites him. The mechanism of transmission is clearly somewhat similar to that of *Filaria bancrofti*. Enormous numbers of papers on the *Plasmodium* cycle have been published. There is no question of going into the details of the subject here. Very recently the cycle has been elucidated in the initial phase of the infestation of the mammalian host, following on the bite of the mosquito. Infection of this host is not betrayed by fever until several days have elapsed. It was recognized by H. E. Shortt and his colleagues¹²² that this latent period corresponds to a first phase of schizogonic multiplication taking place in the liver. It is after this that *Plasmodium* passes into the blood and fever ensues. Fig. 57 shows the whole cycle as known today.

Hæmoproteus columbae of the pigeon is transmitted by a pupiparous fly, *Lynchia maura*, which lives on the pigeon, but in this case the part of the cycle which is accomplished in the invertebrate is reduced to the pairing of the gametes; the ookinete does not leave the stomach of the insect and is inoculated into the pigeon without having developed. This cycle has been studied in particular by Ed. and Et. Sergent¹²¹. *Hæmoproteus noctuae* of the little owl is, according to Schaudinn¹¹⁹, transmitted by *Culex*.*

The hæmogregarines that are principally found in the blood of cold-blooded vertebrates have an analogous cycle. The invertebrate host is generally one of the Hirudinea (for Hæmogregarinæ) or an acarine (*Lyponyssus saurarum* for *Karyolysus lacertarum*). *Hepætozoon perniciosum* of the rat has for its invertebrate host an acarine, *Lelaps echidninus*, a parasite on

* The researches of Schaudinn (1904) on this last parasite achieved fame because this author was led to suppose that the Haemosporidia, the Hemo-flagellata and spirochaetes were all identical. But his conclusions must have been based on a misunderstanding of mixed infections and are no longer valid.

the rat; *Leucocytozoon canis* has the tick, *Rhipicephalus sanguineus*.

The Hæmoflagellata are transmitted in much the same way as the Hæmosporidia and the study of the factors involved is now a matter of exceptional importance on account of the pathogenic forms; moreover, it is highly complex. Today, one may

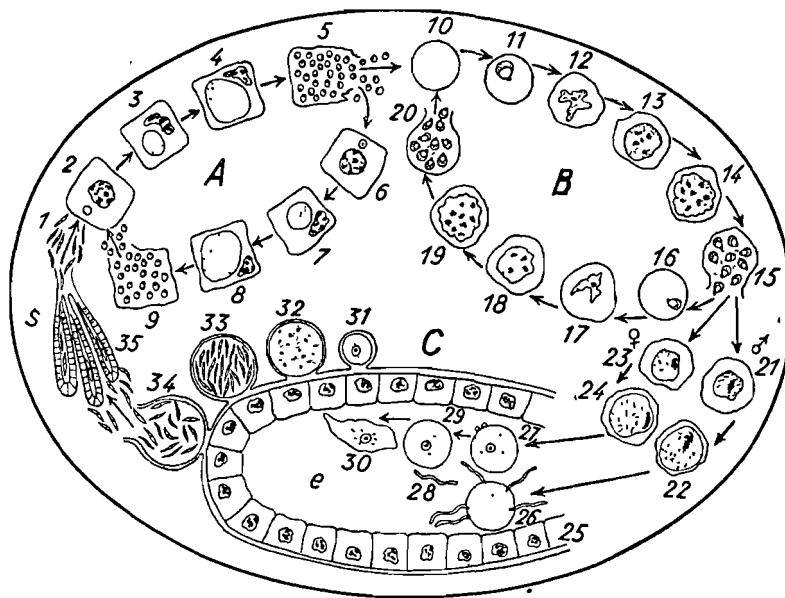


Figure 57. Developmental cycle of *Plasmodium cynomolgi* (after H. E. Shortt).

A, phase in the liver, and *B*, phase in the blood of the mammal host (schizogony). *C*, phase in the mosquito (sporogony): 1–9, schizogonic cycle in the hepatic cells; 10–20, schizogonic cycle in the red corpuscles in the blood; 21–22, microgametes; 23–24, macrogametes; 25–30, their development and conjugation in the stomach, *e*, of the mosquito; 31–34, oocysts and formation of sporozoites; 35, their passage through the salivary gland of the mosquito.

consider it established that there are two categories of transmission. In one of them the invertebrate vector truly deserves the name of host because there is development of the flagellate within it before reinoculation, and reinoculation is only possible after this development has been completed; in the other, the

invertebrate is only a mechanical agent in passive transmission. In the first case the organisms transmitted are specific; in the second case there is no such limitation.

The invertebrates that transmit the hæmoflagellates are naturally bloodsucking species, primarily the biting insects, either Diptera (flies, *Glossina*, *Stomoxys*, *Tabanidæ*, *Simulium*, *Phlebotomus* and mosquitoes) or fleas, lice and Hemiptera, and secondarily the ticks and leeches.

Species of *Glossina*, the tsetse flies, are the vectors of trypanosomes which are of the first importance on account of their pathogenic nature; in the first place, there are *Trypanosoma brucei* causing nagana and *T. gambiense* causing sleeping sickness, and then there are other species such as *T. cazalboui* causing souma, and *T. pecaudi*, etc. The part played by *Glossina* was first shown by Bruce in 1894; in exact experiments on nagana he showed that the transmitting agent was *Glossina morsitans* and that big game in Africa acted as a reservoir of the causative agent. *Trypanosoma gambiense*, the cause of sleeping sickness, is principally transmitted by *G. palpalis*; but in certain regions (Rhodesia) there is another trypanosome, *T. rhodiense*, infecting man, transmitted by *G. morsitans*. *T. cazalboui* is transmitted by different species of *Glossina*. In all these cases *Glossina* is the true host in which some development occurs, its degree varying according to the species. Some authors maintain that this development takes place exclusively in the proboscis, others that it is completed in the stomach, whence, after some delay, the trypanosomes pass either to the proboscis, or else to the salivary glands (this would be the case with trypanosomes of man). The details of this development are still not clear. Koch observed a dimorphism which suggested gametocytes to him, but the reality of the phenomenon of sexuality has not yet been demonstrated.

Trypanosoma lewisi, a non-pathogenic form in the rat, similarly completes its life cycle in a flea, *Ceratopsyllus fasciatus*, and perhaps in a louse, *Hæmatopinus spinulosus*. *T. theileri*, in cattle in the Transvaal, is said to be transmitted by a hippoboscid. *Schizotrypanum cruzi*, causing South American trypanosomiasis in man, has for its intermediate host bloodsucking Hemiptera of the family Reduviidæ (*Triatoma*, *Rhodnius*, etc.), with development analogous to that found in species of *Glossina*.

Wild animals such as armadillos act as reservoirs of the organisms.

Trypanosomes of aquatic vertebrates are transmitted through the agency of leeches (*Trypanosoma granulosum* of the eel by *Hemiclepsis*, *T. rajæ* by *Pontobdella*, *T. inopinatum* of the frog by *Helobdella*, etc.), as was shown by the researches of Léger and Brumpt. But with other trypanosomiases invertebrates are purely mechanical vectors. This is said to be the case with surra (*T. evansi*), transmitted by *Stomoxys* and tabanids, and for debab (*T. berberum*) of camels, also transmitted by tabanids. *Stomoxys* also spreads the trypanosomiases for which *Glossina* is the specific host, as was clearly shown by Bouffard in connection with souma (*T. cazaloui*). In the same way mosquitoes can transmit this infection. *Trypanosoma equiperdum*, causative agent of dourine in horses, is directly transmitted across the mucous membranes at coition, thus differing from all other trypanosomes.* But it has been possible to transmit it experimentally by insects.

The leishmaniases (canine leishmania, kala azar in man, Oriental sore, South American leishmania, etc.), also caused by flagellates (*Leishmania*), are usually transmitted by *Phlebotomus*, a biting fly belonging to the Psychodidae, a fact first recognized by Ed. Sergent in Algeria for "clou de Biskra" and also observed in connection with Oriental sore and most other leishmaniases, particularly kala azar, the leishmaniasis of the spleen in infants.†

The transmission of the piroplasmoses (or babesioses) is effected by acarines, the ticks (Ixodidae), which are true hosts in which the parasite completes its development, and even passes in the eggs from one generation to another. Moreover, these acarines transmit other types of disease.

The precise mechanisms of transmission of the different parasites are far from uniform and many are still debatable. There

* Koch, however, believes that certain facts of conjugal contagion show that *T. gambiae* can be transmitted in the same way.

† Incidental to these data, I shall here relate a curious fact first pointed out by A. Lafont in Mauritius⁴⁸⁴: teeming numbers of a flagellate, *Leptomonas davidi*, caused an infection in the latex of one of the Euphorbiaceæ (*Euphorbia pilulifera*). It was a truly parasitic disease of the plant, a *flagellosis*. Out of 114 plants examined, 49 were infected. Lafont⁴⁸⁵ was able to produce experimental transmission of the parasite through the bite of a hemipterous insect, *Nysius euphorbiae*, that frequently lives on the plant. This fact is certainly not the only one of its kind.

may be inoculation in the true sense, by a sucking invertebrate, or deposition of the parasite on the skin, either in saliva or excrement, and active or passive penetration, either through healthy skin or through wounds.

A special question arises in connection with the migrations of these parasitic Protozoa. With the Metazoa it is obvious that the definitive or final host is that in which the parasite attains sexual maturity. In the Protozoa the criterion is much less clear, the phenomena of sexuality are often completed in stages in each of two hosts, or are not known. We do not know for certain, at least up to the present time, the sexual stages of trypanosomes, and with the Hemosporidia the gametes are really differentiated in the gametocyte stage in the blood of vertebrates, but they only complete development and copulate in blood-sucking invertebrates. Under these conditions, which is the definitive or main host? Two theories exist. Certain biologists such as Léger consider, for instance, that the trypanosomes were originally intestinal parasites of non-biting insects, in the state of *Crithidia* or *Leptomonas*, and that they were modified in biting and blood-sucking insects, so becoming adapted to the internal environment of vertebrates; Roubaud supports these ideas. Minchin, on the contrary, considers the vertebrate to be the fundamental host in which the trypanosomes were originally parasites in the intestine and then later in the blood; finally, they would have passed into blood-sucking insects. Mesnil supports this last hypothesis on account of the occasions, by now rather numerous, in which intestinal parasites have been seen passing into the blood; these are distinct from pathological cases.

For the Hæmosporidia this second hypothesis seems the more natural; they are derived from Coccidia which were originally present in the intestine and later in the blood: there are some types of true Coccidia which, from their situation and even in their development, indicate the possibility of this transformation. Their passage through the Culicidæ would be a secondary complication of the cycle. The vertebrates would then be the principal hosts. The latter term, moreover, is more suitable here than that of definitive (or provisional) host. If we admit Léger's hypothesis for hæmoflagellates, we see that the migrations, after having arisen secondarily, can finally disappear as in the

case of dourine, and this must be compared with the suppression of migration that we have seen in certain species of *Hymenolepis*, where the tapeworm develops without an intermediate host and where this type of development is evidently secondary.

Some plant parasites, like those of the animal kingdom, migrate to successive hosts which are more or less indispensable for the completion of their whole cycle. The classical example is that of certain Uredineæ the sporophyte of which (with uredospores and teleutospores) lives on one host, and the gametophyte (with oöcidiospores and spermogonia) on another. With *Puccinia graminis*, the rust of wheat, the first host is a cereal, particularly wheat; the gametophyte, on the contrary, lives on barberry.

CHAPTER VIII

ADAPTIVE MODIFICATIONS IN THE REPRODUCTION OF PARASITES

THE examples studied in the preceding chapters show how parasitism modifies all the organ systems; the reproductive apparatus is one of those which are most constantly and profoundly affected. The reproductive function in most parasites undergoes considerable hypertrophy; to the usual processes of reproduction others are frequently added which result in increasing them. Without introducing any finalist view one may say that, in fact, reproduction is the goal of all the functions of the organism; but, in free-living forms, the activity of the individual is to a large extent exercised independently of reproduction and in the higher animals it even survives it. In parasites, on the other hand, this function preponderates and all else is subordinate to it; nothing is retained, one may say, except in so far as it helps reproduction.

The parasitic life limits the function of reproduction by tying the parasite closely to the host and thus restricting the usual possibilities for the meeting of the sexes. On the other hand, it introduces a new condition into development, that of meeting the necessary host at a definite time. From these two facts arise the essential characteristics of reproduction in parasites.

HERMAPHRODITISM AND CHANGE OF SEX

To the first of these two facts are related the most frequent modifications of sexuality in parasites; these can be placed in two principal categories: hermaphroditism and exaggerated sexual dimorphism.

Hermaphroditism is a very widespread condition in parasites, whether it existed already in ancestral free-living forms and is therefore primitive, or whether it appeared secondarily and as a result of parasitism. Thus, one may consider as primitive her-

maphroditism that of the trematodes and cestodes, the Rhizcephala, even the Hirudinea (the oligochætes are already hermaphrodite). But in most other groups hermaphroditism is secondary, as one may see by comparing related forms. In the Myzostomaria, which are certainly derived from the polychætes, hermaphroditism must have been established or at least reinforced (for it exists in a more or less rudimentary state in a certain number of polychætes) by parasitism. Among the isopods, which are essentially unisexual animals, the Cymothoidæ show sex reversal, as do also the Cryptoniscidæ amongst the Epicaridæ, and there it is obviously a secondary condition. In the Orthonectidæ, with separate and dimorphic sexes, hermaphroditism is introduced as an equally secondary modification (*Rhopalura julini*, and *R. pelseneeri*, *Stacharthrum giardi*). In the nematodes, which are normally unisexual, the parasitic forms include a certain number of hermaphrodite types (*Rhabdonema nigrovenosum*, *Bradylnema rigidum*, *Allantonema*). In the prosobranch gastropods, where unisexuality is the rule, parasitism, as we have seen in certain forms, involves hermaphroditism, particularly in the most degenerate forms (Entoconchidæ). Hermaphroditism is, moreover, a simplification of reproduction in parasites only if there is self-fertilization, and this is the case in a certain number of groups such as the cestodes, the Rhizcephala, hermaphrodite Orthonectidæ, etc. But change of sex leads to the utilization of all individuals for egg production and therefore turns out to be an arrangement that favours the species; it happens, besides, to converge with the second of the two conditions referred to earlier, the exaggeration of sexual dimorphism, to the extent that it has been and still is sometimes difficult to decide which of the two arrangements one is dealing with. The exaggeration of sexual dimorphism almost always consists of gigantism in the female in comparison with the male. The converse is a rare exception (*Bilharzia*). But in both cases the sexes live together; generally then the dwarf male lives on the female. Thus, the meeting of the sexes is assured. Moreover, the permanent union of the sexes is to be seen even in parasites that are but little modified and show only slight sexual dimorphism, notably in many Crustacea (*Ichthyoxenus*), even in simple commensals or inquilines (see Ch. 1). It is the permanent union of the sexes that is the truly characteristic and fundamental

feature; but one may say that from this arise sexual dimorphism and the dwarfing of the male. These phenomena occur, after all, for the same reason, in organisms that are simply sedentary. One could compile long lists of parasites with intense sexual dimorphism and with the sexes living in permanent association: it is so with most of the Epicaridæ (Bopyridæ, Entoniscidæ, Dajidæ), with almost all copepod parasites (excepting *Xenocæloma*, which is hermaphrodite and self-fertilizing), with the Ascothoracica, with most parasitic gastropods (Capulidæ, Eulimidæ, *Entocolax*, *Pædophorus*), with different parasitic nematodes (e.g., *Syngamus trachealis*).

In the Cryptoniscidæ and some of the Myzostomaria the external aspect of both sexes is similar and precise investigations have been necessary to show that hermaphroditism really exists. In the male phase the animal is dwarfed and lives on a large female, a form into which it will change after having functioned as a male. Practically, it is a dwarf male. Using abundant material, which was carefully observed *in vivo*, I was myself able to follow and make quite certain of the stages of transformation in several types as the male changed into the female (in *Hemioniscus*, *Danalia*, *Liriopsis*, *Ancyroniscus*). In the special case of the Myzostomaria all the transitional stages have been found, from protandrous hermaphroditism, with the simultaneous presence of two unequally developed glands, to a true change of sex, as Wheeler established¹⁸⁵, the males having been for a long time regarded as special individuals, independent of the females.*

The truly characteristic change in sexuality in parasites is, then, the permanent proximity of the sexes, ensuring fertilization, either in unisexual states with a dwarf male living on the female, or in hermaphroditism, involving a change of sex, as we have just seen, or by the establishment of a condition allowing of self-fertilization.

Here I shall mention a fact that is both very curious and unexpected in its connection with parasitism, as it occurs in animals

* In certain parasites (Myzostomaria, Entoniscidæ), as well as in some sedentary animals (cirripedes), *complemental males*, in addition to hermaphrodite individuals, have been described. In each case it is necessary to be sure that these males will not finally develop into females: the existence of such dwarf males in the Myzostomaria is not generally admitted nowadays. The existence of males in the Entoniscidæ, accepted by Giard and Bonnier, needs to be investigated again. The cryptoniscan larvae, which they considered as such, are perhaps merely young stages of ordinary males.

that are perfectly free—the abyssal fishes of the family Ceratioidea (related to the angler, *Lophius piscatorius*). There is in some of these animals a high degree of sexual dimorphism, *the male being a dwarf and living as a permanent parasite on the female*. In studying specimens of this family collected by the Dana, Tate Regan⁵⁹⁴ recognized that on some individual females in three of the species collected (*Photocorynus spiniceps*, *Edriolynchus schmidti*, *Ceratius holbollii*) there were dwarf males

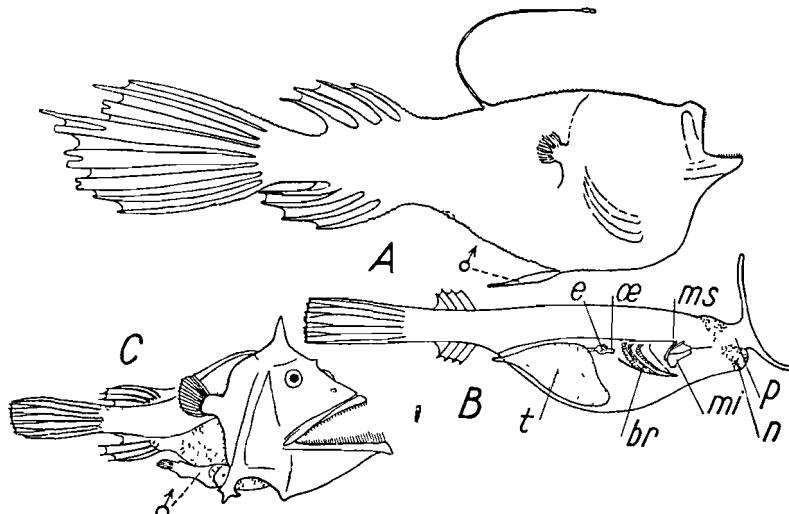


Figure 58. Dwarf males parasitizing females in the Ceratioidea (after C. Tate Regan).

A, *Ceratius holbollii* ♀ with ♂ attached to its ventral region. B, anatomy of the male. C, *Edriolynchus schmidti*, ♀ with ♂ attached ventrally; br, gills; e, stomach; mi, mandible; ms, maxilla; ae, oesophagus; p, attaching papilla formed by the tissues of the female; t, testis.

fixed by the mouth to the surface of the female. The contact is intimate. A perfect continuity of the tissues of both partners, and especially of their vascular systems, is established. The male then feeds at the expense of the female. It is an unequivocal case of parasitism and as complete as could be. Nevertheless, the male has retained his gills and breathes independently. The achievement of this paradoxical association is evidently tied up with the extreme unlikelihood that the sexes would meet if they lived apart. The males must attach themselves to the females shortly

after hatching from the egg; those that do not succeed in this probably perish. It would obviously be of great interest to verify this in living material, but that is practically impossible.

INCREASE IN EGG NUMBERS

The necessity of meeting the right host at the propitious moment of development and, in forms undertaking migrations, that of passing successively into different hosts, affects the parasites to an even greater degree than the need for ensuring fertilization of the eggs. From these circumstances there arises an enormous loss of eggs or embryos which, under the usual conditions of reproduction, would rapidly bring about the disappearance of the species. Parasitic forms have then only been able to maintain themselves by arrangements that compensate for this extreme degree of mortality in their young.

The simplest and the most widespread of these arrangements is a considerable increase in the number of eggs produced. Increase in fecundity is a very general characteristic in parasites and to a large extent the hypertrophy of the female in comparison with the male is due to it. A clear idea of this increase in fecundity is gained by comparing the contents of the brood pouch of one of the Epicardidæ—tremendously developed and with the embryos to be counted by thousands—with that in a normal isopod such as *Sphæroma*, where there will be scarcely a hundred or two. Individuals of *Sacculina*, *Lernaea*, *Xenocaloma*, all constantly produce large batches of eggs: the egg strings of parasitic copepods are much longer than those of normal forms. Egg production in the parasitic nematodes is enormous. It was long ago calculated that *Ascaris lumbricoides* in man annually produced 64 million eggs, representing 1,700 times its own weight; a queen bee, which is considered to be endowed with quite exceptional fertility, annually produces only thirteen times her weight in eggs. In *Sphaerularia bombyi*, a nematode parasite of bumble bees, there is produced on the female herself an extroversion of the uterus, forming an enormous sac to which the body of the female remains attached as a minute appendage (Fig. 59A-C); the sac contains a very large number of embryos. The related genera *Allantonema* and *Attractonema* show similar arrangements. The trematodes and cestodes lay eggs con-

tinuously and those laid annually by *Tænia solium* have been estimated at 80 millions.

But an increase in the number of eggs is not the only means of ensuring compensation for the great loss of larvæ and embryos. In a fairly large number of groups there is intercalated in

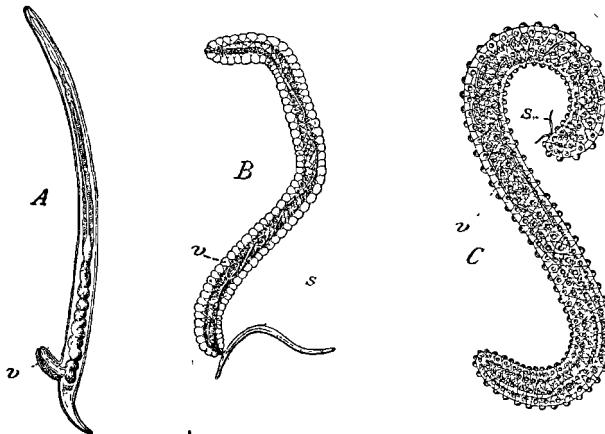


Figure 59. *Sphaerularia bombyi*.

A, young female showing the uterus, *v*, beginning to extrovert ($\times 50$).
B, a later stage; the body, *s*, of the female is very small in comparison with the extroverted uterus ($\times 9$). *C*, final stage; the body, *s*, of the female is not more than a minute appendage on the uterus, *v*, in which the embryos are developing ($\times 5$) (after Leuckart).

the course of the individual's development a phase of reproduction depending either on parthenogenesis or on budding. We shall review the principal examples of this.

ACCESSORY REPRODUCTIVE PHASES

PROTOZOA. In many parasitic types, and notably in the Sporozoa (Coccidia, Hæmosporidia, schizogregarines, etc.), there is, during the initial phase of infestation of the host, asexual reproduction leading to very large numbers of individuals. This is what is termed *schizogony*. It is a phase of intense multiplication followed by the sexual phase, termed *gamogony*, during which the transfer from one host to the other takes place. The link between the two phases is far from obvious and cannot be exactly determined except through experimental infestations.

We shall briefly recall a typical example, that of the Coccidia. Gamogony was first described in the genus *Coccidium*, and schizogony as occurring in a distinct genus, *Eimeria*. It is to Schaudinn and Siedlecki¹²⁰ that the honour accrues of having recognized that it was a question of one and the same parasite. Irrefutable experimental proof was given later by Simond¹²⁶ on Coccidia in the intestine of the rabbit; he induced newly born rabbits to swallow spores of *Coccidium* in milk and thus obtained *Eimeria*, which multiplied in the gut.

DICYEMIDA. These animals are known to swarm in the kidney of cephalopods, which they must infest soon after the latter leave the egg. In young cephalopods they exist as elongated vermiform individuals called *nematogens* and seem to multiply by entirely asexual means for several generations, as in schizogony mentioned above. The germ cells of the axial cell do not, in fact, show any trace of fertilization, nor of the emission of polar bodies and, indeed, seem to be agamonts, the process being one of *agamogony* (equivalent to schizogony). In the adult cephalopods, on the other hand, where the infection is long standing, one finds almost nothing but *rhombogens*, which give birth in their axial cell to special individuals called the *infusoriforms*, arising from germ cells detached from multicellular clusters termed *infusorigens*; and these elements, as Hartmann showed¹³⁸, arise from eggs which give off a polar body and are fertilized. Production of the infusoriforms then results from a sexual process, a gamogony; the cells of the infusorigens are gamonts. The significance of the infusoriforms cannot be considered as definitely established. Hartmann, depending principally on an observation of Keppen's, who sketched spermatozoa in them, considers them to be males. But if one accepts this interpretation the cycle would become even more paradoxical, for fertilization would take place only for the production of males. The certain existence of spermatogenesis in these infusoriforms has still to be established. The other and more probable interpretation is that the infusoriform is the vector of the infection from one cephalopod to another; this fits in with the fact that it is resistant to the external medium, which is not the case with the vermiform individuals. The observations of Lameere¹³⁹ lend weight to this second interpretation. To decide the question definitely fresh observations and experi-

ments are needed, in which attempts could be made both to follow the changes in the internal cells of the infusoriforms outside the cephalopods where they are formed, and to infect young cephalopods as they leave the egg. Although no one has succeeded in this up to the present, it cannot be considered as an impossible task.*

However this may be, the cycle in the Dicyemida allows of the intercalation of a long period of agamogenetic multiplication.

ORTHONECTIDÆ. The cycle of their development includes a phase of asexual reproduction in the host. Let us consider the case of *Rhopalura ophiocomæ*, which is the best known. The larvæ arising from fertilized eggs penetrate into the genital apertures of the ophiuroid *Amphiura squamata*. They give birth to intracellular bodies with one or two nuclei, which become plasmodia in which the nuclei multiply and where, at their expense, germ cells differentiate and give rise to sexual individuals, male or female. These plasmodia constitute a true agamogenesis, such as that of the Dicyemida. Each larva which succeeds in gaining a host gives birth in this host to very numerous individuals and thus compensates for the loss of the larvæ that are unsuccessful (cf. Fig. 48, p. 114).

CŒLENTERATA. In this group asexual multiplication is very general. Its existence in the parasitic forms is not then significant. However, it is interesting to note that among the rare parasites in the group there are several which show precocious asexual reproduction. Such is the case with *Polypodium hydriforme*, a parasite of the eggs of the sturgeon, in the midst of which it forms tubes that develop as numerous buds, each one becoming a hydroid polyp. Larval budding is also shown in the parasitic Narcomedusæ (*Cunina*, *Cunoctantha*, etc.): the *planula* larva lives as a parasite in the manubrium and gastrovascular system of other medusæ of the family Geryonidæ (*Carmarina*, etc.) and at a very precocious stage, scarcely more differentiated than the *planula*, gives rise to a series of buds.

CESTODA. The tapeworm is often considered as a chain of individuals resulting from strobilization. Each proglottis

* The recent researches of H. Nouvel¹⁴⁰ confirm the preceding conclusions that the infusoriform is the vector between one cephalopod and another, and is not a male. The so-called spermatozoa that have been reported (Keppen, Hartmann) must be the cilia of the cells that limit the anterior part of the internal cavity of the infusoriform.

encloses, indeed, the group of organs that could characterize an individual, and is comparable with the group of lower cestodes or *Cestodaria* (*Amphilina*, *Gyrocotyle*, *Caryophyllæus*, which are fish parasites, and *Archigetes*, a parasite of *Tubifex*). The new proglottids form in the initial region of the scolex, in the vicinity of the zone of attachment to the host, usually called the head of *Tænia*. But the study either of *Archigetes*, or of the cysticercoids of *Hymenolepis* and related types, shows, by the position of the hooks springing from the hexacanth embryo, that the point of attachment of tapeworms, and of cestodes in general, is their posterior extremity and that it is on the latter that the formation of new segments takes place in cestodes. The interpretation that the segmentation of the body of *Tænia* into proglottids represents an increase in the number of individuals, remains subject to these discussions which, at bottom, are more verbal than real. In fact, from the point of view with which we are concerned, strobilization presents itself as a highly efficient process favouring the production of a very large number of eggs. Above all, once the cestode has become established in its host this production is continuous over a very long period, during which the proglottids ripen and detach themselves one by one.* Thus the whole of egg-laying is not subject to the hazard of a single batch of embryos; this is an arrangement very well suited to the conservation of the species and one that we shall find again in the trematodes and in many nematodes.

But the cestodes have another method of reproduction intercalated in the development of the individual after it leaves the egg. This occurs when the cysticercus, instead of producing only one scolex, produces a series; from a single hexacanth larva there is thus derived a number of tapeworms, more or less perfect. This is accomplished in very various ways: in *Tænia nilotica* (of *Cursorius europæus*) multiple invaginations develop in the wall of the cysticercus, known as polycercus, which lives in lumbricids. The same occurs in the long-established classical instance of *T. canurus*, the cysticercus of which is usually found

* This process may be related to the schizogenesis of various oligochætes (*Lumbriculus*, *Chætophæster*, *Nais*, etc.) and particularly the schizogamy of the syllids, especially of *Autolytus* and the *Myrianidæ*, which physiologically corresponds closely enough to proglottis formation and also ensures prolonged dissemination of the genital products. Giard grouped the facts of this kind under the rather expressive name of reproductive autotomy.

in the brain of sheep. The process reaches its culminating point in *T. echinococcus* where, as we know, the cysticercus buds off secondary cysts and sometimes even tertiary cysts, each of which behaves like a cœnurus and gives rise to several scolices. Here it is possible for very large numbers to be produced and at the same time to multiply in many different organs. A cysticercus of *Glomeris* (= *Staphylocystis*), instead of budding off scolices by invaginations, produces externally and in grape-like clusters a series of secondary, vesicular cysts, each one of which develops a scolex.

There is, moreover, a certain equilibrium between these reproductive processes and the final development of the tapeworm. In *T. echinococcus*, where multiplication of the scolices is very vigorous, the tapeworm itself is very much reduced, possessing only three or four proglottids: although these are continuously renewed, egg production must be more restricted than in the large tapeworms. On the other hand, *Tænia echinococcus* is gregarious in a high degree, as one might expect from the development of its cysticercus.

TREMATODA. The endoparasitic trematodes which are heteroxenous are at the same time digenetic and the reproductive phenomena occurring during their development are classical. I shall not stress them here. These phenomena occur in the sporocyst stage, when numerous rediæ become differentiated; there may be several generations of them; the rediæ themselves finally give rise to numerous cercariae.

It is necessary to look for the exact significance of the cells from which the rediæ and cercariae develop. Is it a matter of asexual, internal budding, or of larval parthenogenesis (progenesis)? It is the latter interpretation which tends to be accepted today. In the sporocyst of *Distomum duplicatum*, a parasite of *Anodonta*, Reuss¹⁷¹ saw rediæ developing from a single cell; this gave off a structure which he took to be a polar body, and it would therefore be equivalent to an oocyte. The most exact confirmation of this opinion is due to Cary¹⁴⁶, who studied *Diplodiscus subclavatus*, parasitizing various amphibia. However, the drawings given by these workers are not altogether convincing and in any case we are far from being able to find in most forms the equivalent of what they described. R. Dollfus¹⁴⁸, who could not succeed in confirming the data of Reuss and

Cary, proposes that the internal cells of sporocysts and rediae should be considered as belonging to the linear succession of germ cells in trematodes, which continue uninterrupted as far as the cercaria. The formation of rediae and cercariae is compared by him to repeated polyembryony, that is to say, to a kind

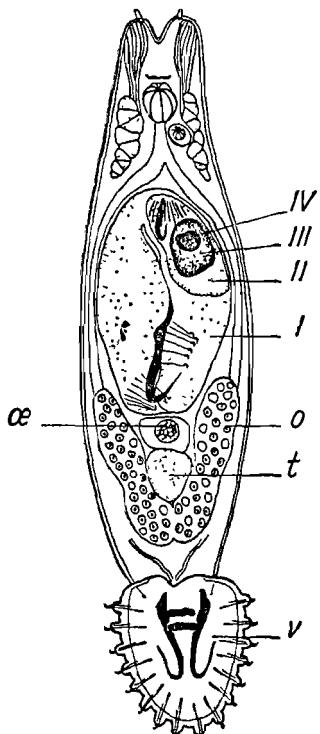


Figure 60. *Gyrodactylus elegans* (after Fuhrmann).

o, ovary (oocyte); α , ovum; *t*, testis; *v*, posterior discs with hooks.
I-IV, four successive generations enclosed one within the other.

of budding. But it is the nature of germ plasm to develop, as a prelude to a new generation, into oocytes and spermatocytes showing the phenomena of reduction divisions.* In poly-

* The continuity of the germ plasm and the precocity of its evolution are shown in a striking way in certain ectoparasitic trematodes, such as *Gyrodactylus*, which lives on the gills of freshwater fishes and also some saltwater ones, in which one may see four successive generations enclosed, one within the other (Fig. 60). Lameere (*Précis de Zoologie*, vol. 2, p. 248, 1925) interprets this as polyembryony. It seems preferable to me to see in it a demonstration of the continuity of the germ plasm through successive generations.

embryony, which we are coming to, the facts are much more naturally interpreted as corresponding to an asexual process; that is to say, they have nothing to do with the germ plasm. In reality the question demands further research.

RHIZOCEPHALA. We have seen already that in some of these so highly modified parasites there occurs typical asexual reproduction, which is especially remarkable in the Crustacea. In *Thompsonia*, instead of a single "nucleus" differentiating on the root system, as in *Sacculina*, a considerable number form, which fall off periodically and are regenerated. We shall not describe the process again here. It is equivalent to the production of a large number of scolices in the cysticercus of a cœnurus or an echinococcus. And here again we find the equilibrium that we have pointed out in the cestodes. The organization of an individual *Thompsonia* is simplified by comparison with that of *Sacculina*. There are no longer nerve ganglia, a pallial cavity, nor even testes, and there is only one batch of eggs, which must develop parthenogenetically.* In *Peltogaster socialis* there is, very probably, precocious fragmentation in the undifferentiated internal phase. It is then a question of budding or, if one likes, of polyembryony, and the process is not peculiar to this species, since it has been found in a distinct form, *Peltogasterella socialis*, in the Pacific. Asexual reproductive phenomena, then, exist in the Rhizocephala with a certain variation in type, and we probably do not yet know all the forms they take.

POLYEMBRYONY IN ENTOMOPHAGOUS HYMENOPTERA. This process, which is so remarkable when one considers the systematic position of the Hymenoptera, was discovered by Marchal³⁰² in the Chalcidoidea and the Proctotrypoidea. It was studied in detail by him in *Encyrtus* (= *Ageniaspis*) *fusci-collis*, a parasite of the caterpillars of *Hyponomeuta cognatellus*, *H. mahalellus* and *H. padellus*. The egg of this encyrtid is laid in that of the butterfly during July and August; development starts before the winter but comes to a complete stop, to be resumed about April. The egg of the parasite is surrounded, as soon as it begins to develop, with a wall of epithelium belonging to the host. From the beginning a large nucleus is differentiated, the *paranucleus*, very rich in chromatin, which will play a vegetative and trophic role, and small nuclei which are not

* The larvæ hatch directly in the cypris stage.

easily stained (Fig. 61A) and are the true embryonic nuclei. The paranucleus undergoes very extensive development, becomes lobed and divided into an infinite number of fragments, while the embryonic larvæ give rise at an early stage to small groups of cells resembling morulæ, each one of which becomes an embryo (Fig. 61B). About one hundred are formed in this way. These embryos develop, like those of the Orthonectidæ, in the middle of a cytoplasmic mass strewn with fragments of the paranucleus containing fat. The paranucleus thus plays the part both of the amnion and of a trophic layer. The whole of the primitive egg is gradually transformed into a long tube in which the

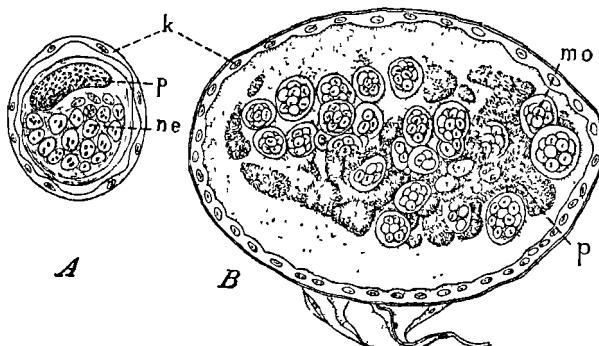


Figure 61. Polyembryony in *Encyrtus fuscicollis* (after Marchal).

p, paranucleus; *ne*, embryonic nuclei; *mo*, moruliform mass giving rise to various individuals; *k*, epithelial sheath of cyst produced by the host, *Hyponomeuta*.

embryos are arranged in line and which continues to be enveloped in the epithelial cyst of the host. In short, differentiation of the embryos is extremely precocious and is highly reminiscent of the Orthonectidæ and their plasmodia, or of rediæ and cercariae in the sporocysts of trematodes.

Polyembryony is an exceptional phenomenon in the parasitic Hymenoptera, but there must be, however, a fair number of examples. Marchal found it in another encyrtid, *Ageniaspis testaceiceps*, a parasite of the caterpillars of *Lithocolletis*, also in a proctotrypoid, *Polygnotus minutus*, which develops in the gastric sac of *Cecidomyia destructor* and of *C. avenae*. In this *Polygnotus* each egg gives rise to about fifty embryos.

Silvestri recognized polyembryony in *Litomastix truncatellus*,^{*} a parasite of the caterpillars of *Plusia gamma*, and here a single egg produces about 1,000 larvæ, without counting a certain number of abortive ones, called by Silvestri asexual larvæ; these lack the rudiments of gonads and degenerate without ever metamorphosing.[†] The details of the process in *Litomastix* appear to be rather different from those in *Encyrtus*.

Patterson³¹⁰ found and studied a certain number of cases of polyembryony in chalcidoids related to *Encyrtus*: *Litomastix* (= *Copidosoma*) *gelechiæ*, a parasite of *Gnorimoschema salinaria*; *Paracopidosomopsis floridanus*, a parasite of the caterpillar of the white cabbage butterfly, *Pieris brassicæ*; *Platygaster rubi*, parasitizing the larvæ of two Diptera living on conifers (*Sabina*). In *Paracopidosomopsis* he again found the asexual larvæ of Silvestri, the existence of which was doubted by Wheeler, and he proved, by rearing them in conditions which excluded the possibility of contamination, that they could not be the larvæ of another insect parasite, such as an ichneumonid, which Wheeler had suggested.[‡]

More recently other cases of polyembryony have been pointed out amongst the parasitic Hymenoptera, notably in the Braconidæ. H. L. Parker³⁰⁸ has described it in *Macrocentrus gifuensis*, a parasite of the caterpillar of the corn *Pyralis*; Paillot³⁰⁷ has found that it occurs in other species of *Macrocentrus*, and in *Amicroplus collaris* parasitizing the caterpillars of *Euxoa segetum*.

* Giard²⁹⁶ had stated that it must be present in this species, at the time of Marchal's discovery.

† This suggests that from the start these larvæ do not contain the cell derived from the line of germ cells, and it would follow, accordingly, that the initial groups of cells normally contain both somatic and germinal elements.

‡ These last researches of Patterson brought up the question of the bearing of polyembryony on sex determination. In the cases already considered, indeed—Bugnon had already noted it in *Encyrtus fuscicollis* before the work of Marchal—all the individuals issuing from one egg were of the same sex. Sex then appeared to be determined from the beginning of development and this was confirmed by polyembryony in the armadilloes amongst the mammals. Similarly, Silvestri observed that in *Litomastix truncatellus* the fertilized eggs gave rise to females and the unfertilized eggs exclusively to males. This was not so in the encyrtids studied by Patterson. In *Paracopidosomopsis*, for example, out of 177 batches of eggs studied, there were 154 in which the sexes were mixed (about 84 per cent.), and analysis of the data showed that this could not be explained by the simultaneous development of several eggs of different sexes in the same host.

DISCUSSION

It follows from the brief preceding review that the processes of reproduction in individuals after leaving the egg are both common and very varied in parasitic forms. The result of these processes is so obviously favourable to the perpetuation of the species, since it compensates for the destruction of a large number of larvae which will not reach the necessary host, that the mind is much attracted towards a teleological explanation. Quite evidently these are adaptations. But the problem is to know how they have been achieved and how these modifications of the development of the individual have come to ensure the propagation of the species.

Since we reject, *a priori*, the teleological interpretation, there remain two possibilities: either these are pre-adaptations retained and developed by natural selection, or else—and it is the solution to which I am drawn—these processes manifest themselves on account of the conditions in which the egg of the parasite happens to develop, but without an essential connection with parasitism or with the need of conserving the species.

We may, indeed, note that none of the processes that have just been reviewed is peculiar to parasitism, but that almost all of them recur under ecological conditions which are more or less comparable, particularly among sedentary animals. We have already had occasion to make comparisons between these and parasites. Sedentary animals exhibit a very pronounced tendency towards asexual reproduction. Amongst them it results, in short, from the effacement and dissociation of individuality. In free-living animals, which may be considered to have a normal type of behaviour, individuality comprises two essential characteristics: one of a physiological nature—the individual is a complex of organs, self-sufficing functionally but indivisible; the other of a morphological nature—the individual is an indivisible whole composed of tissues arising from the development of an egg. Development provides the conditions which are necessary and sufficient for the formation of the complex organic individual; between its parts rigid and necessary correlations become established.

The change in conditions resulting from a sedentary life consists, above all, in modifying these correlations, some of which

lose their obligatory character while other ones become possible. Hence the diminution of individuality which is common in fixed organisms. Now, the conditions of a sedentary life are realized in numerous parasites which, in effect, are fixed. In addition, their very special conditions of nutrition are another factor in changing the correlations and hence in effacing individuality, and one may explain, moreover, the existence, apart from parasites, of certain processes of embryonic reproduction, which must also be dependent on nutrition. Such is the case with polyembryony and with the processes which can be compared with it (formation of rediæ and cercariæ, production of sexual individuals in the Orthonectidae). We find them again in non-parasitic animals where the ovum develops in a nutritive medium analogous to that which the parasite finds in the host. It happens in the Cyclostomata (Polyzoa), where polyembryony was discovered by S. F. Harmer even earlier than Marchal's discovery of it in Hymenoptera. The eggs of *Crisia*, *Lichenopora*, *Tubulipora*, etc., develop in an ovicell which plays the part of a nutritive chamber, providing conditions analogous to those which the egg of *Encyrtus* meets with in a caterpillar. The polyembryony of some mammals is certainly connected with the very precocious grafting of the egg on to the uterine wall and with the conditions of nutrition which result from it.

But it is evident that the phenomena of embryonic reproduction shown by parasites are not explained by a superficial analogy of this kind, any more than, for that matter, those of free-living forms could be. It follows that they must not be envisaged as necessarily deriving from parasitism in its true sense and considered as an entity, nor as a response to the mystical necessity for conserving the species. For they are to be seen apart from parasitism, under more or less analogous conditions.

In each case they arise from some special present cause and, above all, a past one. Marchal, dealing with polyembryony in *Encyrtus* and *Polygnotus*, has sought to analyze it. He attempted, by blastotomy, to find in the conditions to which the eggs of the parasites were subjected, the circumstances which led to the experimental production of polyembryony. He believed that he had discovered a factor of this nature in the egg

of *Polygnotus*, which, in the stomach of cecidomyid larvæ, undergoes very abrupt osmotic changes and at the same time is submitted to considerable movement. On the other hand, he connected polyembryony in *Encyrtus* with the fact that its development is arrested during the winter, and that the subdivision of the embryos takes place in the spring, that is to say, at the moment when the caterpillar host again begins to feed, which also involves abrupt osmotic changes in the medium in which the parasite is plunged. But these suggestions are still very tentative.

The results obtained of late with tissue culture also appear to me to be very suggestive, by showing how the development of cell types may be modified when one succeeds in substituting truly novel conditions for those normally found in the organism. Several processes of asexual reproduction found in parasites must be the consequence of a similar process occurring naturally, and they must be envisaged apart from any teleological idea. Each organism has reacted in its own way, by virtue of its constitution, that is to say, of internal factors which, linked with the variety of external conditions resulting from parasitism, has produced the diversity of examples that we see.

CHAPTER IX

SPECIFICITY IN PARASITES AND MODES OF HOST INFESTATION

ONE of the characteristics of parasitism and, as we have already seen, of commensalism is the specificity of these associations; they always occur between definite species. It is a fact of general importance, but it allows of subdivisions which we are going to review. Specificity in parasites is, indeed, not an absolute characteristic, the expression of a pre-established harmony between host and parasite; it is relative and contingent.

STRICT SPECIFICITY

There are numerous cases and even extensive groups in which parasitic specificity is very strict. It is so in the Sporozoa and particularly in the gregarines. Each host has, as a rule, its characteristic gregarines. We, that is, Mesnil and myself⁵⁹², observed a very significant example of this in *Dodecaceria concharum*. In the plates of *Lithothamnion*, where this annelid lives, it occurs in three forms that we termed A, B and C; the feeding habits of these three are precisely similar. Now, B invariably contains a cœlomic gregarine, *Gonospora longissima*, that is never found in A and C.*

* I support A. Dehorne's decision⁵⁸⁵ to create for form B a new species which he has named *Dodecaceria caulleryi*, characterized by the peculiarity of its spoon-shaped chaetæ, by the localization of *Gonospora longissima* in it, by many details of histology, and by its development. Dehorne, who found it at Portel (near Boulogne-sur-Mer), studied it there and watched the remarkable process of schizogenesis, in which a segment of the middle region of the body (tetragemmal segment) spontaneously generates an individual or even a series of individuals. Mesnil and I have never seen this proceeding at La Hague. Dehorne, for his part, has never found the epitokal forms which I have had occasion to find in abundance among *Dodecaceria caulleryi* which is plentiful on limestone blocks collected by fishermen from the sea bottom in the Straits of Dover; I have also found these epitokal forms swimming freely when I have been fishing at night by the aid of a lamp.

Finally, these different processes (epitoky, schizogenesis) have also been found on the American Atlantic coast by E. A. Martin⁵⁹¹ in a closely related species described in 1879 by Verrill under the name of *Heterocirrus fimbriatus*, which

In a given family one will frequently find that different species contain gregarines which are similar in appearance but specifically distinct. Such are the species of *Anchorina* in the Capitellidæ. Léger and Duboscq¹⁰¹ made the same observation about the gregarines in myriapods: "Les *Pterocephalus*", they said, "se trouvent seulement chez les Scolopendres, les *Dactylophorus* chez les *Cryptops*, les *Rhopalona* chez les Géophiles. Mais ce qu'il semble encore, c'est que chaque espèce de Scolopendre a son espèce de Ptérocéphale et même une simple variété de Scolopendre aura sa grégarine spéciale". E. Hesse⁹³ came to similar conclusions for the Monocystidæ of lumbricids.

Coccidia and Hæmosporidia are as a rule strictly confined to one particular host. Generally speaking, the hæmatozoa one finds in nature can be identified by the species in which they occur. However, in the laboratory it is sometimes possible to inoculate related hosts successfully.

Different groups of parasitic Metazoa show us the same characters of specificity. Such are the Orthonectidæ, and to a large extent the Dicyemida.

The parasitic Crustacea are also highly specific in their hosts. Giard and Bonnier considered that there was absolute host specificity in the Epicaridæ. But in the absence of morphologically distinct characters which could be assessed, they gave different specific names to two epicarids found in distinct hosts. Systematic carcinologists, such as G. O. Sars and H. J. Hansen, criticized this conception as being too sweeping; the latter evidently went too far in the other direction since, in a more recent memoir²⁴⁵, he reunited in a single species, *Cumæchus insignis*, three epicarids that occur in three distinct genera of Crustacea; the females are similar, but Hansen himself pointed out the differences between the males collected from the different hosts. J. Bonnier, discussing the question, has brought forward important arguments in favour of specificity. He cites, for example, the case of the parasitism of *Portunus holsatus* by the entoniscid *Portunion fraissei*, which was a new species always contains a gregarine identical with *Gonospora longissima*. These *Dodecaceria* were found in Bryozoa collected in Vineyard Sound and Martin recognized in them a type of polymorphism analogous to what we had seen at La Hague: a sedentary form (corresponding to our form A *but consisting of both males and females*) without gregarines; a form corresponding to our form B (with epitokal individuals and gregarines) and a form with asexual reproduction. The chætae have the same characteristics as those in the European forms.

created by Giard and himself although there were no precise characters by which they could distinguish it from other species of *Portunion*, but they always found it in this particular species, *Portunus holsatus*. Now, later, they found that the male of this *Portunion* was quite distinct, so much so that they made this species the type of a special genus, *Priapion* (on account of the great length of the penis). The same authors, on receiving from Naples a lot of *Callianassa* parasitized by Epicaridæ and considered as belonging to a single species, found that the parasites were of two different sizes: they then carefully examined the hosts and discovered that these belonged to two species that were related but distinct, *C. subterranea* and *C. truncata*, each carrying one of the two forms of parasite. Having carried out research with large numbers of epicarids on various hosts they saw that in two related species living side by side, and under the same conditions, only one was parasitized. Thus, at Wimereux, *Porcellana platycheles* often contains a *Pleurocrypta*, while *P. longicornis* never does so. These observations, made on large numbers and under natural conditions, have a special value, and are very superior to conclusions drawn from scanty material in museums.

In order to make sure of the identity of two similar epicarids found on two hosts A and B, it is desirable to be able to rear the larvæ and infect both hosts equally with parasites from one batch. In practice this is impossible. In applying the criterion of Giard and Bonnier one may retain doubts on the reality of the distinction between the two species but, as Bonnier remarks, a mistake of this kind is preferable to the opposite one, for by inappropriately uniting two species one suppresses all idea of careful comparison between them.

The parasitic copepods as a rule show strict specificity. This is true for the species parasitizing fishes, ascidians and annelids (Monstrillidæ, *Xenocæloma*, *Staurosoma parasiticum* on *Anemonia sulcatum*, etc.). With the Rhizocephala Giard applied the same rule of specificity, identifying species of *Sacculina* by their hosts; this practice has not been generally followed, but it could not really be condemned without practical attempts to produce experimental infestation of several hosts with nauplii from the same *Sacculina*, experiments which, in practice, are difficult to carry out.

In the Protista (protozoa, bacteria) parasitic specificity can be very strict without being reflected in obvious morphological characters in the parasite; thus Laveran and Mesnil⁹⁶ have been led to distinguish between pathogenic trypanosomes, which are morphologically similar, by their immunity reactions. That shows that the morphological criterion may be inadequate for the separation of parasitic forms and supports the general idea of the specificity of parasites.

MODIFIED SPECIFICITY

There is thus in many cases strict specificity in parasites. Contrarily, it is averred that other parasites are to be met with in a series of distinct hosts; specificity may even present a different aspect for the same parasite, depending on whether it is a question of the intermediate host or the final one in heteroxenous parasites.

Thus, in the trematodes the molluscan host of the sporocyst is generally rather strictly specific. For *Distomum hepaticum* in Europe, it is almost exclusively *Limnaea truncatula* (= *L. minuta*); direct experiments have shown that in *L. stagnalis*, for example, the miracidium only passes through the first stages of development (cf. Kendall, p. 136, footnote), but in regions other than Europe different species replace *L. truncatula* as the host of the miracidium: *L. viator* in South America, *L. humilis* in North America, etc. Facts of this kind are also known for *Schistosoma*; the miracidium of *S. mansoni* has *Planorbis guadalupensis* for its host in the Antilles, *P. olivaceus* and *P. centrometralis* in Brazil, etc. But the definitive host in trematodes is much less specific. *Distomum hepaticum* is found in a whole series of mammals. Similarly, it has been possible to infest various species with cercariae of *Schistosoma*.

In the cestodes specificity seems also to be stricter for the cysticercus or the cysticercoid than for the adult; there are, however, many species in which the cysticerci can develop in numerous hosts. This is notably so in the case of *Tænia echinococcus*. On the contrary, host specificity can be strict for the adult. This was shown in experiments carried out by Joyeux¹⁵⁸ on *Hymenolepis* in rodents and man. *H. nana* in man cannot be distinguished by any precise morphological character from

H. fraterna (= *murina*) in the rat and other Muridæ. Now, while it is easy enough to bring about infestation in rats with *Hymenolepis* eggs from any of their congeners, *Hymenolepis* eggs from man constantly fail to develop in these animals. Apparently we have in this instance two species which are morphologically almost identical and localized in different hosts.

Specificity often appears to be less strict in the laboratory than in nature. Thus, although Hæmosporidia are usually specific under natural conditions, some of them can be inoculated into different species. Natural specificity may be related to the fact that the conditions suitable for infestation do not occur in connection with other hosts. At other times infestation of other hosts may take place but will not be maintained in them. Thus, under natural conditions, fleas and lice are rather strictly confined to a definite host, or to a small number of hosts related to one another, although this is not always so. The human flea, *Pulex irritans*, is found on various mammals (dog, cat, fox, jackal, rat, horse, etc.). One can, moreover, feed one particular flea on different mammals under laboratory conditions. However, as Joyeux observed¹⁵⁸, if one begins rearing fleas on a host which is not the normal one it soon becomes obvious that reproduction is going badly and that the whole brood is soon in jeopardy. In other words, a case of this kind shows that there is a *normal host* which provides the most favourable conditions, and that is why, under natural conditions, the parasite is, as a rule, found only on this host. Léger and Duboscq¹⁰³ came to this conclusion for *Aggregata* on crabs. *Portunus* is more successfully infested with spores from cephalopods than are other genera from which, nevertheless, the parasite can be obtained.

In experiments with *Bothriocephalus*, Rosen⁸⁴ obtained developing oncospheres in several species of *Cyclops* and *Diaptomus*. But it is in *Cyclops*, and particularly *Cyclops strenuus*, that development is best completed.

The normal host in nature is not, however, necessarily that in which the parasite develops most actively. We may suppose, as Woodcock has done, that the animals in which pathogenic species cause acute infections are exceptional hosts and not the normal ones. The latter must tolerate the parasite as it has become accustomed to it, and must have acquired immunity relative to it, but not so the former. It is thus that we can interpret

the very virulent trypanosomiases in domestic animals and in man. *Trypanosoma brucei*, for example, the cause of nagana which does not occur in man but is a disease fatal to most domestic animals, dog, ass, horse and cattle, cannot be considered as a normal parasite of these species. Its natural hosts are big game, such as antelopes, where it exists without causing serious damage. It is when colonial development has brought about the introduction by man of susceptible animals that the parasite has attacked those species which were not adapted to it. Surra in cattle and human trypanomiasis must doubtless be considered as analogous examples. Thus, with these parasites, specificity is relative since they can exist in very different species. Seen from the human point of view of prophylaxis, the natural hosts of these pathogenic species constitute what is called a *reservoir of infection*. In the case of nagana this reservoir is constituted by big game, particularly antelopes; for mal de caderas of horses in South America, caused by *Trypanosoma equinum*, the reservoir of infection appears to be a large rodent, *Hydrochaerus capybara*, which, moreover, dies from it.

The specificity of the vectors of these different blood parasites is likewise very varied. Thus the malarial parasite of man is transmitted by *Anopheles*, but not by *Culex*, its development only being able to proceed in the former, and conversely *Proteosoma* (near *Plasmodium*) in birds develops in *Culex*. Among the different species of *Anopheles* there are some which become infested more easily than others.

It is clear from the facts brought out in the preceding pages that parasitic specificity is a very complex matter with aspects varying very greatly from one case to another, from strict limitation to very great lability.

TROPHIC PROPHYLAXIS

If one considers the struggle against these pathogenic parasites from the practical point of view, the question has a multitude of aspects, clearly brought out by Roubaud³⁸⁴ and not lacking in paradox. Some of these conclusions are closely connected with the analysis of parasitic specificity and must be summarized here. Besides, since these opinions are both ingenious and interesting and were inspired by a factual study

undertaken under natural conditions, I shall dwell on them at some length.

The destruction either of the reservoir of infection or of the vector when, for example, it is a biting insect such as a *Glossina* or *Anopheles*, may be an impossibility. Moreover, the examination of facts in nature leads to the conclusion that in at least some infections such destruction is by no means indispensable. Thus, endemic malaria has progressively diminished in France and has almost disappeared without *Anopheles* having been exterminated. It was feared that in the 1914-1918 war, when numerous sufferers from malaria were brought into France, the disease might develop there. Now, in searching for *Anopheles*, it was found that it was extremely widespread in France and that it had never been uncommon: nevertheless, endemic malaria had disappeared. This is because it never depended solely on the presence of *Anopheles*, but on other factors such as living conditions, soil cultivation, etc.

To explain facts of this kind and to solve the practical problems of prophylaxis, Roubaud arrived at a general conception which he termed the *trophic method*, or *protective nutrition*, or, again, *trophic prophylaxis*. It consists of satisfying the needs of the species conveying the dreaded parasite, thus turning it away from man or from some domestic animal. He conceives this method as more easily applicable in countries new to human activity where the faunistic equilibrium has not yet become solidly stabilized in connection with this activity, than in old countries where all the equilibria have long been established. In new regions, the changes in the environment achieved or provoked by man, and the species that he consciously or unconsciously introduces there, create new relationships.

Thus, in Senegal a termite which ravages the plantations of groundnuts is by no means a specific parasite of this plant; outside the zone of cultivation it attacks various other plants; its localization on the nuts of *Arachis* is due, according to Roubaud, to its still finding supplies of water there when the surrounding soil is completely desiccated. By maintaining a certain soil humidity at the time when the termite attacks the nuts which are still green, that is to say, in satisfying its needs, it can be diverted from the groundnuts; this will be simpler than to attempt to exterminate the termite itself. Similarly, in certain

zones of tropical countries, drought is said to be the reason why so many flies are attracted to the eyes of man and animals, whose lacrymal fluid they can drink; accordingly, this would be the indirect cause of the common and serious eye diseases in these regions. Hence the suggestion of turning the flies from man by offering them water.

In the same way man could protect himself against biting insects by providing them with prey that they prefer. In woodlands, large cattle or horses, for instance, are attacked by tabanids or *Glossina* to a much greater extent than is man. Roubaud considers that to many parasites, especially to those living on the skin, the pig is an animal which offers the same possibilities of nutrition as man, the epidermis of both being naked. This simple factor allows of the successful penetration of many parasites which are stopped by the hairy covering of other species. Moreover, this similarity has brought parasites to prey on man which originally must have been specific to the pig or to other mammals with bare skin.

Auchmeromyia, the Congo floor maggot, now adapted to the negro race, must have been in the first place a parasite of mammals with bare skin, such as *Phacočærus* or *Orycteropus*, on which *Chæromyia* lives under the same conditions, and Roubaud has seen this last spread into human dwellings. Similarly, a tick, *Ornithodoros moubata*, vector of tick fever, seems, according to observations made in the Belgian Congo, to be, in Africa, a natural parasite of mammals with bare skin, such as *Phacočærus* in whose den it is found, and it resorts to man in proportion to the degree of rarity of its natural host. Ed. and Et. Sergent have made interesting observations in Algeria on the *Œstrus* of sheep. It attacks the eyes and nostrils of the shepherds in Kabylie, producing a myasis known under the name of *Thimni* (*Tanné* amongst the Tuaregs), and since then it has been found in very different regions. Now, the incidence of infection in man varies in inverse proportion to the density of the local population of sheep. Man is not attacked when the numbers of sheep are sufficient to ensure the normal egg-laying of the fly.

In the same way, the local incidence of sleeping sickness in Africa bears no relation to that of *Glossina*; the converse is often true, which Roubaud explains by the fact that the normal host of *Glossina* is big game and not man. It breeds in the forests,

where big game is abundant, and normally does not attack man there. One of the best means of attracting it openly to one place is to expose an ass or a horse as a trap. Where these natural hosts are missing the rare *Glossina* falls back on man; it is in such situations that its parasites are best propagated in man in spite of the rarity of the fly.

The gradual decrease and disappearance of endemic malaria in France and other European countries, although *Anopheles* has not become at all rare, has been studied by Roubaud, especially in the marshes of the Vendée and in the environs of Paris, and as a result he explains as follows the facts which had previously been established by Ed. and Et. Sergent. In the Vendée, a malarial district, the anophelines enter houses from which they are absent in the Ile-de-France. What is typical is their presence in stables. They are there in both regions. But they swarm in the Vendean stables on account of the extent of the marshes, which leads to the development of great numbers of larvæ. The result is that the mosquitoes do not find a population of cattle sufficient for them to feed on, and invade the houses, while in the environs of Paris there are sufficient cattle and they do not attack man. The cow is, then, a *protective shield* for human beings and the improvement in health achieved in the 19th century is easily understood. The cultivation, drainage and reclamation of the marshes has diminished the population of *Anopheles* to whom the increased numbers of cattle have offered sufficient prey. Man is thus naturally free from attack. The problem of prophylaxis thus comes down, following a happy expression of Roubaud's, to an *alimentary equilibrium* in the surrounding fauna. It seems to result, moreover, from observations made in the suburbs of Paris that, once adapted to feeding on cattle, *Anopheles* ceases to attack man.

It so happened that the material studied by Roubaud which led him to the conclusions just summarized, independently suggested the same sort of problems to C. Wesenborg-Lund in Denmark, and led him also to similar conclusions—to see in cattle a protective shield against *Anopheles*—which, with the progress of human habitation, has resulted in Denmark, as well as in France, in determining the regression and then the disappearance of malaria. One reads, then, with the most lively interest the fourth chapter (pp. 157-195) of Wesenborg-Lund's

great work³²⁷ on the biology of the Danish Culicidæ, where it is clear that his conclusions are almost identical with those of Roubaud.

These very ingenious ideas, which give us all at least a precise programme of prophylactic experiments, are of particular interest for the questions envisaged here in having been suggested by direct observation of nature and, above all, in showing parasitic specificity as a relative property. They fall in well with the conception of the normal host previously set out. There are not rigid pre-established relationships between species, but more or less stable equilibria which are relatively easily disturbed. In virtue of this Lamarckian conception, the environment recovers in this context the place which suits it, and even the facts of absolute specificity fall naturally into order as limiting cases of perfectly stabilized equilibria.

HOST PARASITE EQUILIBRIUM

By their enormous extent and the way in which they deal directly with the natural environment, the researches into applied entomology undertaken by the United States Bureau of Entomology have provided very important data on parasitic specificity, as far as entomophagous insects are concerned. For the most formidable insects there have been instituted, as we have seen, investigations on an unprecedented scale, and as the parasites of these insects have appeared to be one of the most efficacious weapons against them, the problem of parasitic specificity comes naturally under consideration.

The Bureau of Entomology draws up a special list of the parasites of each noxious insect, their habits and their parasites or hyperparasites—the first being friends, the second enemies, of man. In organizing these dossiers one sees the complexity of the relationships which govern the natural expansion of species.

Let us take, for example, the studies made on a cotton weevil, *Anthonomus grandis*, which became widespread and was forcefully dealt with. As early as 1913, it was recognized that there were 54 species that parasitized this insect. A table relating to 25 of these parasites (which is reproduced in the book by P. Marchal already cited) shows that their specificity is very unequal, at least in the present state of our knowledge. Five

from among them are known to parasitize respectively from 18 to 12 different species, while ten others are so far known positively only from *Anthonomus grandis*, and five also from a second species.

In researches on two lucerne weevils, *Hypera punctata* and *Phytonomus posticus*, W. R. Thompson³²⁴ established data which plead in favour of a rather restricted parasitic specificity. In fact, the two species live in the same fields and in very similar conditions. Now, of the nine parasites of *Phytonomus*, only two occur in *Hypera*.

The most varied and the most important information has been obtained in connection with *Lymantria dispar* (Gipsy Moth) and *Euproctis chrysorrhæa* (Brown Tail Moth), which have already been referred to. The European parasites of these species, introduced purposely into the United States, have found themselves under new conditions there. Let us consider the tachinids; their specificity is very variable. Certain species have so far only been found in *Lymantria dispar*, while *Carcelia excisa* is also known on 24 different hosts, *Compsilura concinnata* on 51, and *Tachina larvarum* on 39.

The case of *Parexorista cheloniae* is of a particular interest. This fly is found both in America and in Europe, where it develops in rather varied insects and in particular in *Lymantria chrysorrhæa*. Now, the American race of the fly never attacks the caterpillar of this moth, and it has been found that the fly is not immune to the urticating properties of the caterpillar. It happens that the introduction of the European race of *Parexorista* has not been efficacious because it hybridizes with the American race and the hybrids behave towards the caterpillar as the American race does and not as the European one.

RELATIVE SPECIFICITY

All in all, the preceding facts show that one cannot consider the reciprocal specificity of parasites and their hosts as an absolute and uniform property. It is evidently one of the fundamental characteristics of parasitism; but it is essentially relative, and is displayed in highly variable degrees. There are certainly many cases where it is very strict, a given parasite never being met with except in a single host species. But it is no less certain

that many parasites, under natural conditions, infest several different species of hosts and sometimes even rather a large number. Specificity must, then, be considered separately for each parasitic form.

It is necessary, besides, to distinguish between specificity in fact and in principle. The first is specificity shown by the direct observation of natural phenomena; the second that which results from experiment. The restriction of a parasite to a single host in nature may simply be due to the absence of circumstances in which it could penetrate into other hosts but not to its being unable to develop in them. We have already quoted the case of parasites which are localized on mammals with bare skin, which have easily been induced to infest mammals with hairy skin simply by partly shaving the latter. On the other hand, there really exist some parasites, above all endo-parasites, which can only adjust themselves to the internal environment of a single species to which they are adapted. This is notably the case with the hæmatozoon of human malaria that cannot be cultured in any other animal species.*

Even in cases where experimental infestation is obtained in several species, it is clear, as we have already seen in several instances, that it is more successful in certain species than in others. One is thus led to distinguish between normal hosts and those that are exceptional. On this distinction depends the usually limited localization of parasites in nature, either on one definite host or on a small number of hosts. Moreover, whenever observations of facts in natural conditions are made on a sufficient scale, one meets with parasites that have strayed on to exceptional hosts. That is particularly true of parasites that migrate, such as the trematodes or cestodes. Many cysticerci and metacercariae encyst in hosts which will never be the prey of an animal in which the adult stage of the parasite could be reached.

Specificity also results, as Roubaud shows very clearly, from a progressive adaptation of parasites and their hosts, that is, from an equilibrium of increasing stability in long-established faunas. New equilibria and new parasitic associations are

* Except, perhaps, in the anthropoid apes. Mesnil and Roubaud¹¹¹ have, indeed, succeeded in infesting a chimpanzee. Their memoir contains a statement on the specificity of various species of *Plasmodium*.

realized when a fauna is disturbed by the introduction of new forms.

All these problems have their equivalents in bacteriology, where the experimental study of pathogenic organisms has allowed cases to be handled on a vast scale. Experimental research into syphilis, for instance, such as has been made in the last forty years, has shown that this disease, hitherto considered as strictly limited to man, can be communicated to numerous species but that it is far from developing in the same way in them. It is clear that most of the general facts of bacteriology apply to parasitism and it is only for reasons of expediency that they are left out here.

Taken as a whole, the preceding observations, then, lead us in the last analysis to consider specificity of parasites as very real but of a relative order and as the result of an evolution; they depend on extrinsic conditions encountered in the past and in the present by the species under consideration, and in no way on a pre-established harmony; there can be no question of regarding parasites as forms specially conceived by Providence as complementary to the life of definite hosts.

SPECIFICITY AND ACCESS TO THE HOST

One of the important elements in the problem of parasitic specificity lies in the factors governing the access of parasites to their hosts and their penetration into them. The study of these factors is then complementary to the preceding question. It is clear that all the methods by which parasites penetrate cannot be reviewed. Each species has its special one. But a few examples will give an idea of the variety and interest of these processes, and of the part they can play as far as parasitic specificity is concerned. It is with internal parasites that the question principally arises, although with external ones the problem of access may be equally interesting. Two chief methods of infestation may be distinguished: one that is passive and another in which the parasite plays an active part.

Passive infestation takes place either by the ingestion of spores or of eggs, or by that of an intermediate host containing the parasite, or by inoculation through the bite of some vector organism. If there is ingestion of eggs, spores or cysts the

organism is usually liberated by the action of the digestive juices of the host on the protective envelopes, and this action implies a certain specificity which has been shown plainly, for instance, with the Sporozoa. The spores of gregarines, or of Myxosporidia, only open when acted on by the gastric fluids of certain hosts, or at least open better than. The organism liberated must be able to resist the action of these fluids and there, again, is a specificity which is generally limited in extent. Between the liberation of the organism or of the ingested larva and its arrival in its final location, where development will be completed, there often occur complicated journeys.

Direct inoculation into the internal medium of the host is the most perfect method of transmission. The malarial parasite, *Plasmodium malariae*, may be taken as an example of this. It passes from man to the culicid, *Anopheles*, by suction, undergoes an elaborate development in the mosquito, ending with the localization of the sporozoites in the salivary glands and the proboscis; these organisms are finally *inoculated* directly into man. Most of the Hæmosporidia are transmitted in an analogous way by various intermediate hosts: mosquitoes, leeches, etc.

But this complete adaptation is not always achieved. Thus, with *Filaria bancrofti*, the larvæ which have developed in the mosquitoes do not penetrate into the proboscis, but accumulate in the labium of the insect. At the moment when the latter bites they are simply deposited on the skin which they break through by their own efforts. Here, then, there is passive transport to the host and active penetration into it. It is the same in a certain number of cases where blood-sucking insects are the vectors of the parasite. The latter is deposited by them on the skin with the saliva or even with excreta, and finally penetrates by means of an abrasion, excoriation or bite of the insect; this must be the method of penetration of a certain number of microbes such as plague bacilli, various spirochætes, particularly that of recurrent fever which comes into contact with the skin principally by the crushing of a louse. It is clear, then, that a number of mechanisms are concerned in the transmission of parasites by intermediate hosts.

The ways and means of penetration of parasites not involving an intermediate host are, however, much less simple than one might suppose, as we shall be able to show by some examples.

That of *Sacculina* is typical in this connection and the reality is quite different from what one could have supposed *a priori*. For many internal parasites of invertebrates the method of penetration is unknown. We do not know how animals such as *Fecampia* or the eunicid parasites of annelids enter their hosts. So far, the penetration of Dicyemida into the kidney of cephalopods has not been seen.

One of the groups in which the facts are most varied and unexpected is that of the nematodes, which show extreme diversity in their ways of life, both as parasites and saprophytes, and also in their localization in their hosts. We have already seen what is known of species of *Filaria* in the blood. There is still a certain number of these parasites whose method of penetration is unknown. We know nothing yet about the penetration of parasites such as *Eustrongylus visceralis* into the kidney of the dog and different mammals. But even with the intestinal nematodes, which appear to penetrate by simple ingestion and to develop directly in the intestine, the reality is sometimes much more complex.

Such is the case with *Ancylostomum duodenale*, the cause of miners' anaemia. For a long time it was believed to be ingested either in water or in food soiled by the hands. The researches of Looss¹⁹⁴, confirmed by other workers, showed that this could not be the most usual method. The eggs evacuated with the faeces develop externally, provided that the temperature is high enough (hence the localization of the parasite in warm countries and in mines); the larvae usually penetrate into man *through the skin*. Looss happened to observe this accidentally on himself, under conditions in which contamination *per os* was impossible, and he carefully proved it. Larvae of *Ancylostomum* deposited on damp skin penetrate into it in a few minutes; he established this particularly on a leg infected an hour before amputation. In experiments with dogs and monkeys, using *A. duodenale* and *A. caninum*, the larvae were placed on areas of shaved skin and he was able to follow all the phases of their penetration and their final journey. As they penetrate they cause irritation and redness, and, in heavy doses, temporary oedema. They pass into the blood vessels and lymphatics, where some are destroyed by phagocytosis in the lymphatic ganglia. They reach the heart by way of the veins, and from there pass to the lungs, in which it is

possible to bring about a heavy infection within a few days. From the lungs they pass to the trachea and thence to the oesophagus, finally reaching the intestine. Outside, these larvae are very susceptible to desiccation; a few moments' drought suffices to kill them, which happens most often on food. On moist skin, and principally thanks to sweat, they find favourable conditions. In the galleries of mines they easily pass up the damp walls and from there move on to the hands of miners. This is a very significant example of the complexity which is sometimes found in the mechanism of penetration by parasites.

Strongyloides stercoralis follows a similar course, and probably other nematodes too. Lühe reports, in connection with the experiments carried out by Looss, that at the autopsy of a panther he found a lung full of nematodes, probably resulting from a similar migration.

Ascaris lumbricoides, the common intestinal parasite, has a no less complicated life history. Stewart²⁰⁴, then Ransom and Forster²⁰⁰ (confirmed further by Yoshida²⁰⁹, working on rats, mice, young pigs, rabbits and guinea-pigs) showed that the larvae emerging from the eggs ingested *per os* do not develop directly in the intestine but pass into the intestinal circulation and after that complete a circuitous course analogous to that of *Ancylostomum*, passing through the lung on the way. By making young pigs ingest large doses of the eggs of *A. lumbricoides*, over a period of two weeks, Ransom and Forster produced fatal pneumonia in these animals within eight days; at the autopsy the lung was found to be full of young *Ascaris*, while the controls were in good health. At the end of ten days the worms were found in the mouth and the oesophagus. In the rat and mouse the initial stages are the same but infestation is not completed and goes no further than the mouth. Pig and man are the normal hosts; in the sheep, which must be an accidental host, intestinal infestations have been obtained. Experiments of this kind show the elasticity of the idea of parasitic specificity. They indicate, moreover, how many interesting discoveries remain to be made in the domain of parasitism, concerning the conditions of penetration into the host.

The life history of *Ancylostomum* will naturally be compared with that of *Schistosoma* (= *Bilharzia*) outlined earlier, in which the cercaria also passes through the skin.

MYIASES

The larvæ of flies, which show considerable ecological variation, ranging from a saprophytic to a strictly parasitic life, also supply some extremely interesting instances of access to the host.

The tachinids, whose entomophagous larvæ play so important a part, as has already been said, reach the host in very different ways, which Townsend³²⁶ has studied and which he classifies in the following manner:

1. The laying of eggs on leaves where they are ingested by the host.—The larva hatches in the gut of the latter and passes into the general body cavity where it develops in the adipose tissue. The eggs of these species are small and dark, and only hatch under the influence of the intestinal fluid of the host (e.g., *Crossocosmia sericariæ* parasitizing the silkworm; *Blepharipoda scutellata* parasitizing *Lymantria dispar*, etc.).

2. The laying of the eggs on the host.—The egg laid, for instance, on a young caterpillar hatches fairly quickly and the larva penetrates into it. In its last larval instar it pierces the body wall from within, so as to have a respiratory opening. This method was the earliest known (e.g., *Thrixion halidayanum*, studied by° Pantel; *Parexorista cheloniæ*, parasite of *Euproctis chrysorrhœa*).

3. The laying of larvæ which are deposited on the skin of the host (Dexiidæ).

4. The laying of the larvæ beneath the skin of the host.—The female uses the ovipositor to pierce the caterpillar, and introduces the larva under the skin (e.g., *Dexodes nigripes*, *Compsilura coccinata*, parasites of *Euproctis chrysorrhœa* and *Lymantria dispar*).

5. The laying of larvæ on leaves or stems.—Case of *Eupeletaria magnicornis*, which deposits its larvæ on branches where it has recognized (probably by smell) the presence of caterpillars, the larvæ being placed in the track they will take on returning to the nest. The larvæ hook on to the caterpillars as they pass by and penetrate into them.*

In matters of detail we see curious adaptive characteristics

* The Nycteribidæ which live on bats also lay larvæ, which are ready to pupate, on branches in the neighbourhood of *Pteropus* but not on the animal itself, as Rodhain and Bequaert³¹³ described in the case of *Cyclopodia greeffi*.

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in the eggs and larvæ of tachinids relating to these various
conditions.

I shall show this by referring to *Pollenia rudis*, which has been very well investigated by Keilin²⁹⁹. Here the egg is laid on the soil. The larva, after hatching, penetrates into a lumbricid, *Allolobophora chlorotica*, through the openings of the seminal vesicles in which it passes the winter and spring. In the month of May it burrows through the host's tissues to its anterior end which it perforates, making an opening through which its posterior extremity together with the respiratory openings juts out.

Flies with larvæ parasitic on vertebrates (causing myiases) provide us with numerous data of the most interesting nature. Some of them are rather saprophytes than parasites, living in ulcers, doubtless at the expense of the bacteria which multiply there. They show the beginnings of adaptation to parasitism. Certain of these larvæ are by no means specific, others tend to be specialized and produce very definite myiases; such is *Pycnosoma bezzianum*, which lays its eggs on the hairs of Bovidæ and Equidæ; the larvæ finally burrow into the skin and cause ulcers; never does the fly lay in already existing ulcers. Such also are *Lucilia argyrocephala* and *L. sericata*.

Certain species have blood-sucking larvæ, living near the host and coming into contact with it intermittently in order to suck its blood. This is the case with *Auchmeromyia*, thoroughly investigated by Roubaud³¹⁶. The larva, the Congo floor maggot, is biologically tied to the negro race as we have already seen; the species only maintains itself in settled tribes that sleep on the bare floor of the cabins. The larvae, inert during the day, leave the ground at night to suck the blood of the sleepers. They are not found amongst nomadic tribes. *Chæromyia*, found in the burrows of *Phacochærus* and *Orycteropus*, is similarly adapted to those animals which have bare skin like man. And there exists a series of flies, *Phormia sordida*, *P. (Protocalliphora) azurea*, and *Passeromyia heterochæta*, which live in birds' nests at the expense of their young.

Other flies producing myiases lay eggs on the ground and the larvæ actively seek the host into which they penetrate. Such is *Cordylobia anthropophaga*, whose larva, Caylor's worm,* pro-

* Lund's larva, which lives in analogous conditions, belongs to another species, *Cordylobia* (= *Siassia*) *rodhaini*.

duces in the depth of the skin of the host (rat, dog, and, in addition, man) a furunculous tumour with a permanent opening through which it breathes.

Some of them reach the host in a very curious and indirect way, being carried by another insect. This is the case with the South American fly *Dermatobia hominis*, whose larva, the Macaque worm, produces a cutaneous myiasis. It lays its eggs on insects (*Stomoxys*, and particularly a culicid, *Janthinosoma lutzi*) when they are biting horses. These insects, principally *Janthinosoma*, are the agents by which the larva reaches man (see Neiva ³⁰⁶).

Others lay directly on the host, particularly *Œstrus ovis* of sheep which lays during flight on the nostrils or eyes; the larvæ develop in the nasal fossæ, producing false staggers. The botfly, *Gastrophilus equi*, of horses, lays its eggs on the hair in places where the horse can lick them. The roughness of the lips during licking causes the egg to open and set free the larva which, on reaching the host's mouth, burrows into the epidermis, as Roubaud ³¹⁸ has shown, and makes its way by the œsophagus to the stomach, where it completes its growth, fixed to the wall. It is cast out in the dung at the moment of pupation. The warble fly of cattle, *Hypoderma bovis*, which causes sub-cutaneous tumours on the back in the vicinity of the vertebral column, does not develop there but penetrates under the same conditions as the botfly of the horse, burrows along the wall of the œsophagus, then follows the diaphragm, crosses the vertebral column and finally reaches the skin of the back, where it causes a sub-cutaneous tumour. The fully developed larva passes outside when the tumour festers. Certain birds (magpies, starlings, wagtails) frequently extract and feed on these larvæ by breaking open the tumour.

From these various data relating to the Diptera we come to the case of the jigger, *Sarcopsylla penetrans*, a flea whose larva burrows actively under the skin, mainly of the foot, and grows there, forming a small swelling which remains open exteriorly.

These different examples show how the final position of the parasite is insufficient in itself to teach us how infestation came about.

HEREDITARY TRANSMISSION

Another class of facts relating to methods of penetration in parasites is provided by cases in which infestation is hereditary and transmitted by the egg. We now know a certain number of examples of Protozoa, bacteria and Protophyta. The most classical case is that of the Microsporidia, and in particular that of pebrine, *Nosema bombycis*, in the silkworm. It was through noticing that the egg was contaminated by *corpuscles* that Pasteur conceived the method of dealing with the eggs, which allowed of the establishment of healthy broods. Direct contamination occurs by the mouth, the caterpillar eating leaves soiled by excrement carrying the spores of the parasite. These develop in the gut and the Microsporidia penetrate into the intestinal epithelium, then into the various tissues that they invade, finally reaching the ovary. It is very probably the same with many other Microsporidia; Mesnil, for instance, has confirmed the presence of spores of *Nosema incurvata* in the eggs of *Daphnia obtusa*.

Piroplasma is also transmitted in ticks from one generation to another by infestation of the eggs. Theiler has even established that infection can persist throughout two generations without being renewed by fresh parasites. It is thanks to this hereditary transmission that bovine piroplasmosis is transmitted; for certain ticks, *Boophilus annulatus* and *B. decoloratus*, do not again leave the animal to which they become attached in the larval stage and where they have become infected. Transmission can thus only take place through the daughter ticks; and, moreover, *Piroplasma* has been found in the eggs. The same type of hereditary transmission, by *Rhipicephalus sanguineus*, occurs in canine piroplasmosis. Spirochætes are also hereditarily transmitted by ticks, particularly species of *Argas*. In the light of recent research the role of ticks in the transmission of various infections of man and other animals appears to have a very considerable importance.

Brumpt has similarly shown that *Trypanosoma inopinatum* in the green frog is hereditarily transmitted by the intermediate host, a leech, *Helobdella algira*. The leeches, born of an infected mother and having had no other source of infection, contain

trypanosomes in the proboscis and the gastric cæca. But their presence in the egg itself has not been established.

Finally, hereditary transmission by the egg plays a major role in infections which have a particular significance, as we shall see: we find this in the yeasts (green bodies, pseudova, pseudovitellus) which regularly occur in various groups of insects, notably the aphids. We only mention them here and will study them in connection with symbiosis.

CHAPTER X

RECIPROCAL REACTIONS OF PARASITE AND HOST

THE effect of parasites on their hosts is a problem of very great extent, which, in the last instance, includes all the infectious illnesses and the problems they set us, such, in particular, as that of immunity. There can be no question of dealing with them here. In restricting ourselves to non-bacterial parasites it is evident that the effect depends largely on the circumstances of parasitism. Many parasites, practically harmless in small numbers, become formidable and even fatal in the case of a heavy infestation. Thus some kinds of trichina only cause slight trouble as a rule, though the ingestion of large numbers of these nematodes brings about an illness which is rapidly fatal. One could cite analogous examples for trematodes. The hedgehog, for instance, harbours some which under ordinary conditions are inoffensive; such are *Distomum leptosomum* and *D. spinulosum*, whose sporocysts live in *Helix hortensis* and *Helix nemoralis*. But when Hofmann¹⁵⁶ fed hedgehogs with infested individuals of *Helix*, he produced a heavy fatal infection in them.

In considering infestations which are not acute, one may say that a parasite, particularly an internal parasite, when once established on its host forms with it a functional system in a state of equilibrium, the whole of which is opposed to the external environment. It is what Giard⁵⁸⁶ expressed by the term *complexe hétérophysaire*, each of the two organisms being a *complexe homophysaire*. The equilibrium thus conceived results from effects and mutual reactions, and we shall examine the principal types of these.

PARASITES AND FOREIGN BODIES

Since the parasite is primarily a foreign body introduced accidentally into the host, we may expect to see the latter attempt to eliminate it, or at least to isolate it from the internal environ-

ment, by a cellular or non-cellular barrier, such as is formed around an inert body. One may, indeed, cite a certain number of examples of this. *Trichina* larvæ in muscles are surrounded by a cyst membrane which is generally calcified. The production of pearls in molluscs seems to be, at least to a large extent, a reaction of the same nature, for in the middle of most pearls there is a parasite, most frequently a larva of a trematode or of a cestode. The pallial epithelium, on coming into contact with it, has secreted a layer of mother of pearl which has isolated it. This reaction continues and concentric layers are formed and accumulate to constitute the pearl—mother of pearl if the process remains external and in contact with the shell, a true pearl if the process is completed within the visceral mass of the mollusc. The parasitic origin of pearls, recognized in 1852 by de Filippi in *Anodonta*, has since then been the subject of numerous works, notably by Seurat³⁸⁵ in Tahiti, by Herdman and Hornell in Ceylon, by L. Jameson³⁷⁷ on mussels of the French coasts (Billiers, Morbihan), by R. Dubois, Giard, etc.

PHAGOCYTOSIS IN NORMAL AND ABNORMAL PARASITES

The production of a membranous cellular envelope around the parasite is a rather rare phenomenon, at least in the case of normal parasites; even though amoebocytes accumulate very rapidly around inert foreign bodies, most normal parasites living in an internal environment remain free from them. Thus, as Cuénot has pointed out⁸⁹, the cœlomic gregarines are never enveloped by amoebocytes as long as they are in the vegetative phase.

The formation of an envelope occurs as soon as they encyst or even prepare to encyst. Léger⁹⁷ showed this perfectly clearly in the case of *Lithocystis schneideri*, a gregarine living in the cœlom of a sea urchin, *Echinocardium cordatum*. Around the cysts, on the other hand, amoebocytes form enormous blackish masses.* Metacercariæ of trematodes, encysted, for instance,

* We, that is, Mesnil and myself⁵⁹², nevertheless observed phagocytes enveloping a cœlomic gregarine, *Gonospora longissima* (form B), in *Dodecaceria concharum*. But it is possible that the cases in which we saw this phenomenon were the prelude to the encystment of this gregarine.

in annelids, are also surrounded by a thick mantle of amoebocytes, as I have myself seen with cercariae of *Echinostomum* in the coelom of *Arenicola*, the lugworm of anglers. In the case of Entoniscidae (Crustacea, Isopoda, cf. pp. 77-80) the recent researches of Veillet²⁷⁷, too, have shown that the cryptoniscan larva, immediately after its penetration into the crab that it infests, is covered over by an envelope of amoebocytes. Similarly with nematodes encysted in the coelom of lumbricids; thus,

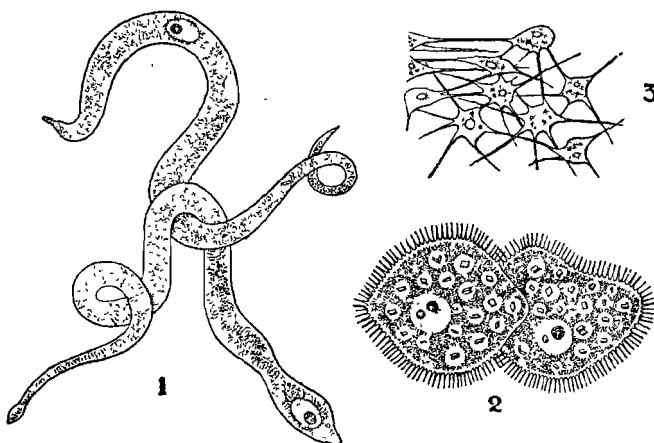


Figure 62. *Lithocystis schneideri*.

- 1, phase when the gregarine is free-living and motile (two individuals entwined) and without a phagocytic sheath in the coelomic fluid of the urchin *Echinocardium cordatum*; 2, prelude to the encystment of two individuals, paired and contracted, and already covered with a sleeve of phagocytes; 3, some of the phagocytes greatly enlarged (after Léger).

the larvae of *Pollenia rufa* are enveloped in winter, during their resting stage. But when these various parasites are in an active state they are not surrounded. It appears that normal parasites possess immunity against amoebocytes and phagocytes. This is what happens in particular, as a general rule, in entomophagous parasites. But with abnormal parasites it seems to be otherwise. Timberlake³⁸⁸, for example, induced the hymenopteron *Limnerium validum*, which normally parasitizes *Hyphantria cunea*, to lay eggs in *Euproctis chrysorrhœa*. Now, although very

many eggs were laid, he found only very few larvæ in the caterpillars. Most were destroyed or strongly attacked by phagocytes. W. R. Thompson³²⁴ found that it was much the same in *Sturmia scutellata*, a tachinid normally parasitizing *Lymantria dispar*. The eggs of this fly are deposited on leaves which are finally eaten by the caterpillar; the eggs hatch in the alimentary canal and the larvæ pass from there into the general body cavity. Thompson fed these *Sturmia* eggs, on leaves, to various caterpillars; the larvæ developed in members of the Lasiocampidæ, but not in caterpillars of *Vanessa urticæ* and *Parorgyia antiqua*, where they were found to be attacked by phagocytes. In these several cases it was unfortunately not possible to determine whether the phagocytes attacked healthy larvæ or only those that were dead or had already had their vitality greatly reduced.

On the whole, it appears that normal parasites do not as a rule provoke a phagocytic reaction, or else they inhibit it by appropriate secretions which are not possessed by abnormal parasites. The absence of reaction in normal parasites is then doubtless the result of an adaptation of a secretory nature. We may believe that such a mechanism makes it possible for the parasite to live in the intestine or internal environment of the host. It must be able to resist the enzymes and other substances of this medium. The problem has been solved in the case of those intestinal parasites which are not digested. According to Dastre and Stassano³⁷³, tapeworms resist by producing an antikinase, neutralizing the intestinal kinase and, as a result, indirectly preventing the action of trypsin. According to Weinland³⁹⁴, the substance produced by the parasite must be an antitrypsin. We have obviously still a great deal to learn about these matters. A class of new facts of major practical importance is involved but cannot be dealt with here, the question of *antibiotic* substances, produced in a strictly specific fashion by certain fungi. This is a process which is probably of very great extent, at least in the vegetable kingdom but probably also in the animal kingdom. We see in the case of penicillin and streptomycin that it is of the first practical importance and we are obviously only at the beginning of this new chapter of biology.

PARASITES AND TOXINS

The apparent effect of many parasites on their hosts is slight, even extremely slight when one considers the enormous bulk of many of these parasites in comparison with the host, and the toll that they must take of the food of the latter.

Often they appropriate reserve substances: thus, the entomophagous types do not prevent the caterpillars from developing and pupating, but the latter have no further material available for effecting metamorphosis.

It is by means of toxic substances that the action of many parasites principally makes itself felt. The feverish reaction in malaria, for example, is produced when after each phase of reproduction the elaborated toxins are liberated in the blood through the breaking down of the corpuscles where schizogony has taken place. The peri-intestinal fluid of *Ascaris megalcephala* contains a toxic substance which, on contact, provokes a lively irritation of the cornea and of the naso-pharyngeal mucous membrane, and it has often happened that zoologists, after having handled specimens of this *Ascaris*, have felt its effects. Weinberg³⁹³, by collecting the peri-intestinal liquid under aseptic circumstances and injecting it into guinea-pigs, has shown that it is, indeed, the irritant substance and is very toxic (a dose of 0·5 cu. mm. rapidly kills a guinea-pig). Dropping this liquid into the eye of a horse provokes a violent reaction but not a constant one. According to Weinberg, the horses which are not sensitive to it are, in general, those that carry a large number of these worms. There is thus ground for thinking that immunity is established against this *Ascaris* toxin. Moreover, heavily infested horses are often thin and their serum contains specific antibodies.*

Ancylostomum duodenale causes, as we know, a severe anaemia which is often fatal but the mechanism of which is not yet known. For a long time it was attributed to haemorrhages provoked by the worm, and L. Löb and A. J. Smith³⁷⁹ have shown that these worms secrete an anti-coagulant substance apparently connected with a diet of blood. Nevertheless, according to Looss¹⁹⁵, they feed not on blood but on debris from

* Sarcosporidia in sheep contain a toxin, sarcocystine, isolated and studied by Laveran and Mesnil³⁷⁸; it is very active in the rabbit, which is killed by a very small dose, but it has only a slight effect on sheep.

the mucous membrane and the haemorrhages are incidental in character. The effect of these worms is said to be due to a toxin. The anaemia caused by *Bothriocephalus* is also said to be the result of the action of a toxin, but this seems to be liberated, and therefore to react, only when the worm is diseased or dead; the toxin is then able to diffuse.

In these various cases the reaction of the host to these toxins is shown by alterations in the blood. Most of these parasites indeed cause a more or less intense eosinophilia, seen in the bearers of echinococci, ancylostomes, filarial worms, trichinas, dermal myiases, etc. Moreover, one can produce this eosinophilia in a guinea-pig by injecting it with extracts from these different parasites.

ANTIBODIES. The serum of the hosts of these parasites has also been found to contain specific antibodies (lysins, precipitins, anaphylactic antibodies) and the existence of these antibodies can become a means of diagnosis, as Weinberg³⁹² has shown with echinococcus. In all these cases, however, it is necessary to take into account the possible effect of bacteria introduced by the parasites through the lesions they produce, and to guard against this cause of error.

THE EFFECT OF THE PARASITE ON THE GENERAL METABOLISM OF THE HOST

Certain parasites profoundly affect the nutrition of the host by modifying its metabolism in a remarkable way. Wheeler³⁹³ pointed out a very curious fact of this kind in an American ant, *Pheidole commutata*. The workers, parasitized by *Mermis*, are hypertrophied; the volume of the abdomen is eight times greater than the normal; the head, the thorax and all the organs are also hypertrophied. Wheeler distinguishes these individuals by the name of *macroergates*. This hypertrophy is evidently the result of excessive larval growth brought about by overfeeding due to the parasite. The parasitized larvae have to be nourished in an appropriate fashion by the workers.

Sacculina, too, brings about an appreciable modification of the metabolism of the crab that it infests, as was shown by the researches of G. Smith³⁸⁷. In its system of rootlets and at the expense of the crab's blood, *Sacculina* elaborates reserve

substances which in female crabs would be laid down in the ovaries. The chemistry of the blood differs remarkably in male and female crabs. In *Carcinus mænas*, normal blood is more or less colourless except towards moulting when it is pink. In the female it is yellow when the ovary is approaching maturity; these two tints denote respectively the presence in the blood of tetroerythrin and lutein. The fat content of the blood is 0·198 per cent. in females with yellow blood, 0·086 per cent. in males with pink blood, and 0·059 per cent. in males with colourless blood. The liver, like the blood, shows considerable and parallel variation in the fat content, which varies from 4 to 12 per cent., the largest amount being found in females in which the ovary is nearly ripe.

Now, in the crabs of both sexes that are carrying *Sacculina*, the liver is always very rich in fat and the blood is pink or pale yellow. The blood of the parasitized males contains a great excess of fat in comparison with the normal, and approaches the composition of the female's. Thus, *Sacculina* causes in the host, whatever its sex, the development of a metabolism that is characteristic of the female.* These modifications are reflected in the crab's morphology, as was shown by Giard⁵⁸⁶, who considered it to be a very common result of parasitism and dealt with it under the name of *parasitic castration*.

PARASITIC CASTRATION

In parasitic castration, as Giard conceived it, there are in reality two sets of facts: on the one hand, actual castration, that is to say more or less complete atrophy of the gonads caused by the parasite; on the other hand, a correlated alteration of the secondary sexual characters leading to the production of individuals more or less intersexual in appearance.

Giard distinguished between direct and indirect castration. In the former the parasite develops in the genital organs themselves, and takes their place; thus an oestrid, *Cuterebra emasculator*, develops in the testes of a squirrel, *Tamias listeri*; *Distomum megastomum* destroys the gonads of a crab, *Portunus*

* In short, *Sacculina* acts like an ovary on the metabolism of the host and diverts assimilated substances towards itself. Keilin²⁹⁹ proposed the term *nutrition déviatrice* for facts of this order, very widespread amongst entomophagous insects.

depurator; many trematode sporocysts and rediæ invade and destroy the hermaphrodite or unisexual glands of the molluscs that they infest, either pulmonates or prosobranchs. *Amphiura squamata* is sterilized by the orthonectid, *Rhopalura ophiocomæ*, which develops in the immediate vicinity of the host's ovaries whose growth is then arrested, but the testes of this hermaphrodite species are normal. *Sacculina* checks the development of the gonads of crabs, either ovaries or testes, but castration is not always total, particularly in the male.

Of much more frequent occurrence is indirect parasitic castration resulting from a distance effect. It is to be seen very generally in crustaceans that are carrying Epicaridæ, as Giard and Bonnier were the first to point out. I myself ²²⁶ had occasion to see a very significant example of it in some specimens of *Peltogaster curvatus* attached to hermit crabs and parasitized by a cryptoniscid, *Liriopsis pygmaea*. During growth, this parasite feeds by sucking up the host's juices; in the adult stage it feeds no more. Now, in individuals of *Peltogaster* carrying *Liriopsis*, the oocytes in the ovary are always undergoing degeneration and appear to have been emptied. This evidently results from the epicarid's diverting to itself the substances from which the ovary of the rhizocephalan should be built up; but this state of affairs terminates when the parasite itself ceases to feed. It is quite easy to find and recognize specimens of *Peltogaster* which have previously carried *Liriopsis*, as the latter leaves a lasting hole in the mantle. Now, in these individuals the ovary has regenerated and regularly ripens its oocytes. Their degeneration was then due to the diversion of food substances by the epicarid.

Parasitic castration also occurs in plants: either direct castration by the development of fungi in the floral organs; or, what is more interesting, indirect castration effected at a distance by various parasites. These parasites cause nutritional disturbances which act on the whole plant and lead to the virescence of the parts of the flower, or the transformation of the stamens and pistil into petals. Molliard ⁴⁰⁶ has pointed out a certain number of cases of this kind: *Knautia arvensis* attacked by *Peronospora violacea*; *Matricaria inodora* attacked by *Peronospora radii*; *Viola sylvatica* infested by *Puccinia violæ*; various Umbelliferæ and Cruciferæ under the influence of acarines. In *Primula officinalis* the pistil and stamens become petaloid as a result of

a fungus invading the roots. So does *Scabiosa columbaria*, on stems where the roots bear galls of a nematode, *Heterodera*. Molliard put forward the hypothesis that most double flowers, if not all, result from parasitic associations. This is typical castration.

The same interpretation may be given to an alteration in an inflorescence that Giard³⁷⁴ had pointed out in one of the Compositæ, *Pulicaria dysenterica*, and about which he had put forward certain very ingenious suggestions. In some places, for several years running, one sees stems on which the peripheral flowers of the capitulum have lost their ligulate form and are tubular like those of the centre; they present divers other anomalies: in particular, the flowers of these plants have a strong tendency towards unisexuality. Now, Molliard⁴⁰⁷ observed that in the plants of *Pulicaria* displaying these anomalies the roots were attacked by a weevil, *Baris analis*, and it is to the effect exercised by this parasite that the modifications of the inflorescences must be attributed. Indeed, these modified stems, after being rid of their weevils, eventually produce normal flowers. Molliard has, besides, had occasion to find analogous modifications which are always connected with the presence of parasites: a plant of *Sinapis arvensis*, with virescent flowers, proved to have weevil larvæ in the collar region; larvæ of a weevil, *Hylastinus obscurus*, were present and ate out long galleries in the equally virescent stems of some plants of *Trifolium repens*; they are not found in normal stems. *Primula officinalis* and some kinds of *Senecio* have provided similar data. In particular, some plants of *Senecio jacobæa*, with their general aspect completely modified and their inflorescences altered into compact balls without peripheral ligules, had their stems mined by larvæ of *Lixus*.

Let us now consider the alterations in the secondary sexual characters correlated with parasitic castration. The first of these cases was pointed out by J. Pérez³⁸² in Hymenoptera of the genus *Andrena*, parasitized by *Stylops*. Members of either sex lose their distinctive characters to some extent and tend to acquire those of the opposite sex. In the female, at the same time, the ovaries atrophy and their oocytes no longer reach maturity. In the male, only the testis on the side where the parasite is situated is altered; the other remains functional. It is to

be noted that in America these modifications have not been found in the same parasitic associations.

The most striking case, discovered by Giard⁵⁸⁶ and carefully re-investigated by G. Smith³⁸⁷, is that of crabs parasitized by *Sacculina*. The female scarcely undergoes any modification, while the male resembles the female type. These modifications are very variable in extent: they can reach a point where the diagnosis of sex becomes very difficult. They affect the form of the abdomen, the independence of its segments, the abdominal appendages and sometimes also the chelæ. Let us take two examples: *Carcinus mænas* and *Inachus scorpio* (= *mauritanicus*).

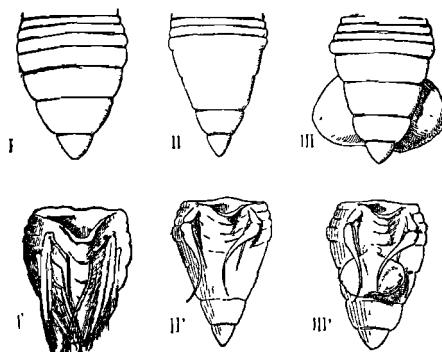


Figure 63. Modifications in the abdomen of *Carcinus mænas* (dorsal and ventral aspect) under the influence of *Sacculina* (after Giard).

I-I', abdomen of normal female; II-II', that of normal male; III-III', that of a male parasitized by *Sacculina*.

In *Carcinus mænas* the abdomen of the female is wide and rounded and all the segments are quite distinct; the abdomen of the male is pointed and triangular in form; furthermore, segments III, IV and V are united into one whole. Now, in males parasitized by *Sacculina* these segments become independent and at the same time the abdomen becomes enlarged and rounded (Fig. 63).

In *Inachus scorpio*, of which a special study was made by G. Smith, working on abundant material collected at Naples, the facts are still more striking. The shape of the abdomen differs very considerably in the two sexes, as is the rule in the oxyrhynchous crabs. That of the male is rectangular and very

narrow, that of the female wide and rounded. Now, one finds males parasitized by *Sacculina*, in which the abdomen has assumed the female form. But here the modifications also extend to the abdominal appendages. The female possesses on each segment a pair of pinnate appendages, on to which are hooked the packets of eggs; the male, on the contrary, has only one pair of copulatory stylets in the anterior region of the abdomen. Now, amongst the parasitized males, one finds female appendages in all stages of development, as is shown by the top series

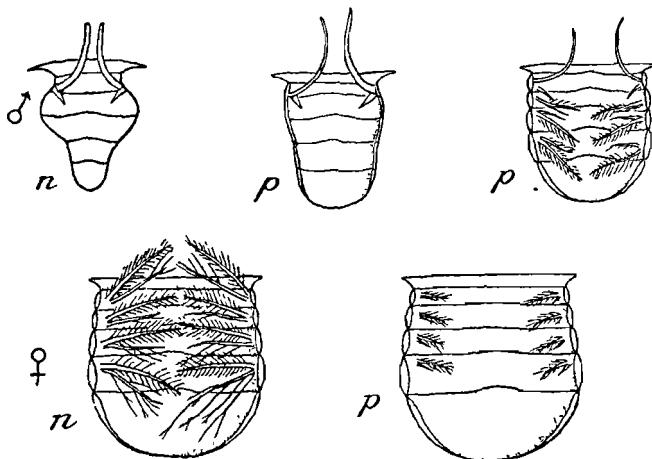


Figure 64. The abdomen of *Inachus mauritanicus* showing modifications due to *Sacculina* (ventral aspect), after G. Smith.
 n, normal individuals; p, parasitized individuals: the males in the first row and the females in the second.

of drawings in Fig. 64. Certain males have the appendages complete and their true sex can no longer be recognized externally except by the more or less visible vestiges of the copulatory stylets. With some of them dissection is necessary and the information it provides is sometimes of doubtful value on account of the atrophy of the testes and the vasa deferentia. Finally, in the genus *Inachus* the alteration of characters also extends to the chelæ; those of the male are normally much stronger than those of the female, but in a certain number of males parasitized by *Sacculina*, the chelæ are feebly developed and of the female type.

On examining crabs which had previously carried a *Sacculina* and which may be recognized by an annular scar in the former region of insertion, Smith found some which had originally been males and in which the gonads, after the loss of *Sacculina*, were undergoing regeneration but contained young oocytes; that is to say, that the gland then had an orientation towards the female sex.

I shall cite a further analogous case in the crab *Eriocheir japonicus*, studied more recently by Yo K. Okada and Y. Miyashita²⁶¹ in Japan. Here again, the males parasitized by *Sacculina* showed all stages of modification in the shape of the abdomen and in the development of the appendages of this region, even to the extent of completely resembling females. The chelæ are also modified in the female direction and, under the influence of the parasite, the gonads are greatly reduced in those feminized males, sometimes being changed into an ovary or a hermaphrodite gland. It is clear, then, that these cases occur very generally in the crabs.

If we relate all these facts to what we have said above on the metabolism of the crab that is parasitized by *Sacculina*, we see that in the male, parallel with the deviation in metabolism, the secondary sexual characters are modified in the direction of the female sex and that this influence may even extend as far as a modification of the polarity of the genital gland itself.*

* One can today classify the preceding modifications as cases of intersexuality, as defined by Goldschmidt⁵⁸⁷ and F. R. Lillie. The former, working on the genetics of *Lymantria dispar* (this bombycid, as its specific name indicates, shows sexual dimorphism very clearly), has pointed out that by appropriate crossing of races one obtains at will individuals showing a mosaic of male and female characters, that is to say, gynandromorphs, and that these individuals, from the point of view of the sexual instincts, are intermediate between males and females. He was able to standardize the different races and, with the help of these data and by crossing two suitably selected races, to obtain an expected degree of intersexuality, extending as far as complete sex reversal in one group of individuals. Evidently a similar state of affairs occurs in *Inachus* under the influence of *Sacculina*. The changes in the crabs are also comparable with the anomalies shown by a free-martin, explained by F. R. Lillie⁵⁹⁰. Such an individual is the heifer twin of a male calf, which, since the days of antiquity, has been known to be sterile, and which, anatomically, is an intersex, showing a varying mixture of male and female characters in the genitalia, with a more or less pronounced deviation towards the male sex. Lillie showed that these deviations were the consequence of a precocious anastomosis which, in the case of a twin pregnancy, exceptional in the cow, established itself between the vessels of the foetal membranes. Thus, the female embryo, at a very precocious stage, is submitted to the effect of male blood and the hormones it contains. Under the influence of these hormones there is inhibition of female characteristics and development of male ones.

In pagurids carrying *Peltogaster*, F. A. Potts has also observed that the males to some extent take on the characters of the female, without the converse occurring. Giard had previously noticed that in male pagurids parasitized by an epicarid, *Phryxus paguri*, the abdominal appendages often resemble those of the female. Rathke, half a century earlier, believed that only female prawns (*Leander*) were parasitized by *Bopyrus*. Now, actually males are often parasitized as well, but as a result they adopt the secondary sexual characters of the female, which misled Rathke.

Cases of this kind are probably rather widespread in the Crustacea but their discovery and analysis demand precise observations on abundant material. More recently an English zoologist, B. W. Tucker (1931), has also observed that, in *Upogebia littoralis* parasitized by a bopyrid, *Gyge branchialis*, females were not modified, whereas in the males the chelæ and first abdominal appendage assumed the characters proper to the female. The genital glands are reduced and more or less feminized. At the root of all these changes there must be hormonal activities released or modified by the action of the parasite, which will doubtless be better known in the near future.

In some homopterous Hemiptera, *Typhlocyba hippocastani* and *T. douglasi*, parasitized by a hymenopteron, *Aphelopus melaleucus*, and by a dipteron, *Atelenevra spuria*, Giard⁵⁸⁶ observed a very marked atrophy of the ovipositor in the females of both species. In males parasitized by *T. hippocastani*, the penis is equally reduced.

In plants one may quote the case of one of the Caryophyllaceæ, *Lycnis dioica*: in female stems of specimens of this dicœcious plant parasitized by *Ustilago antherarum*, the presence of the parasite has the effect of inducing the appearance of anthers, which, moreover, are invaded by the fungus.

The numerous examples of a morphogenetic effect produced by the gonads through a hormonal mechanism clarify the facts observed in the case of parasitic castration. There is, however, an apparent paradox in the data relating to crabs and insects. For in arthropods experimental castration appears to have no effect on the secondary sexual characters, even when carried out very early. But within the mechanisms of the two actions there are evidently considerable differences in the conditions.

Recent data on the endocrinology of the arthropods open up numerous fertile perspectives in this connection.*

SPECIAL CASES OF REACTION OF HOSTS TO PARASITES

At the beginning of the chapter we saw that parasites, at least when they are active, do not as a rule provoke a phagocytic reaction. But that is not to say that there is never a cellular response to their presence. One could cite various examples of such a response.

Around the egg of entomophagous Hymenoptera a sheath is formed from the cells of the host, forming an epithelial layer, which very certainly plays an important part in the exchanges between host and parasite.

The larva of the timbu fly, *Cordylobia anthropophaga*, causes the formation of an open cutaneous tumour (furunculous myiasis) consisting of a neoplastic proliferation of dermal tissue around the larva. These cells rest on a kind of cellular purée on which it feeds and which must not be confused with suppuration; there is suppuration only if the larva is diseased or dies, and if the opening of the tumour closes up (Roubaud ³¹⁷).

In fishes there is a reaction of the same kind around the glochidium larvæ of Unionidae. In a few hours they are encased in a thick vascular cyst, the elements of which are phagocytized by the pallial cells of the young mollusc. F. H. Reuling ³⁶³ observed the interesting fact that this reaction of the host does not continue indefinitely. After two or three successive infestations of *Lepidosteus* by glochidium larvæ of *Lampsilis anodontoides*, there is no further reaction and development is unsuccessful. Using *Micropterus salmonoides*, the same author was able to obtain two massive infestations by glochidium larvæ of *Lampsilis luteola*, but a third was abortive, resulting in abnormal cysts from which the parasite was expelled after forty-eight hours, although infestation succeeded perfectly when glochidium larvæ

* As an example which will render this statement more precise, I shall cite a very curious case studied by Panouse ²⁶³. In removing the eye stalks of prawns (*Leander serratus*) he not only produced a reaction in the chromatophores but caused rapid development of the ovary and thus obtained eggs out of season. There is, in the eye stalk, an endocrine gland which, directly or indirectly, acts on the growth of the ovary. It is clear, then, that the parasites, in modifying the hormonal balance, can act on the genital glands and the secondary sexual characters.

from the same batch were used on fresh controls. Immunity is thus rapidly acquired by the fish, whose serum then destroys, *in vitro*, the tissues of the glochidium, while the serum of fresh controls is without effect.

With certain Protozoa we see localized cellular reactions. Various Coccidia and gregarines cause hypertrophy of one cell or of a group of cells. Thus *Caryotropha mesnili*, a coccidian parasite of the spermatogonia of an annelid, *Polymnia nebulosa*, studied by Siedlecki¹²⁵, brings about the hypertrophy of the cell in which it develops, as well as of its nucleus. Some adjacent spermatogonia can undergo analogous modifications and fuse

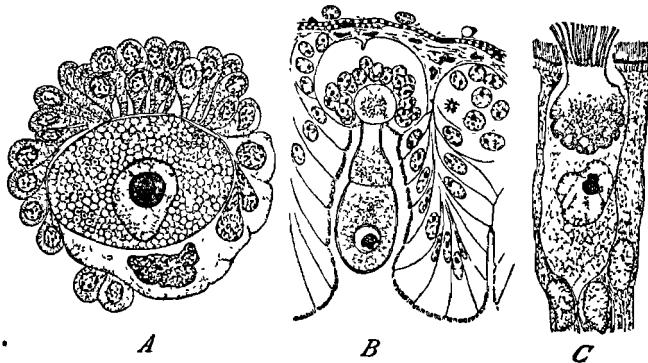


Figure 65. Cellular reactions of the host to Coccidia and gregarines. A, *Caryotropha mesnili* (after Siedlecki). B, *Clepsidrina davini* (after Léger and Duboscq). C, hypertrophy of an intestinal epithelial cell of *Blaps* parasitized by *Styloynchus longicollis* (of which only the epimerite is visible) (after Léger and Duboscq).

with the first to form a giant multinucleate cell; the rest of the group of spermatogonia do not develop normally into protozoa but remain in the condition of epithelial cells forming a compact envelope around the parasite. Here, then, is direct partial castration.

Analogous cases have been observed in various gregarines. *Pyxinia frenzeli*, a parasite of the intestinal epithelium of larvae of *Attagenus pellio*, produces hypertrophy of the host cell, followed by atrophy (Laveran and Mesnil). *Clepsidrina davini*, in *Gryllomorpha*, causes the epithelial cells of the intestinal crypts, to which it is attached, to fuse into a syncytium (Léger

and Duboscq¹⁰⁰). Hesse^{93A} has pointed out cases of the same nature in the gregarines of oligochaetes: *Monocystis agilis* and *Rhynchocystis pilosa* act on spermatogonia in the same way as *Caryotropha mesnili*. *Nematocystis magna* hypertrophies the epithelial cell which supports it. These examples of hypertrophy have sometimes led to mistakes. The genus *Myxocystis*, described as a type of special parasitic Sporozoa in *Limnodrilus*, has been recognized as being only a microsporidian parasite of the lymphocytes or spermatogonia of the worm, causing hypertrophy of the parasitized cell and of its nucleus, and the fusion of several cells into a giant cell. Various Microsporidia, such as *Nosema anomalam* in the stickleback (Stempell), *Glugea* in *Balanus amaryllis* (Ch. Pérez), and a species that I have myself studied in the liver of the sand eel, *Ammodytes lanceolatus*, produce giant and polymorphic nuclei at the periphery of the infected area. Stempell¹²⁷ considered them to be an actual part of the parasite with the significance of vegetative nuclei. It is more probable that they are elements belonging to the host, hypertrophied and fused into giant cells. In all likelihood the same applies to the cell with a large nucleus and a brush-like border which envelops the cysts of *Giltruth* in the stomach of the sheep, studied by Chatton⁸⁶. A sporozoan, *Selysina perforans*, of obscure affinities, parasite of an ascidian, *Stolonica socialis*, and studied by Duboscq⁹⁰, also causes the formation of giant multinucleate cells by the fusion of cells in large or small numbers.

In the cells of the sabellid *Potamilla torelli* invaded by *Haplosporidium potamillae* (frequently accompanied by a yeast, related to *Monospora* in *Daphnia*) there is a proliferation of peritoneal endothelium into a sort of papilloma (Caullery and Mesnil³⁸⁰).

One could add to this series of examples, and it is clear that we are concerned with the effect of substances continuously secreted by the parasites.

GALL FORMATION

These very localized cellular reactions lead us naturally to a type of modification due to parasites and very widely spread in plants. I refer to galls. There are some analogous formations in animals which we shall examine first of all. Giard⁵⁸⁶ proposed

to give them the name *thylacie* ($\thetaυλάκιον$ purse). According to whether the parasite is animal or vegetable one may say that it is a question of *zoocecid*s or *phytocecid*s, of *zoothylacies* or *phytothylacies*.

A certain number of sedentary Myzostomaria, on the pinnules of crinoids, cause the formation of cavities with a thick, calcareous wall and a small external opening, within which they hide.* Similarly, a copepod, *Pionodesmotes phormosoma*, studied by J. Bonnier ²¹⁵, forms a true gall in an abyssal sea urchin, *Phormosoma uranus*, with a soft test: in contact with it the test becomes strongly calcified to form a sphere jutting into the cœlom (Fig. 66) and contrasting with the general frailty of the wall of the sea urchin. In these galls there is a narrow opening through which the hypertrophied female copepod cannot pass; the male, a great deal smaller, must still be able to make its exit. H. J. Hansen (1902) found a similar case, that of the copepod *Echinoheres globosus* on the sea urchin *Caliteria gracilis*. Finally, Mortensen and Stephensen ²⁵⁶ have also pointed out the formation of a gall by a copepod, *Astrochordeuma appendiculatum*, at the expense of an ophiuroid, *Astrocharis gracilis*.

A crab, *Hapalocarcinus marsupialis*, modifies the growth of one of the Madreporaria, *Pocillopora cæspitosa*, by its presence at the tips of the branches, where it causes the formation of cavities in which it remains concealed. This case, pointed out by Semper, has been thoroughly studied by F. A. Potts ²⁶⁷, who followed out the gradual development of the cavity in which the crab dwells; a line of openings persists there, ensuring the circulation of the water. *Hapalocarcinus* modifies other corals, *Seriatopora hystrix* and *Sideropora*, in the same way. Other crabs of the genus *Cryptochirus* similarly inhabit cavities in a massive polyp, *Leptoria*, where they live in pairs, the male being much smaller than the female.†

* Analogous malformations in fossil echinoderms show that this type of parasitism is ancient. J. Mercier (1936) pointed out that in the sea urchin *Collyrites dorsalis* of the Callovian phase, protuberances of the test were caused by galls produced by a parasite which he placed near *Pionodesmotes* (= *Castexia douvillei*). Parasitism by Myzostomaria appears also to be of long standing (Clark, 1921).

† Let us here recall that, as we have already seen, the parasitic gastropod molluscs (*Megadenus*, *Stylifer*, etc.) also provoke malformations resembling galls or thylacies on the echinoderms where they live (*Stylifer celebensis* on the starfish *Certonardoa*, Hirase ³⁴³; *Megadenus arrhynchus* on the starfish *Anthenoides rugulosus*, Ivanov ³⁴⁵; *Megadenus cysticola* on the spines of *Dorocidaris tiara*, Kœhler and Vaney ³⁵⁰).

Giard⁵⁸⁶ created the term thylacie in connection with individuals of *Typhlocyba* parasitized by *Aphelopus melaleucus*; the hymenopteron is indeed carried in a voluminous pocket, placed laterally on the abdomen.

The pocket in the host, *Polycirrus arenivorus*, where *Xenocæloma* is situated, may also be considered as a gall; the presence

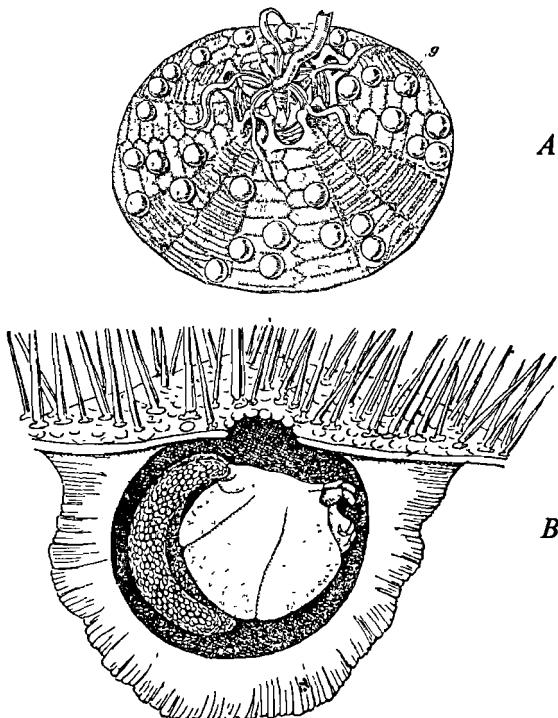


Figure 66. A, fragment of the test (inner face) of *Phormosoma uranus* with numerous prominent spherical galls, *g*, of *Pionodesmotes phormosomæ*. B, interior aspect of one of the galls with its external opening and the parasite (♀) (after J. Bonnier).

of the parasite causes the tissues of the annelid to undergo special proliferation and differentiation.

Finally, one may include amongst temporary galls the formation of the vascularized cyst in which glochidium larvae develop in fishes, as well as the tumours of the furunculous myiasis produced by the larvae of the timbu fly.

But this type of reaction remains exceptional and is little developed amongst animals.

On the contrary, galls are of major importance amongst plants and are as interesting from the physiological point of view as they are from the morphological one. I shall restrict myself here, however, to some remarks of a general nature on this subject.

Animals that produce galls in plants, the cecidozoa, belong to various groups. The most important are nematodes (helminthocecids), particularly *Heterodera*; acarines, principally *Eriophyes* and *Phytoptus* (phytoptocecids); but, above all, the insects. Almost all the orders include gall-forming types, but those that play the most important part are the aphids, Diptera (Cecidomyidæ) and the Hymenoptera. Among these last, the Cynipidæ constitute a vast family, attacking species of *Quercus* by preference and supplying data of great interest to the biologist (parthenogenesis, polymorphism, etc.); the Tenthredinidæ and the Chalcididæ have also very great importance as gall formers.*

Galls are formed at the expense of all parts of the plant: root, stem, leaves, flowers, buds; each gall former produces as a rule a definite gall on a fixed part of a given plant. There is usually very strict specificity between gall formers and plants, a specificity subject, however, to the same vicissitudes as parasitism in general. Many gall formers attack only one kind of plant and are *monophagous*; others are more or less *pleophagous*, as we find with *Heterodera radicicola* and with a chrytidinid, *Pycnochrytrium aureum*, that is known on about one hundred plants. Sometimes, on the contrary, on very closely related species, gall formers, without being morphologically distinct, constitute quite separate physiological races. One can cite, for instance, the case of *Isosoma graminicola*, which is represented by two distinct races on *Triticum repens* and *T. junceum*.

The morphology, structure, dimensions and colour of the galls are as strictly determined as in normal organs. I refer the reader to the work of C. Houard⁴⁰², who has devoted a considerable amount of work and careful documentation to galls in the French and in exotic floras. There is a precise mor-

* True gall formers must naturally not be confused with the commensals and inquilines which sometimes live there in great numbers. In the galls produced by *Biorhiza aptera* (Cynipidæ), 79 parasitic species and 11 commensals have been enumerated.

phology in galls; in general, they are the result of two processes: cellular multiplication, or *hyperplasia*, and a *hypertrophy* of the cells and nuclei. We have a very striking example of cellular hypertrophy in the swelling produced by *Heterodera radicicola* in the roots of melon, where the nematode causes the formation of giant cells, sometimes containing as many as 200 nuclei (Fig. 67).

In general, particularly in parenchyma, the tissues have a clearly embryonic character; the cells and nuclei are much larger

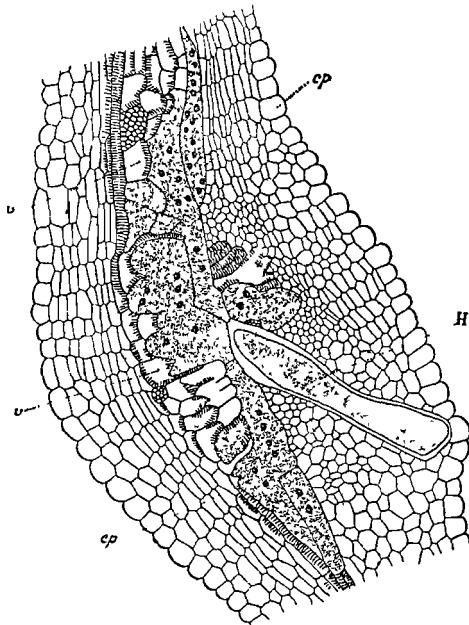


Figure 67. Longitudinal section of the root of a melon attacked by *Heterodera radicicola*, *H*; *cp*, multinucleate cells (after Molliard).

than in normal tissues; the chlorophylllic apparatus is reduced; frequently there is production of anthocyanin. From the chemical point of view, galls are richer in water than normal tissues, and also richer in soluble nitrogenous compounds, in starch and in tannin.

The point which here will interest us most is the mechanism of gall production. It must be noted that galls are only formed on plant organs that are undergoing development, and

that they are only formed by animals in the state of eggs or larvæ. The most natural hypothesis—it had already occurred to Malpighi in the seventeenth century and is generally admitted today—is that these structures are due to the action on the plant of irritant substances, deposited in the tissues by the gall-forming animal either at the moment when the eggs are laid or in the course of larval growth. These substances must cause nutritive material to be diverted from the tissues. One sees, moreover, a general parallelism between the histological and morphological differentiations which develop in many galls and those which result from alterations in plant nutrition due to other causes and which are expressed, for example, by fasciation or virescence of the flowers. There is also a good deal that is analogous between galls and fruit, and this must be based on similar conditions of nutrition when both of them are being formed. Galls would then be, in short, the plant's reaction to substances inoculated by the gall-forming parasite, and their morphology would be determined by the plant's actual constitution. Gall production occurs only when there is inoculation into a tissue that is embryonic in character. After that all the correlations which regulate the development of the plant itself and which intervene in the formation of new parts, so determining their symmetry, come into play but under modified conditions. Thus, a truly new *organ* is produced, whose structure and development depend upon the intrinsic properties of the plant and are thus determined in advance.

In spite of the apparent adaptation of the galls to the circumstances in which the cecidogenous larvæ develop and emerge, the galls must be considered as a characteristic reaction of the plant, independently of all finality concerning the parasite. If there had been evolutionary adaptation of the one to the other, one could hardly imagine it other than as a modification in the irritant action of the parasite as, for instance, a variation in the substances by which the parasite acts on the plant or in the nature of the action of these substances.

It is only at a recent date that it has been possible to obtain some experimental results supporting the preceding hypothesis. The conditions of gall production certainly involve a very precise causal mechanism which crude experiments cannot imitate.

Some very suggestive observations and experiments on this subject were made first of all by Beijerinck ³⁹⁹ on the galls of Hymenoptera, and more recently by W. Magnus who, in confirming the conclusions of Beijerinck on certain points, nevertheless diverged from him on others.

Beijerinck studied in particular the galls produced on willow leaves by *Nematus* (=*Pontania*, Tenthredinidæ). He noted that when the insect deposited the egg in the wound she had made in the plant, she also deposited a droplet of liquid secreted by abdominal poison glands. According to him, it is this liquid that causes the formation of the gall, for the latter is produced even if—as sometimes takes place—the egg is not laid and also when the egg has been killed by means of a needle. Under these conditions the galls do not attain the normal final dimensions, but one sees them begin to take shape without the agency of the egg and of the larva. These experiments have been repeated and verified by Magnus ⁴⁰⁵ with various species of *Pontania*, in particular *P. proxima* on *Salix amygdalina*. Magnus even improved on them by removing the egg from the plant almost immediately after it had been laid and without injuring it. He was able to compare the whole course of events in gall production in the plants thus treated and in others serving as controls, in which the egg had been left. Now, in those in which the egg had been extracted the gall formed well but more slowly and remained smaller. It develops, then, without the intervention of the egg itself, or of the larva. It is not so in all galls. According to the experiments of Magnus with those of the Cynipidæ (*Rhodites*, *Biorhiza*) the presence of the egg and of the larva is necessary.

Beijerinck concluded from his experiments on *Pontania* that the determining factor is the secretion deposited by this insect in the wound on the plant. But when the substance in question was directly inoculated into the leaves of the willow neither he nor Magnus succeeded in provoking a reaction of the plant, nor any definite reaction such as that of the natural gall. That must depend on the conditions of inoculation. The wound made in the plant by the insect's ovipositor involves a very great precision so far as the torn tissues are concerned, and, consequently, of the cells which react. Magnus, then, does not consider it as absolutely established that the gall is really the

direct result of the action of a definite chemical substance on the cells of the plant. For him the wound itself is a decisive factor.

He distinguishes, moreover, two stages in the development of galls: an initial phase in which undifferentiated tissues are formed by cell multiplication, and a second phase in which these tissues differentiate. The latter, in all galls, would be constantly dependent on the living and developing larva which acts through its secretory products. An injection, made once, of a chemical substance would thus not suffice to bring about the complete development of a gall.

If the secretions introduced by the parasite are indeed the effective cause of gall formation, the active substance in them remains to be discovered. It is natural to think of enzymes, and it has been proved that various eggs and larvæ of gall-forming animals are, indeed, rich in proteolytic enzymes; this fits in with the fact that galls contain nitrogenous compounds, particularly in the soluble state and not in the form of proteins. In discussing these problems Magnus arrived at a hypothesis of a general nature that I give here on account of the analogy that it suggests with the conditions of parasitism in animals. The production of galls would be the result not of the direct action of enzymes but of that of substances secreted by the gall-forming animals, which would prevent or delay the action of the plant's own enzymes. These would be, in other words, antibodies produced by the parasite and introduced by it into the plant, and these would modify the conditions of cell metabolism. The specificity of the antibodies would condition the specificity of the different galls produced by distinct parasites on the same plant. For the moment this hypothesis awaits confirmation.

Whatever may be the exact way in which substances inoculated by the parasite act in the production and the differentiation of galls, it is interesting to point out some positive results obtained recently without the intervention of gall-forming organisms, by the introduction into the plant of substances elaborated by the latter. These results are from work by Molliard and E. F. Smith.

Molliard's experiments⁴⁰⁸ were first performed on *Rhizobium radicicola* on the roots of Leguminosæ; it was isolated from the roots of the bean, in a pure culture. The culture liquid, passed through a porcelain filter, finally served as a nutritive

medium for peas which had previously been germinated aseptically on moist cotton wool. Controls were grown under the same conditions but in spring water. Under the influence of the *Rhizobium* culture liquid the roots of the peas showed a hyperplasia of the pericycle, and hypertrophy of the cortical cells; but there was no question of a specific action nor of any considerable changes.

More recently, Molliard⁴¹⁰ succeeded in reproducing, at least partially, the gall which a cynipid, *Aulax papaveris*, produces in certain poppies, *Papaver dubium* and *P. rhoæas*. This insect is gregarious. There are as many as 50 larvæ in a single gall. Molliard pounded up a batch of these larvæ and, with the aid of a syringe provided with an asbestos filter so as to obtain a clear liquid, he injected the product of this pounding into the middle of the stigmatic platform of a flower bud of the poppies, on the axis of the pistil. The plant was then protected against all access by the hymenopteron. After some days the treated flowers showed hypertrophied placentæ, the appearance being remarkably similar to that of the natural gall. But further stages, subsequent to this preliminary change, were not obtained for lack of fresh doses of the irritant substance, which, under natural conditions, must be the better assured and controlled, the greater the number of larvæ.

E. F. Smith⁴¹¹, in the United States, carried out a series of researches, parallel to these preceding ones, on crown galls produced by *Bacterium tumefaciens*; he caused substances elaborated by this bacterium to react on the plant. He cultured the bacterium on a very simple medium.* After culture, this medium was found to contain formaldehyde, ammonia, amines, alcohol, acetone and formic and acetic acids. Smith observes that many of these substances are amongst those which have been shown to be the most effective stimulants in experimental parthenogenesis carried out by J. Lœb. He painted the buds of the young plant with these substances, or injected them with it. The plants utilized were cauliflower, castor oil (*Ricinus*) and tomato. But, again, the operation could not be repeated continuously as it would have been under natural conditions. Smith

* Distilled water with 1 per cent. dextrose and 1 per cent. peptone added, and sufficient calcium carbonate to neutralize the acids formed which inhibit the development of the bacterium.

obtained tumours which remained small and showed hyperplasia of the vessels and hypertrophy of the cells. The cells were more compact than in normal tissue; they lacked chlorophyll. Their volume became almost a hundred times that of normal cells. The changes brought about were thus similar to those which are characteristic of the natural gall.

In short these results, without establishing the complete development of the galls, are nevertheless sufficient to justify the hypothesis from which the experimenters set out, particularly if one takes into account the difference existing between experimental and natural conditions.

Galls may, then, be considered as the specific reaction of the young tissues of plants to chemical substances introduced into these tissues by the cecidogenous organisms. The frequency of galls on plants and their high degree of differentiation, in contrast to the rarity of analogous structures in animals, is doubtless only the expression of the predominance, in plants, of local reactions over general ones. That is clear if one considers the constitution of both of them, and the difference of the physiological relationship between the parts in both cases, and if, in particular, one envisages the role of the circulatory system in animals.

CHAPTER XI

SYMBIOSIS BETWEEN ANIMALS AND PLANTS

THE last part of this book will be devoted to the study of symbiosis. This term was created by A. de Bary in 1879, to designate the intimate and constant association of two organisms with mutual relationships assuring them of reciprocal benefits. Even if one lives at the expense of the other and can be considered as a parasite, its metabolism provides the partner with more or less essential elements. Symbiosis is the extreme form of mutualism. Once again we see that a strict continuity exists between all categories of associations of organisms.

The typical example of symbiotic associations as conceived by de Bary was the case of the lichens, whose nature had just been established by Schwendener⁵⁷⁸. O. Hertwig⁴¹⁶, extending the conception to certain associations between animals and plants, defined symbiosis as the common life, permanent in character, of organisms that are specifically distinct and have complementary needs. As I have said above, the delimitation of symbiosis and of commensalism, or even of parasitism, is not always easy. One sometimes brings into it associations such as those of *Eupagurus prideauxi* and *Adamsia palliata* which, on other occasions, one considers as belonging to mutualism, while restricting symbiosis to cases where union is particularly intimate. The analysis of examples of symbiosis thus understood will show that it is not always purely mutualistic and that one of the two associated organisms is in reality more or less parasitic on the other.

There is also a category of facts which, without really belonging to symbiosis, can be compared with it in certain respects and which I shall evoke in this introduction. It concerns the social animals and particularly societies of insects—the social Hymenoptera, especially the bees and ants, and the

termites. These societies are groups in space of distinct individuals, apparently independent but in reality united to one another in a definite fashion, which involves in each one of them complementary functions, involving for the group as a whole a definite collective individuality and at the same time modifying in a definite direction the structure and fate of each individual. In short, a kind of symbiosis exists between all the members of the community.

I shall here restrict myself to pointing out some of the chief features concerned. The dominant one is the division of labour amongst the associates, localizing certain functions in definite categories and stamping them by definite anatomical and physiological characters, so that castes are formed, forming a unity related to symbiosis itself.

In the most typical societies of bees, ants and termites the reproductive function, fundamental property of every individual under ordinary circumstances, becomes the privilege of an individual or a caste. Sex itself results from fertilization or alternatively from parthenogenetic development of the egg, leading in the first eventuality to the female sex, in the second to the male. The males have only an ephemeral existence, their role being limited to the accomplishment of the act of fertilization. Reproduction becomes the monopoly of a sole female individual, the *queen*; but she, on the contrary, is incapable of leading an independent life or of rearing her progeny. The supplying of food to this queen and her larvæ becomes the exclusive business of a numerous caste of male and female workers who come to be excluded from the reproductive function by reason of the atrophy of their gonads, this being determined deliberately by the quality of the food provided for them in the larval state. Here is a definite and labile mechanism functioning with perfect regularity, like a laboratory experiment.

I do not wish to enter here into a detailed examination of the variations of these processes; that would lead to a complete analysis of the life of social insects, which is outside the scope of this work. I limit myself to remarking that even if they do not enter into the category of actual symbiosis they are connected with it and that is why I have drawn attention to them on the threshold of the chapters which follow. We shall study separately the different types of symbiosis, grouped according to

the degree of intimacy of the connections between the associates, and with regard to the nature of the latter.

One is led, indeed, by the constancy of the association and of the relationships between the associates to consider as cases of symbiosis the regular association of two definite species without the fusion of individuals with one another; we shall designate these associations by the term *ectosymbiosis*, in contrast to the typical form of symbiosis, where there is interpenetration of the two associates with the formation of a mixed complex, which we shall call *endosymbiosis*.

Furthermore, separate chapters will be devoted to symbiosis between animals and plants and that between two plants. In the first of these two cases one of the associates is always a microscopic organism belonging to the lower plants (fungi, algae or bacteria) or to the Protozoa.

ECTOSYMBIOSIS

ANTS AND FUNGI. Our first example of ectosymbiosis is provided by associations between ants and fungi. The American ants of the genus *Atta*, called *leaf-cutting ants*, shred leaves into tiny fragments which they pile up, and on these heaps there regularly develops a mycelium whose hyphae are utilized as food by these ants. Thus the latter habitually establish mushroom gardens. These associations have been studied in detail by many eminent naturalists for three-quarters of a century: Belt, Fritz Müller and his nephew Alf. Möller⁴⁹⁸, H. von Ihering⁴⁷⁰, Göldi⁴⁵¹, Huber⁴⁶⁴, etc. Exact determinations have been made of the fungi so cultivated. The most constant is an agaric, *Rhzites gongylophora*, that has been found associated with all species of *Atta*. Some other fungi belong to the genera *Aptero-stigma* and *Cyphomyrmex* (Xylariaceæ). It has been observed that, when swarming, the ants carry bundles of mycelium in pockets in the hypopharynx and that when new colonies are first being formed the queen cultivates the fungus; later, this task is the business of the workers.

TERMITES AND FUNGI. We find analogous cases in the termites of the family Metatermitidæ, and particularly those of the genus *Odontotermes*. The termitarium regularly contains a mushroom garden. This was observed as early as 1779 by Koenig

and in recent decades has been the subject of very numerous researches amongst which I should like to make special mention of those of Doflein⁴⁴², Petch⁵⁰⁸, Jumelle and Perrier de la Bathie⁴⁷⁵⁻⁷, and Bugnion⁴³¹⁻², and more recently those of Bathellier⁴²⁵, P. Grassé⁴⁵³, and R. Heim⁴⁶².

The fungi develop on "combs" constructed by the termites with small balls of excreta; they form a mycelium with "spheres". The fungi themselves are agarics, which have been methodically cultivated by R. Heim, who obtained fructifications; he made the genus *Termitomyces* for them. But there are also some Ascomycetes (*Xylaria*). It was generally agreed that in the termitarium the fungi were an essential larval food and that they were indeed cultivated by the termites. The careful observations of Grassé⁴⁵² run counter to this opinion. According to him the termites use the fungi, mycelium or spheres, for food only in a very accessory way and these are not one of their basic foods. One cannot allow that intentional cultivation occurs. The spores are introduced passively with the plant debris forming the material of the combs. The conditions of temperature and humidity are at an optimum for the development of the fungus. The culture having thus developed spontaneously, the combs, as Smeathman had already said at the end of the 18th century, are nurseries where the termites deposit their eggs, which there find optimum physical conditions; the larvæ, however, do not in fact feed on the fungus. Their mouth-parts would not allow them to tear the spheres apart and Grassé was able to prove that nearly all the latter remain intact. They do not constitute a basic food but have at most only an accessory value.

It is clear, then, that anthropomorphic tendencies have greatly exaggerated the precision and purpose of the relations between termites and fungi. Their constant association with Termitidæ is an undeniable fact; in the etymological sense of the term a symbiosis exists here, but this does not correspond at all to a close physiological relationship, and one may suppose that it is the same for associations between ants and fungi.

OTHER ASSOCIATIONS OF INSECTS AND FUNGI. Other regular associations between insects and fungi have been discovered. For instance, the beetle *Xyleborus* (Bostrichidæ) makes galleries in wood, and these same galleries are habitually covered

with the mycelium of fungi sown passively by the insect and utilized as food by its larvæ. It is the same with some other forms that are equally xylophagous, such as the Platypodidae and the Lymexylonidae (*Hylecætus*) and certain Hymenoptera, the Siricidae. Similarly, in the galls produced by certain Cecidomyiidae in Leguminosæ, the internal cavity of the gall is also covered with a mycelium on which the larvæ feed. But it is not necessary to let oneself become involved in finalist interpretations of these associations, constant and definite though they may be.

ENDOSYMBIOSIS

We now come to the cases in which the two associated organisms interpenetrate and tend to constitute a more or less perfect morphological and physiological unit, an endosymbiosis.

The number of works which relate to this subject has considerably increased in recent years, resulting in an important increase in our knowledge and a growing precision in the analysis of the data. One of the workers who has devoted himself to it with the greatest tenacity and penetration is P. Buchner, who, in addition to numerous studies on particular cases executed by himself or his pupils, has made a profound and methodical study of it in his book, *Tier und Pflanze in Symbiose* (1930), and *Symbiose der Tiere mit pflanzlichen Mikroorganismen* (1939), containing substantial important evidence which has been utilized in the following pages.

PROTOZOA AND INTESTINAL BACTERIA. To begin with we shall examine a class of facts which is provided for us by cases of the constant presence of lower organisms, protozoa or bacteria, in the alimentary canal of the host. Properly speaking, they are there as parasites, but, through being finally absorbed by the host or through making an effective contribution to its nutrition by means of their own metabolism, they may constitute an essential element in its physiological functioning.

Let us note, first of all, in a very summary fashion, the fact that in various phytophagous insects such as lamellicorns (cock-chafers) and Lucanidae amongst beetles, and Tipulidae amongst Diptera, there is in the larval gut a vast dilatation in which bacteria swarm. It has been definitely established that these bacteria,

cultured *in vitro*, ferment cellulose and thus contribute to the digestion of this substance in the host. The intestinal dilatations in which they accumulate are, in fact, fermentation chambers.

The precise interpretation of the role of these symbionts in the physiology of the organism which houses them presupposes an extremely thorough knowledge of the host's metabolism which, in general, we are far from possessing. I shall cite, as a typical example, the case of the hemipteron, *Rhodnius prolixus*, which is the subject of some remarkable researches by Wigglesworth⁵⁴⁷; the following quotation, which appears to me to be very suggestive, is borrowed from a recent work by this author (1948, p. 743): "But the normal *Rhodnius* always harbours in its gut a symbiotic bacterium, *Actinomyces rhodnii*, which is essential for the nutrition of its host; apparently, it produces certain vitamins of the B group which are deficient in blood. If *Rhodnius* is reared under sterile conditions so as to be freed from its *Actinomyces*, it goes into a state of diapause and will not grow beyond the fourth or fifth instar. Perhaps the vitamins synthesized by this micro-organism provide the raw material for the production of the moulting hormone." These few lines give an idea of the very numerous and important problems, which are also very complex, that arise out of the facts of symbiosis in insects and also in other groups. We shall come to them again in the pages that follow.

INTESTINAL FLAGELLATES OF TERMITES. A particularly striking example is furnished by the flagellates that swarm in the alimentary canal of termites, except in those, the Metatermitidæ, that cultivate fungi. These flagellates are large and highly differentiated (Polymastigina, Hypermastigina). They have been the subject of very many papers; amongst recent ones I shall cite those of Kofoid, Swezy, Cleveland, Hungate, Pierantoni and Grassé. The hind-gut of the termites forms, as in the cases mentioned above, a voluminous sac (especially in the workers) containing a thick, milky liquid in which flagellates and bacteria abound.

The experimental analysis of the role of flagellates in termite digestion was carried out in a particularly precise and brilliant way by Cleveland^{435, 436}, working on a series of species of American termites from California and Panama, etc. Each species of termite has its special flagellate fauna and more than

40 species of these flagellates are known. Their presence is essentially linked up with the digestion of wood. Of the four families of termites, three (*Mastotermitidæ*, *Kalotermitidæ* and *Rhino-termitidæ*) are xylophagous and provided with intestinal flagellates, the fourth (*Termitidæ sensu stricto*) being neither xylophagous nor carrying flagellates.

The flagellates, by invagination at their posterior end (Fig. 68), engulf the particles of wood filling the gut of the termite and digest them. The termites finally feed on the flagellates themselves. The flagellates are thus true symbionts and it is thanks to them that the termites are able to live indefinitely and reproduce on a diet comprising only wood and cellulose (in the form of cotton wool, for instance). Cleveland established this fact by breeding experiments carried out for eighteen months and more. These experiments were made principally on Californian species, *Termopsis angusticollis* and *Reticulotermes clavipes*.

That flagellates are indispensable is shown by experiments on defaunation. They can be completely eliminated in the following ways: (1) by *incubation*, which consists of maintaining the termites at a temperature of 36° for twenty-four hours; (2) by total *fasting* for a sufficient length of time; (3) by *oxygenation*, that is to say by placing them in pure oxygen under pressure. By this last method the death of some species of flagellates results in 30 to 40 minutes when there is a pressure of 35 atmospheres of oxygen, or in a few days at ordinary atmospheric pressure.* The termites are resistant for a much longer period; oxygen is forty to fifty times more toxic to the flagellates than to the termites themselves.

Different flagellates vary in their resistance to oxygen, so that by suitably arranged experiments one can eliminate at will this or that species amongst those that are to be found at any one time in the gut of the termite. Thus, in *Termopsis* there are four species of flagellates, *Trichonympha campanula*, *Leydiopsis sphaerica*, *Trichomitus termitidis* and *Streblomastix strix*. By combining defaunation methods of fasting and oxygenation, Cleveland was able to rid the termites of any one of these species, or all four, and finally by submitting the corresponding termites to

* Cleveland carried out analogous defaunation experiments on parasitic intestinal protozoa (ciliates, flagellates) in cockroaches, earthworms, frogs, urodeles and goldfish. At a pressure of 3·5 atmospheres the cockroaches were resistant for ninety hours, while their intestinal protozoa died in three and a half hours.

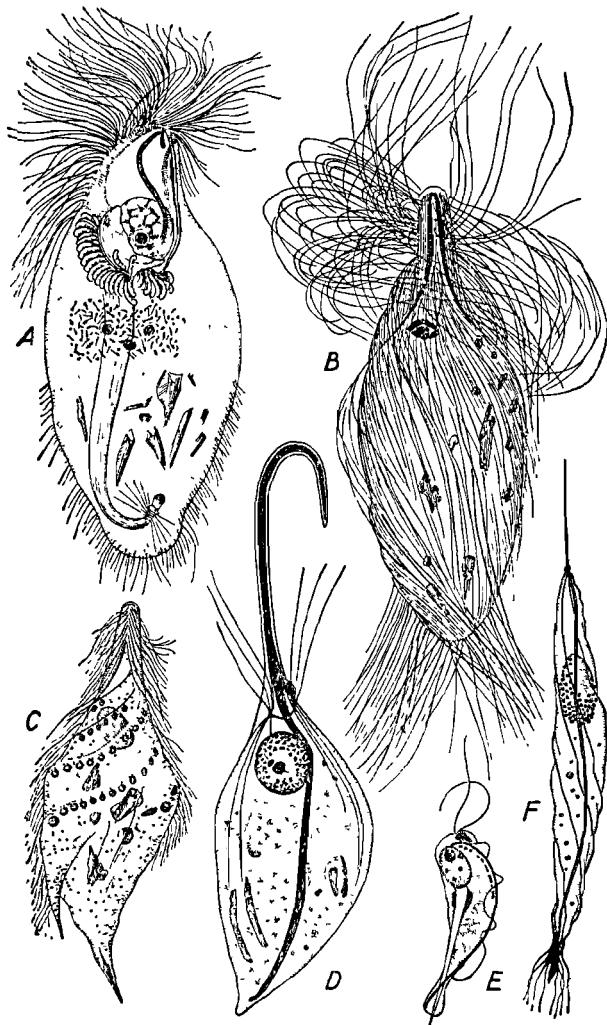


Figure 68. Flagellates in the rectal sac of termites.

A, Jænia annectens; B, Trichonympha chattoni; C, Spirotrichonympha kofoidi; D, Oxyomonas projector; E, Trichomonas trypanoides; F, Pyrsonympha vertens (A-C, E, F after Duboscq and Grassé; D, after Kofoid and Swezy; taken from Noirot and Alliot. Note the particles of wood within flagellates A-D.

a definite diet, particularly to one of wood or cellulose, and seeing whether they could survive under normal conditions, he was able to determine the part played by each species of flagellate.

Here let us only say that in the total absence of flagellates the termites rapidly die off; the same happens if *Streblomastix* is the only species in the gut. With *Leydiopsis* and *Trichonympha* they live. These two species are thus true symbionts which, by their own metabolism, ensure the nutrition of the termite. Analogous experiments carried out with *Reticulitermes flavipes* have shown that the presence of the flagellates is strictly correlated with the

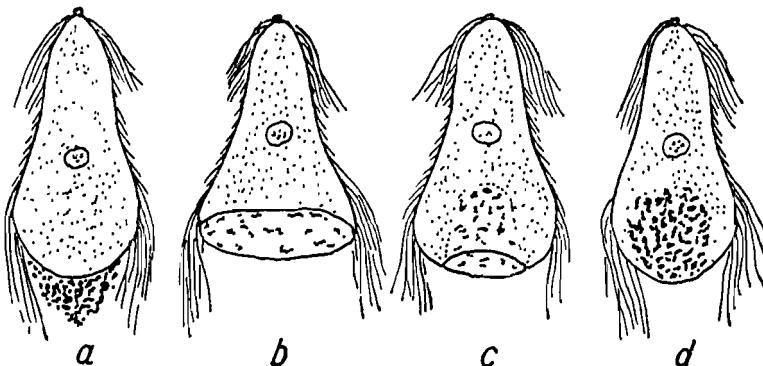


Figure 69. Ingestion of wood by *Trichonympha campanula*, a flagellate in the gut of termites (after L. R. Cleveland).

Ingestion takes place by the invagination of the posterior extremity which engulfs the wood particles.

absorption of wood by the termites. There are, indeed, some castes which, when adult, lose the ability to shred wood owing to the structure of their mouth-parts. Correlated with this there is a loss of flagellates from the intestine; these non-xylophagous castes must then be nourished by other members of the termitarium.

Interest in these researches of Cleveland has since been revived by several workers. Let us cite here the observations made by Pierantoni, who by means of stains analyzed the contents of the cytoplasm of flagellates and found mitochondria there, and, furthermore, some symbiotic bacteria which, according to him, would hydrolyze the carbohydrates of wood into

soluble sugars. Thus there seems to be symbiosis at two levels in the termite-flagellate association.

The gut of the termite itself contains numerous free-living bacteria which must contribute to its nutrition by fixing nitrogen in the form of proteins.

Termites deprived of their flagellates soon die but may be saved by being provided with fresh flagellates either by direct ingestion or by feeding them on the faeces of their congeners. Experiments of this kind have been made by various authors on *Jænia annectens* and *Mesojænia annectens* in *Calotermes flavigollis*, and on *Trichonympha minor* and *T. agilis* in *Reticulitermes lucifugus*; they confirm the earlier researches of Cleveland⁴³⁷ and of Montalenti⁵⁰⁰. Hungate⁴⁶⁵⁻⁴⁶⁸ has studied the metabolism of the flagellates *in vitro* and established that they digest cellulose; according to him, as well as Pierantoni, while they are digesting wood in the termite gut they produce substances such as assimilable glucose which is a source of energy for the termite. Furthermore, the termite thus consumes the oxygen which would be fatal to the flagellates. There is, then, clearly an effective biological symbiosis between the two associated organisms. By quantitative experiments in *Zootermopsis* Hungate came to the conclusion that on the whole, one third of the soluble products of digestion is produced by the activity of the termite and two thirds by symbiotic Protozoa.

How this symbiotic association between termites and flagellates is brought about is what Grassé and Noirot (1945) have sought to determine in detail. The facts vary somewhat according to the groups of termites. In a general way it is possible to distinguish two types of excrement in these insects, one solid or sticky and lacking flagellates, and the other liquid and teeming with these organisms. This last is the *proctodeal food*. Under the influence of various stimuli exercised by its congeners, the termite empties its rectal pouch, and this liquid food is greedily eaten up. Furthermore, during larval moults and, in *Cryptotermes*, the imaginal moult, almost all symbiotic flagellates pass to the exterior. The fresh contamination of individuals defaunated by their moult is achieved by the ingestion of proctodeal food ejected by a non-defaunated termite. After this, a large proportion of the ingested flagellates are digested, which represents an important contribution of proteins to the consumer.

The preceding statements, although very summary, show that the termite-flagellate association, while presenting at first sight all the signs of simple intestinal parasitism, is in reality an effective physiological symbiosis.

INFUSORIA IN THE PAUNCH OF RUMINANTS. Vertebrates provide us with some cases of associations which are

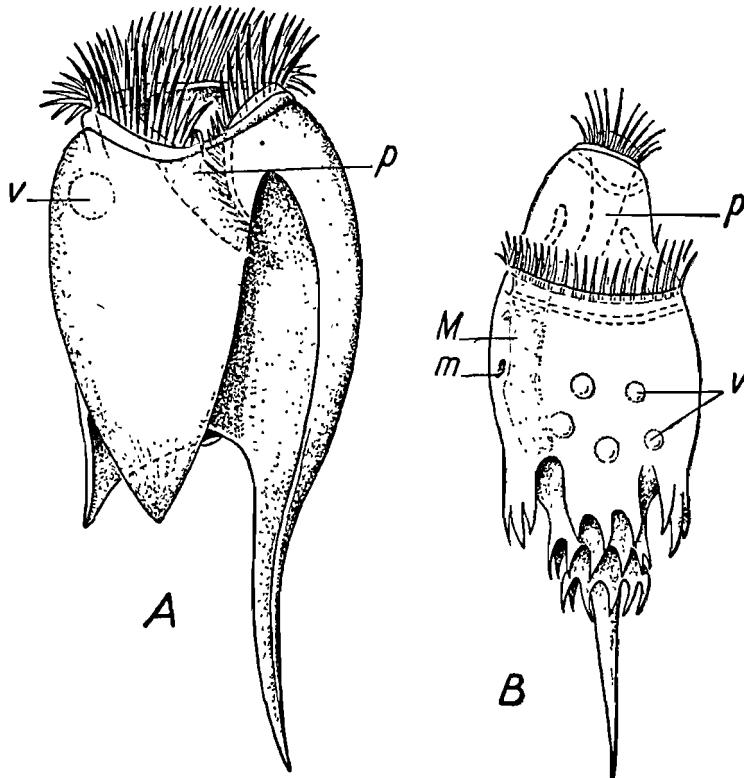


Figure 70. Ciliates in the paunch of ruminants (after Doflein).
A, *Entodinium caudatum*. *B*, *Ophryoscolex caudatus*. *M*, macronucleus;
m, micronucleus; *p*, peristome; *v*, contractile vacuole.

analogous to those above; Protozoa or bacteria regularly live and multiply in the digestive tube of vertebrates and by their own characteristic physiological activity play a role in digestion as effective as that of actual food.

The most striking of these cases is that of the ruminant

mammals, but there are analogous instances in other forms such as the horse, certain rodents (hamster, guinea-pig), and even in the anthropoid apes.

First of all, let us consider the ruminants. Everyone knows how their stomach is differentiated into a series of successive chambers (rumen, reticulum, psalterium and abomasum). In the rumen, where ingested and triturated vegetable matter first accumulates, there habitually occur considerable numbers of ciliates which are of large size, highly differentiated and belonging to the Ophryoscolecidae (*Ophryoscolex*, *Diplodinium*, *Entodinium*), the Isotrichidae (*Isotrichia*) and Enchelidae (*Bütschlia*). Ferber enumerated nineteen species of these ciliates in sheep. Their numbers have been estimated at about 100,000 per cubic centimetre. This ciliate population is established in the rumen as soon as lactation ceases, infestation taking place by means of cysts which had previously been cast out with the excreta. The rate of reproduction is considerable (at least one division every twenty-four hours); nevertheless their final numbers remain approximately constant. They must therefore either be regularly evacuated with the faeces or digested by the host, thus providing the latter with a constant and important contribution of proteins. The ciliates themselves live on vegetable matter contained in the rumen, that is to say, on starch and on cellulose. This nutrition has recently been the subject of much work. Trier⁵⁴² has shown that the ciliates incorporate and digest starch for the most part, but also green cell products. Dry straw, on the contrary, does not suit them; the rumen of a ewe fed on dry oat straw for four weeks becomes completely emptied of ciliates. The residues left by their digestion of cellulose are perhaps utilized by the ruminant.

Among the most recent researches on these questions are those of Hungate⁴⁶⁶. He cultured one of these ciliates, *Diplodinium* (= *Eudiplodinium*) *neglectum*, in a medium obtained from grass and mineral salts and he was able to maintain these cultures for twenty-two months, in the absence of oxygen and at a suitable osmotic pressure. These protozoa are strictly anaerobic. Hungate succeeded in extracting from these cultures an enzyme that would digest cellulose. This *cellulase* is at its optimum activity when the acidity of the medium corresponds to a pH of 5·0, which is equivalent to that of the internal

medium of these protozoa. Glucose is the final product of cellulose digestion; an intermediate product is *cellobiose*, with a corresponding enzyme, *cellobiase*. From this it follows that *Eudiplodinium* is in fact an auxiliary agent in ruminant digestion and that a true symbiotic relationship exists here. Experiments by other workers show, however, that ruminants *defaunated* of ciliates digest almost as much cellulose as those where they are present in the rumen.

Furthermore, from the rate of reproduction of these ciliates in cultures, Hungate has calculated that the proteins with which they provide the host, through themselves being digested, amount to about 20 per cent. of the ruminants' requirements in these substances.

Hungate extended the preceding results to the culture of other species found in the rumen: *Eudiplodinium maggii*, *Diplodinium* (= *Polyplastron*) *multivesiculatum*, *D.* (= *Anoplodinium*) *denticulatum* and *Entodinium caudatum*. The first three of these species also digest cellulose, but not the fourth, nor, moreover, species of *Isotrichia* or *Bütschlia*. Species of *Diplodinium* alone, then, must be regarded as true symbionts.

These results, like those from the work of numerous other authors (Schwartz, 1925, 1926, Ferber⁴⁴⁷, Mangold and his pupils), the details of which we cannot go into here, show the complexity of the relationships between the ruminant and its ciliate population, relationships which may partly be considered as symbiosis, partly as parasitism.

In the horse the cæcum is populated by ciliates and these by themselves represent a notable contribution of protein. In the hamster the stomach is subdivided into two chambers and the one next to the œsophagus contains ciliates belonging to the same types that occur in ruminants. In anthropoid apes the ciliates are localized in the large intestine, and Reichenow (1920) was able to show that they digest cellulose there, and after multiplying very considerably are finally absorbed by the host.

ROLE OF BACTERIA. In addition to the role of ciliates in digestion in these various mammals, bacteria must also be taken into account. Symbiotic activities have been shown to occur with them too. Amongst the researches carried out on this subject I shall cite those of J. Pochon⁵²⁵⁻⁵²⁶, who, working on ruminants,

isolated and maintained a pure culture of a cellulolytic bacterium, *Plectridium cellulolyticum*, from the rumen. The cultures were made in a medium as close as possible to the content of the rumen, and, in particular, anærobic. *Plectridium cellulolyticum* is motile, rod-shaped, ciliated, gram positive, and a facultative anærobe; the optimum temperature for its culture is 40° C. It is only cellulolytic under anærobic conditions. It is capable of fermenting various sugars and alcohols under anærobic conditions; in anærobic culture it is peptidolytic but not proteolytic.

Similar questions which arise in certain birds have recently been dealt with by Mangold and his pupils. In the grain-eating birds (fowls, pigeons and doves, and forest passerines) there are paired intestinal cæca, of greater or lesser extent, which are absent in birds of prey. In these cæca bacteria assist in the digestion of cellulose.

ZOOCHLORELLÆ AND ZOOXANTHELLÆ. A classical and widespread example of symbiosis is that of zoochlorellæ and zooxanthellæ—unicellular algæ that are regularly found in the cytoplasm of various protozoa and in the tissues of invertebrates belonging to different groups.

The constant occurrence of green or yellow corpuscles in the tissues of certain invertebrates was pointed out as early as 1850; their interpretation as intracellular algæ was proposed by Cienkowsky⁴³⁴ in 1871, then by Gesa Entz⁴⁴⁴ and K. Brandt⁴²⁸; it was confirmed in particular by Beijerinck⁵⁵⁶ in 1890 and by Dangeard⁴⁴⁰. Nevertheless, this opinion was opposed for quite a long time, notably by E. Ray Lankester. An excellent summary of these discussions is to be found in a *résumé* of the subject which we owe to Bouvier⁴²⁷.

The yellow bodies (*zooxanthellæ*) are met with in marine animals, the green ones (*zoochlorellæ*) principally in freshwater organisms. Here are some examples of animals where they are present:

PROTOZOA. Various naked amoebæ (*Ameba viridis*) and also shelled ones (*Diffugia piriformis*, *D. nodosa*); some Foraminifera (*Trichosphaerium sieboldi*, *Peneroplis pertusus*, etc.). A large number of Radiolaria, notably the Spumellaria (*Collozoum*, *Sphaerozoum*), and Heliozoa (*Acanthocystis*, *Actinosphaerium*, *Heliophrys*, etc.); flagellates (*Anisonema viridis*, *Noctiluca*, *Lepto-*

discus); very numerous ciliates (*Paramecium bursaria*, *Frontonia leucas*, *Ophrydium versatile*, *Stentor polymorphus*, *Trichodina patellæ*, etc.).

SPONGES. *Spongilla viridis*.

CŒLENTERATES. *Hydra viridis*, *Halecium ophiodes*, some medusæ (*Cotylorhiza*, *Sarsia*, *Rhizostoma*), some Siphonophora (*Veabella*, *Porpita*), Milleporina, Alcyonaria (gorgonians), Hexacorallia (numerous sea anemones), etc.

CTENOPHORA. *Euchlora*.

TURBELLARIA. *Convoluta*, *Vortex viridis*, etc.

ROTIFERA. *Ascomorpha helvetica*, *Itura aurita*, etc.

ANNELIDA. *Eunice gigantea*.

BRYOZOA. *Zoobothrium*.

MOLLUSCA. *Tridacna*, *Elysia viridis*.

The plant nature of these yellow or green bodies, which are generally spherical with a diameter of 3 to 10μ , is seen in the following characters:

1. In structure they are like a unicellular alga: one can actually recognize a cellulose membrane, a chromatophore which occupies most of the cytoplasm, a pyrenoid, a nucleus (visible on staining). There are also starch grains and metachromatic corpuscles.

2. Their presence is not invariable in most of the cases cited above. If, indeed, there are some species that are always found to be infected, such as *Hydra viridis*, *Convoluta*, etc., and some that are nearly always infected, such as *Paramecium bursaria*, and *Ophrydium versatile*, there are others that are only incidentally so, or only in certain localities. Individuals of *Noctiluca*, for instance, contain zooxanthellæ in the Indian Ocean but not in our seas. *Trichodina patellæ*, heavily infected on the Normandy coast (Cape de la Hague), is never so at Wimereux.* Thus it cannot be said that these bodies are organites indispensable to the species in which they are found.

3. It has been possible to observe the process of infestation of the species in which they occur. F. le Dantec ⁴⁸⁷ is noted for having done this in the case of *Paramecium bursaria*, after taking the necessary precautions. After passing a green individual through several lots of filtered water he crushed it so as to set

* There is a tendency nowadays to regard the species of *Trichodina* living on *Patella* in the two places as distinct.

the zoochlorellæ free and then took a *Paramecium* from a colourless culture and placed it in the drop containing them. Under the microscope he watched the ingestion of the zoochlorellæ by this ciliate. They were not digested and he saw them multiply by dividing into four. After a few days the individual *Paramecium*, which had been colourless to begin with, was green. Schewiakoff made an analogous observation with *Frontonia leucas*, but Famintzin⁴⁴⁶ contested its authenticity. Doflein⁸² has infested *Amœba vespertilio* with chlorellæ of *Frontonia*. Awerintzeff has similarly infested *Dileptus anser* with those from *Stentor viridis*. There are also the experiments carried out by Pringsheim on the zoochlorellæ of *Paramecium bursaria*; he was able to reinfect the ciliates after having blanched them.

4. They can survive for a long time outside the species that harbours them, as was shown notably by Cienkowsky, Brandt and Schewiakoff.

5. Their division, very easily seen today in stained material, was first seen *in vivo* by numerous observers, namely Beijerinck and Famintzin. The latter tried to get them to multiply outside the ciliates. He was only successful after many difficulties. To do this he crushed a green *Paramecium* between a slide and a coverslip. The zoochlorellæ tended to adhere to the coverslip under which he passed a drop of saline (containing 1/1,000 of potassium acid phosphate and 1/1,000 of ammonium sulphate). In this medium he saw two successive quadruple divisions, with an intervening period of growth.

6. One can deprive the animals of their algæ, blanch them, either by keeping them in darkness for a long time, where they will cast them out, or by a method described by Whitney⁵⁴⁵ for *Hydra viridis*, which consists of adding 0·5 to 1·5 per cent. of glycerine to the water containing them. The individual *Hydra* blanched in this way flourishes and produces buds; it is interesting to note that it does not become reinfested when placed in an aquarium containing green hydras.

They are then indisputably autonomous algæ. Beijerinck identifies the zoochlorellæ with a free-living alga, *Chlorella vulgaris*, which he has been able to culture in water to which has been added 8 per cent. gelatine, 0·8 per cent. peptone, 0·2 per cent. asparagine, and 1 per cent. cane sugar; it is one of the Proto-coccaceæ. He once succeeded in culturing zoochlorellæ extracted

from ciliates; the culture set up was maintained without difficulty, and was shown to be identical with the free-living *Chlorella*. Famintzin verified these results for free-living *Chlorella* which he cultured in saline, as well as for the zoochlorellæ of *Paramecium bursaria*. The zoochlorellæ of different animals are, moreover, not necessarily all of the same species. Genevois⁴⁴⁹ succeeded in culturing the zoochlorellæ of various turbellarians (*Dalyella viridis*, *Typhloplana viridata*, *Castrata viridis*) and identified them as *Chlorella vulgaris*. According to Chodat⁴³³ the cultured algæ belong to *Protococcus* and resemble a species, *P. ophrydii*, isolated by him from *Ophrydium versatile*. Chodat, as we know, was a great specialist in culturing the lower algæ *in vitro*.

The zooxanthellæ are said to be Cryptomonadineæ. Schaudinn⁵³⁵ places those from Foraminifera in the genus *Cryptomonas* (*C. brandti* in *Trichosphaerium sieboldi*, *C. schaudinni* in *Peneroplis pertusus*). Keeble⁴⁷⁹ considers the green bodies of *Convoluta viridis* to belong to *Chlamydomonas*, characterized in the flagellospore stage by four flagella and a stigma.

In the Metazoa natural contamination often occurs even in the egg, as Hamann observed in *Hydra viridis* in 1882. It is thus a hereditary infection. Hadzi⁴⁵⁷ saw this same transmission by the egg in another hydroid, *Halecium ophiodes*; the zooxanthellæ, which tint the endodermal cells brown, pass into the developing oocyte. In the same way there is regular contamination of the egg in *Millepora*, according to observations made by Mangan⁴⁹⁰.

But, according to the researches of Keeble and Gamble⁴⁷⁸, in *Convoluta viridis*, where the algæ are constantly present, it is otherwise. The young individuals of *Convoluta*, on leaving the cocoon, are colourless; but green bodies exist on the surface or in the interior of the cocoons. It must be noted, too, that workers (Georgievitch, Sekera, von Graff) who have studied the embryonic development of *Convoluta* have not observed the green bodies during the development of the embryo. By taking young individuals of *Convoluta* as soon as they hatched and rearing them in carefully filtered water Keeble was able to keep them in a colourless state for a month, while those that were kept in ordinary sea water became green. By adding green individuals of *Convoluta* to a culture that had remained colourless the latter

turned green in three days. When the embryos have hatched, the empty cocoons become filled after three weeks with small, green, quadriflagellate bodies (*Carteria*, a subgenus of *Chlamydomonas*). It follows that *Convoluta* is infected by green bodies not with the structure of the adult, but in a flagellate state which is a great deal smaller and very difficult to see.

According to the observations of Brandt and Famintzin, the young individuals of *Collozoum* have no xanthellæ and contamination must be made by very small flagellospores which have not yet been seen; but once they have reached the state of yellow bodies in the ciliate or radiolarian, reproduction takes place by binary or quadruple fission. It seems to be the same with *Trichodina*.

Let us consider the nature of the relationships between zoochlorellæ or zooxanthellæ and their hosts. Clearly there is, in general, a symbiosis profitable to both. Brandt⁴²⁸ in particular has developed this conception. The algæ are said to find effective protection in the animal and to lodge in it in such a way as still to receive light. Zooxanthellæ are particularly common in pelagic animals with a transparent surface (Radiolaria, medusæ, Ctenophora, etc.); they find carbonic acid in the animal cell, which is rare in the superficial layers of the sea. On the other hand, they release oxygen, aiding the respiration of the animal tissues. They produce starch, which may be utilized by the animal; or else, since this reserve substance may only be formed in an insoluble state, the soluble and assimilable products which lead up to it may be directly utilized. The animals which normally contain yellow or green bodies (Radiolaria, *Convoluta*) thus no longer feed directly, but indirectly on the products of the synthesis performed by their symbiotic algæ, and the latter, on the other hand, can only with difficulty live in isolation and freedom. Thus there is constituted a new biological unit, the *phytozoon*.

As early as 1889 Famintzin opposed many of Brandt's conclusions. According to his observations, and contrary to what Brandt said, the Spumellaria (*Collozoum*, etc.) directly ingest solid prey (even copepods) with the help of their pseudopodia, not only when they are young and lack xanthellæ, but even when they are adult. And when they are starved, the radiolarians with xanthellæ survive for a long time by digesting the xanthellæ

themselves. The starch which has sometimes been observed in radiolarians comes from these resorbed xanthellæ. It is the same with sea anemones, according to Famintzin. Most animals with chlorellæ or xanthellæ lose their colour after a certain time if they are kept in darkness (ciliates, *Hydra* and sea anemones can be decolourized in this way), their algæ being cast out in a brownish and half-digested condition.

Similar conclusions were reached by Keeble and Gamble working on *Convoluta*. These authors observed, first of all, that, contrary to the accepted opinion, this turbellarian ingests solid bodies (diatoms, algæ, spores, bacteria), at least when it is young, by means of a ventrally situated mouth in the posterior region, which leads into the parenchyma. It feeds independently and not by means of the green bodies. There is evidently profound adaptation of the green bodies to *Convoluta*. According to Keeble, the green cells are finally incapable of a free-living existence, their cell wall atrophies and their nucleus degenerates. Under normal conditions they live thus, but under conditions of famine they are digested by *Convoluta*. The relations between the animal and its green cells are considered to be complex by these authors, and cannot altogether be described as a symbiosis. Keeble states that the green cells act as a sort of excretory system for *Convoluta*. The relations between green cell and animal change with their development, passing from a symbiotic relationship to one in which the animal is parasitic on the algal cells.

It follows from all these facts that the association of algæ and animals is not invariably a true symbiosis and that in certain circumstances the animal lives as a parasite at the expense of its algæ.

Let us note finally that in addition to zoochlorellæ and zooxanthellæ some Cyanophyceæ have regularly been found in certain Protozoa, principally in the rhizopod *Paulinella chromatophora*, where they are present as curved and elongated forms. Pascher (1929) maintained these organisms *in vitro*, where they divided successfully.

MYCETOMES OF INSECTS. We now come to another category of associations between animals and the lower fungi (or bacteria), which take very various forms and have been principally studied in recent decades. We shall first examine one of the

earliest known examples of these, the interpretation of which has gradually become more precise. These are the structures which are generally known as mycetomes in insects.

It is many years since these mycetomes were first observed, but they received a definite interpretation only in 1910. As early as 1858 Huxley⁴⁶⁹ described in aphids a rather variable organ situated in the abdomen beside the ovaries (Fig. 71 *m*), with cells crammed with inclusions that were generally spherical, resembling a vitellus; hence the name *pseudovitellos* given to this

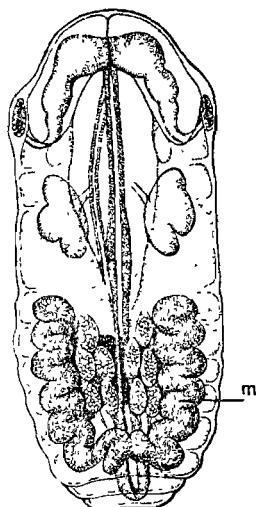


Figure 71. Larva of a green-fly, *Drepanosiphum platanoides*, showing the green body or mycetome, *m* (after Balbiani, taken from Henneguy).

structure. Balbiani⁴²⁴ studied it a little later and gave it the name of *pseudova*, or *green body* on account of its pigmentation. He saw, besides, that it was derived from a particular structure, constantly to be found at the posterior pole of the egg and called by him the *polar mass*. Metchnikoff⁴⁹⁶ followed out its whole development and called it the *secondary vitellus*. This body, which has been seen by numerous observers, gave rise to the most diverse hypotheses until its true nature was established independently and almost simultaneously by Pierantoni⁵¹⁰ and Súlc⁵⁴⁰. In the inclusions of the green bodies, these authors

recognized yeasts or *blastomycetes* (*Schizosaccharomyces aphidis*), which appear thus as living habitually in a stable relationship with the aphids.

Analogous structures were already known in the Coccidæ, and had even been correctly interpreted. They were pointed out, indeed, by Leydig⁴⁸⁹ about 1850, studied by Metchnikoff and other workers, and it was Putnam who, in 1877, recognized that they contained plant elements, and this was confirmed, ten years later, by Moniez⁴⁹⁹. In 1895 Lindner formally identified yeasts in the coccid *Aspidiotus nerii*. Vejdovsky (1906), Conte and Faucheron⁴³⁹ independently gave the same interpretation,

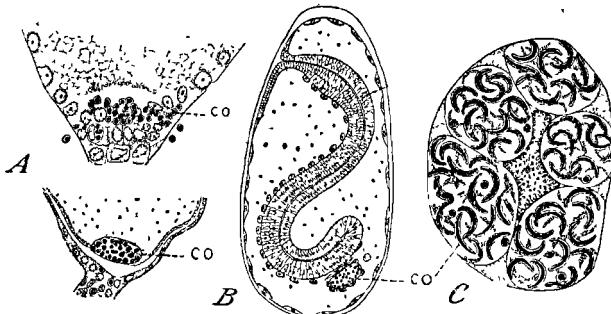


Figure 72. Symbiotic yeasts and mycetocytes in Homoptera (after Pierantoni).

A, two sections showing the penetration of the yeast corpuscles, *co*, into the developing oocyte of *Icerya purchasi*. *B*, embryo of *Icerya purchasi* with its mass, *co*, of embryonic corpuscles. *C*, a mycetocyte of *Dactylopius citri*, with corpuscles in the form of crescents.

which Pierantoni confirmed by relating them to analogous structures in the aphids.

Apart from these two groups and under different forms similar structures occur in the Aleurodidae (where Signoret perceived them in 1867), the Psyllidae (where they were pointed out by Metchnikoff), the cicadas and the Cicadellidae.

Let us take a first glance at these facts by studying them in a coccid, *Icerya purchasi*, as Pierantoni did, and by following out the insect's development. In the ovary, at the posterior pole of the developing oocytes, about a hundred spherical bodies (Fig. 72*A*, *co*) are regularly present; they are very easily stained; they also occur elsewhere in the general body cavity, and, more

abundantly, in the cytoplasm of large cells forming yellowish organs situated on either side of the intestine and limited by a flattened epithelium. In these organs the corpuscles in question are actually dividing. Thus they form, at the posterior pole of all the eggs laid, a constant or polar mass like that seen by Metchnikoff. At the beginning of embryonic development this polar mass is enveloped by special cells, called *mycetocytes* by Súlc; they first adhere to the blastoderm, then fall into the vitellus. They attach themselves then to the germ band (Fig. 72B); finally they come to be situated dorsally, in the posterior region of the embryo, and divide into two masses, placed on the sides of the proctodæum, and these will become the yellow bodies pointed out at the beginning of this description. While this is taking place the blastomycetes are actively multiplying; the mycetocytes become enormous; their compressed nuclei are irregular in shape. Although they are crammed with these fungi, the mycetocytes live and flourish, continuing to divide mitotically. This mass of cells with their blastomycetes constitutes the mycetome.

Pierantoni extracted the mycetome of the animal, dissociated it, and placed the fragments in an 8 per cent. solution of gelatine to which 20 per cent. beet sugar had been added. At the end of four days, during which the medium was kept at a temperature of 15° C., he obtained colonies of saccharomycetes, which he considered to have been derived from the intracellular bodies, with a type of budding characteristic of yeasts, even though in the mycetocytes the elements multiply by equal division. These yeasts are aerobic and, moreover, the yellow bodies are abundantly supplied with tracheæ.

The blastomycetes in the cells are not always spherical; thus, in *Dactylopius citri*, they appear as crescents in each mycetocyte (Fig. 72C, co) and are united in clumps in the intracellular spheres.

The blastomycetes occur in male embryos as well as in female ones, but in the male the mycetome gradually vanishes.

Buchner⁴³⁰ completed the investigation by making a direct study of the mycetome in the different groups of insects cited below and his observations coincide with those of Pierantoni. He studied aphids (*Drepanosiphum*), Coccidæ (*Lecanium corni*), Aleurodidae (*Aleurodes* on the maple), Psyllidæ (larva of the

willow psyllid), cicadas (*Cicada orni* from Japan and Liberia), and Cicadellidae (*Aphrophora salicis*). From them he extracted various blastomycetes, the taxonomic descriptions of which are given in his memoir (genera *Saccharomyces*, *Oospora*, *Kerminicola*, *Coccidomyces*, etc.), with a note of the cultures that were made of them. These observations were extended and systematized in his general work³.

The mycetome shows different arrangements which Buchner classifies as follows:

1. The least differentiated is that of certain Coccidae, Jassidae and Fulgoridae, where the blastomycetes are situated in cells dispersed in the fat body without differentiation of a localized mycetome (Lecaniidae, Diaspididae). The presence of blastomycetes is none the less constant, whatever may be the source of the individuals.
2. The second stage is that where there is a differentiated mycetome (Aphididae, Aleurodidae, Coccidae, *Icerya purchasi*, *Dactylopius citri*) enclosing a single form of blastomycete (monosymbiont species).
3. Certain species are disymbionts, harbouring simultaneously two types of blastomycetes, one in dispersed mycetocytes, the other in a differentiated mycetome (in *Cicada orni*), where all the cells are fused into an enormous multinucleate syncytium in the meshes of which the blastomycetes are situated.
4. Both forms of blastomycetes of a disymbiont species dwell in two distinct superimposed mycetomes (Cicadellidae, *Ptyelus lineatus*).
5. The two mycetomes of the preceding case are fused into one (Liberian cicada, Psyllidae).
6. Finally, it is possible for three species of blastomycetes to exist simultaneously, two in a mycetome, the third in a dispersed mycetocyte (Psyllidae) or even in the same mycetome (*Aphalaro calthae*).

Whatever the various topographical complications may be, the general characteristics common to all cases are that infection is absolutely constant in all localities; that it is transmitted from one generation in the course of oogenesis; that it is localized during development in definite cells which finally come to constitute a special organ with a definite structure and position.

The presence of the mycetome in all the insects enumerated above is correlated with a way of life that is common to them, that of sucking the juices of their food plants.

What, now, are the physiological relations of the blastomycetes and their hosts? All the evidence goes to show that the former exercise no adverse influence on the latter; they have absolutely no significance as pathogenic organisms. It is no less evident, moreover, that they find a favourable culture medium in the mycetocytes as well as excellent means of disseminating themselves through the reproduction of their hosts.

Súlc put forward the hypothesis that the blastomycetes might play a part in the breaking down of urates. Pierantoni has different views. The constancy and precise localization of the blastomycetes in whole groups of insects indicate to him that they fulfil an important physiological function in the host's body. Now, all the insects in which they are to be seen, and primarily the aphids, feed on plants from which they extract considerable quantities of sugary substances and starch. The aphids cannot even make use of all the sugar they ingest and reject large quantities of it in the form of *honey dew*; we have seen the relationships which have been established on this account between the aphids and ants. According to Pierantoni, the blastomycetes produce enzymes which help in the digestion of sugar, and they themselves find excellent conditions for nutrition through the presence of sugar in the tissues. The tracheæ of the mycetome may serve both for supplying oxygen to these ærobic organisms, and for dispersing carbonic acid. The constant association of blastomycetes with these insects, the character of the preceding relationships, and their regular transmission during oogenesis, constitute for Pierantoni the characteristics of a *physiological hereditary symbiosis*.

OTHER EXAMPLES OF SYMBIOSIS IN INSECTS. Numerous examples of symbiosis between insects and lower organisms, Protozoa or bacteria, are now known and have been more or less thoroughly investigated. Work on these problems has multiplied in recent decades and has gradually become more precise. It is not always easy to distinguish a true symbiont from structures that really belong to the organism containing them. The essential and distinctive criterion is their culture *in vitro*; but the difficulty in this case is to eliminate other organisms of a

commonplace character and to be certain that one is indeed culturing the presumed symbiont.

A first group of facts, which are, moreover, rather numerous, relates to insects with burrowing larvæ which feed on leaves, seeds, wood or putrefying debris. The symbionts are localized in a more or less well-defined fashion within a mycetome of variable structure. They are usually transmitted from one individual to another by contamination of the egg, as we saw above.

Such is the case with *Dacus oleæ* (Tryptidae), a parasite of the olive, in which there arise from the gut, in front of the proventriculus, four large diverticula swarming with bacteria (*Bacterium savastanoi*, *Ascobacterium*) that also occur in lesions produced by the insect on the tree.

Keilin (1921) has also discovered a bacterial symbiosis in a dipteron, *Dasyhelea obscura* (Ceratopogoninae), a parasite of the elm. Symbiosis is intracellular here, as the researches of Stummer showed. Similar facts are now known in several families of Coleoptera: Anobiidae, Cerambycidæ (where the symbiotic organism is a saccharomyces), Curculionidae, Buprestidae, Lyctidæ and Cucujidæ. I shall mention, in particular, among the very numerous researches carried out on insects, those of W. Schwarz (1924) on the mycetome of aphids and Coccidae, in which the various morphological and physiological aspects of the problems of symbiosis are clearly brought out in the light of experiment and culture.

One long-discussed case is that of the *bacteroids*, which are regularly found swarming in certain cells of the fat body in the Blattidae. First pointed out by Blochmann⁴²⁶, these structures have been interpreted by several authors (Cuénot, Henneguy, Prenant) as kinds of crystalloids having only a purely external resemblance to bacteria. Mercier⁴⁹⁴, on the other hand, regarded them as truly symbiotic bacteria and gave them the name of *Bacillus cuenoti*; he found them again in the embryo. By extracting them from embryos still enclosed in oothecæ, taking meanwhile the most rigid precautions against contamination, he succeeded in culturing them. Javelly, repeating the experiments, did not, however, obtain any culture and considered that Mercier had cultured an impurity from the surface of the ootheca, probably *Bacillus subtilis*. Buchner, on the contrary, believed that it was clearly a question of symbiotic

bacteria which are to be found in various Blattidæ, indigenous and exotic. Contamination occurs early in development, by means of the eggs. This example shows how difficult these problems are.

The ants provide us with the same kind of data, here, too, pointed out in the first place by Blochmann (1884) in *Camponotus ligniperdus*, then in *Formica fusca*. Here it is the cells of the intestinal wall that are invaded by bacteria. Strindberg (1913) studied this tissue and concluded for his part that he was dealing with mitochondria; but Buchner, who repeated this work with various species of *Camponotus*, thought that true symbionts were present; contamination takes place by precocious infection of the oocytes and is thus also produced in the workers.

Let us note here that apart from insects the same kind of thing occurs in a prosobranch mollusc, *Cyclostoma elegans*. As early as 1858 Claparède studied concretions in one of its glands, and Garnault, in 1887, described large cells there, regularly containing, in addition to the concretions, numerous bacteroid structures. Mercier repeated the work and agreed with Garnault in considering them to be true bacilli. From the gland, he obtained a culture in which the elements appeared to be identical. Recent work (1933-1936), notably by Buchner, has established that it is, indeed, a question of bacteria and that here there is true symbiosis. This has also been found in various other species of *Cyclostoma* and in related forms (Annulariidæ), particularly *Tudora putre* in Cuba and *Chondropoma rubrereticulatum* in Haiti. Symbiotic bacteria have also been found in the excretory organs of various oligochaëtes (*Lumbricus terrestris*) and Hirudinea (*Hirudo medicinalis*, *Hæmopsis sanguinea*).

Let us remember, too, the authentic existence of symbiotic fungi in the kidney of *Molgula* (compound ascidian). Pointed out by Lacaze-Duthiers, they were studied by Giard and named *Nephromyces* by him. More recently, they have been the subject of research by Buchner at Naples. This worker succeeded in observing the formation of zoospores and of gametes, but did not manage to obtain a culture of them, nor to see the onset of infection in *Molgula*. The affinities of the fungus are still uncertain (Oomycetes, Chytridiales or Acanthistales).

EXAMPLE OF SYMBIOSIS IN BLOOD-SUCKING ANIMALS.
We have now another series of facts about symbiosis correlated

with a definite type of life, that of animals feeding on the blood of vertebrates.

The first example of this kind is provided by a fly, *Glossina*. Roubaud⁵³⁴ studied its symbiotic yeasts, which had already been pointed out by Stuhlmann. In the adult tsetse fly there is an area of thickened epithelium in the mid-gut which shows, macroscopically, greyish spots or bands. Sections at this level show cells three to five times higher than those nearby, and thus forming extensive papillæ. They are packed with bacillary structures, 3 to 5 μ in length. These elements, on being freed by the breaking down of the cells, fall into the lumen of the intestine. Smears show that they multiply by a budding typical of yeasts and Roubaud relates them to the *Cicadomyces* of Šulc. The cells that contain them are then true mycetocytes and these structures occur with unfailing regularity in all the species of *Glossina* studied by Stuhlmann and Roubaud. The latter found them also in larvæ and followed their fate through to pupation. In the larva, which lives in the maternal uterus, the mycetocytes are localized at the level of the proventriculus. Roubaud supposes (without being able to give formal proof) that the yeast is transmitted from one generation to the next, either by the egg, as in the Hemiptera, or, preferably, by the maternal lacteal secretion since he has not been able to find any trace of it in the oocytes. These elements are not abundant in the larvæ; they multiply in the adult when digestion becomes active. Roubaud relates their presence to the strictly hæmatophagous diet of *Glossina*. In support of this theory, he makes the observation that one finds neither yeasts nor mycetocytes in the Stomoxydinæ to which *Glossina* is related phylogenetically, nor in the Tabanidæ, the Culicidæ, larvæ of *Auchmeromyia*, nor species of *Lyperosia*, all forms which are not strictly hæmatophagous. On the contrary, in the Pupipara, a group which is quite distinct in origin from *Glossina* but, like it, adapted to strict hæmatophagy, one again finds, by a remarkable instance of convergence, mycetocytes and yeasts. This was shown by the researches of Sikora on *Melophagus* and those of Roubaud on *Liptotena* and the Hippoboscidæ. Observations of the same nature have been made on *Lynchia maura* and on *Ornithomyia avicularia*, which live on birds and the Nycteribidæ (a family of bats).

There must be then, according to Roubaud, a close correlation between strict hæmatophagy and the presence of intestinal symbionts: the enzymes of the yeasts must facilitate digestion of proteins and corpuscles of the blood. This suggestion of Roubaud's finds support today in the fact that a whole series of symbioses has been found to occur regularly in various other hæmatophagous types. Such is the case with certain Hirudinea such as *Placobdella catenigera* and *Piscicola geometra*, where the symbionts are situated in the œsophageal diverticula. The same is true of numerous acarines (Gamasidæ, *Argas*, *Ornithodoros*, *Ixodes*), where the organisms are localized in the malpighian tubes and the intestinal epithelium. These acarines are, moreover, the vectors of pathogenic organisms (notably *Rickettsia*), and propagate diseases such as spotted fever, etc. The presence of symbiotic micro-organisms thus appears to be at least a very widespread condition in the animals that live on the blood of vertebrates.

We find it again in lice (*Pediculus humanus capitis*, *P. humanus corporis*, *Phthirus pubis*), where it has been studied particularly by Buchner, and also in insects that feed on keratin, such as the Mallophaga which live on the feathers of birds (e.g. *Diplourus baculus* on the turtle dove, also studied by Buchner).

ANIMAL LUMINESCENCE AND SYMBIOSIS. Another class of facts shows a close correlation between symbiosis and animal luminescence. The latter appears in many different cases to be determined by the action of symbiotic bacteria transmitted from one generation to the next.

But it is by no means true to say that all the phenomena of luminescence originate from symbiosis. There are, first of all, those which are due to occasional contamination by luminous bacteria and which fall into the category of simple parasitism. Thus we see the decomposing bodies of fishes become luminescent through certain saprophytic bacteria developing in their tissues. Such bacteria can infect the living animal. Thus Giard and Billet (1889), having found some luminous individuals of *Talitrus* (Amphipoda) on the sea shore, recognized that it was a case of bacterial infection. By cutting an antenna on a slide, collecting a drop of the blood and inoculating other individuals of *Talitrus*, they saw the latter become luminous, and were able to repeat the experiment again and again. They

cultured the bacterium itself in a pure state and obtained luminous cultures. There could be no question here of symbiosis. It is simply a case of infectious parasitism.

The luminescence of a freshwater prawn, *Xiphocaridina depressa*, observed by Yasaki⁵⁴⁹ in Japan, belongs to the same category. This worker recognized that it was caused by a pathogenic bacterium (vibrion), which could be easily cultured, and on being inoculated into other Crustacea or insects rendered them luminescent but killed them rapidly.

Similarly, Issatchenko⁴⁷¹ was able to culture *Bacterium chironomi*, which makes chironomids luminous. He observed some swarms of these insects which were entirely luminous; the insects rapidly died off and the infection must have been produced in the larval stage.

Leaving these cases of accidental infection on one side, we come to those in which luminescence is a normal phenomenon in a species, either permanent or intermittent in character. One of the chief initial investigators into this phenomenon was Raphael Dubois. It is necessary in these cases to distinguish between two categories of facts: luminescence may be an intrinsic property of the animal or else caused by a symbiotic bacterium. To the first alternative belong the marine Protozoa, such as *Noctiluca*; other planktonic invertebrates; various luminous insects, notably the Elateridae such as the cucujo, *Pyrophorus noctiluca*, of the Antilles, studied by Dubois; various abyssal fishes and probably also a bivalve mollusc, *Pholas dactylus*, which discharges a luminous liquid into one of its siphons. In this last animal Dubois was able to isolate two substances in solution, one being *luciferin* and the other an enzyme, *luciferase*. The mixing of the two solutions produces light and these facts have since been extended and confirmed by Newton Harvey⁴⁵⁹. On this basis, Dubois tended to generalize about the interpretation of animal luminescence. But another theory, based on many precise researches, has been developed by Pierantoni, according to whom luminescence in many of the animals showing it is due to the existence of a constant symbiosis with photogenic bacteria. He was led to this interpretation by his researches into the mycetomes of insects. One may admit that both conceptions are valid according to the cases concerned. The demonstration of luciferin and luciferase

would be an argument in favour of the first, their absence a presumption in favour of the second.

Let us now look at the facts invoked in support of the symbiotic interpretation. Pierantoni⁵¹¹⁻⁵¹³ was, first of all, struck by the parallelism between the structure of the luminous bodies in *Lampyris* (a glow-worm) and that of certain mycetomes of aphids (*Aphrophora*). In the former animal the luminous organs are constituted by a parenchyma the cells of which are crammed with little bacteriform corpuscles possessing the staining characteristics of bacteria. Furthermore, the egg of the glow-worm, which is also luminous, contains the same bacteroids. Starting with the luminous organs of *Lampyris*, Pierantoni stated that with peptone agar he obtained cultures of two different bacteria, but he does not say whether the cultures were luminous. It remains extremely difficult to affirm that the organisms cultured are indeed the intracellular corpuscles seen in the first place. The interpretation of luminescence in *Lampyris noctiluca* as the result of symbiosis is not generally accepted. It is firmly opposed by various highly qualified workers, notably Vogel (1922), Trojan (1929), Novikoff (1939), etc.

LUMINOUS CEPHALOPODS. But the Italian author developed his researches principally with cephalopods. He has shown, first of all, from the morphological point of view, that there is an intimate tie between the organs known as the accessory nidamental glands and the luminous organs near the anus and the ink sac. These glands have, in reality, no connection with the formation of the egg shell and do not emit an actual secretion. They exist in general only in the females, where they are next to the true nidamental glands, but they are found also in the males of certain species (*Loligo forbesi*). In their most simple form (*Loligo*) they consist of a mass of epithelial ducts embedded in connective tissue, and, within the lumen of these ducts, a mass of granulations is always to be seen, which, according to Pierantoni^{514, 517}, are the bacteria which he succeeded in culturing. In cuttlefish the structure of the accessory nidamental gland is complex; indeed, it comprises ducts of three different colours (white, yellow and orange-red), filled with bacteria different in appearance in each of the three cases (cocco-bacilli, bacilli and cocci). There are also many bacteria in the epithelial cells and the connective tissue. They are said to be

present on the surface of the egg when it is laid, and between the layers of the shell. They would thus be transmitted from one generation to the next, would be localized and would multiply in the accessory nidamental gland, which would be a specific receptacle for them. Cultures of these various bacilli have been obtained (the bacteriological study was made by Zirpolo) and those from the yellow ducts are luminescent. Now, Pierantoni has observed that in female cuttlefish at the mating season the ventral surface is luminescent, a fact that had not been noticed earlier.

Let us consider the cephalopods with ventral luminous organs. Pierantoni was able to study them under favourable

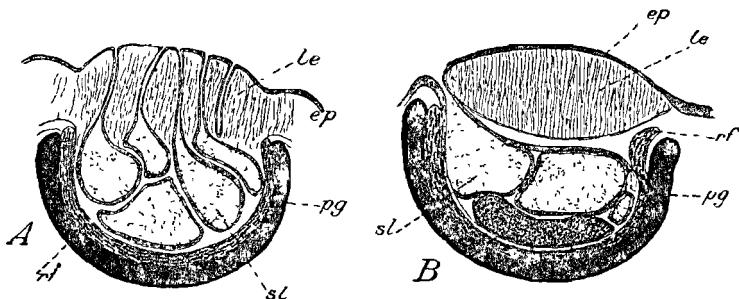


Figure 73. Sections of luminous organs.

A, of *Rondeletia minor*; *B*, of *Sepiola intermedia* (after Pierantoni); *ep*, epidermis; *le*, lens; *pg*, pigment; *rf*, reflector; *sl*, luminous substance.

circumstances in the Sepiolidae, in which these organs were discovered rather recently (in *Rondeletia*, *Sepiola*, *Sepiella oweniana*). The accessory nidamental gland (present only in the female) has just two kinds of ducts (white and red). The light organs (Fig. 73) which, in the female, occupy the central part of the gland, are formed of yellow ducts. It seems very probable that the light organs are a specialized part of this gland in which the yellow ducts are concentrated. In addition, there is a reflector below, formed at the expense of muscular tissue, and, above, a lens developed from connective tissue. The ducts of the light organ, greatly dilated (Fig. 73B), are packed with a finely granular mass, composed, according to Pierantoni, of bacteria and constituting the actual luminous substance. Taking

the most careful precautions, Pierantoni and Zirpolo obtained cultures which they considered to originate from these corpuscles. In cuttlefish broth they form a white film, magnificently luminescent and emerald green, which illuminates the whole liquid when it is stirred.

Pierantoni stresses the precautions employed against contamination and the differences in appearance between the cultured bacteria and those luminous ones which are commonly to be met with on the skin or muscles of cuttlefish and of dead fish. He concludes, then, that the luminescence of the Sepiolidæ must be due to symbiotic bacteria localized in the light organ, which must itself be a result of the differentiation of the accessory nidamental gland of cuttlefish and squids.

He found that this light organ functions in two ways: by internal illumination of its substance (symbiotic bacteria), or by the emission of the contents of its ducts into the surrounding water, which then itself becomes luminous. The photogenic bacteria are transmitted from one generation to the next when the eggs are laid.

There would thus be a hereditary physiological symbiosis which is probably very general; the Italian author has also attempted to undertake research into the luminous organs of deep sea cephalopods, unfortunately difficult to obtain in good condition. First of all, he made observations on a species (*Charybditeuthis*) collected at Messina. The luminescent kernel of the photogenic organs here "serait toujours constitué par des cellules remplies de microorganismes transformés par adaptation à la vie intracellulaire". This interpretation is based on the study of fixed and stained material. It was not possible to make cultures and the intracellular situation of the corpuscles considered as bacteria inevitably raises questions which will be considered later on. More recently (1924, 1926), Pierantoni⁵¹⁹ was able to carry out similar researches on an abyssal myopsid cephalopod, *Heteroteuthis dispar*; there, too, in a ventral luminous organ occurring in both sexes he found corpuscles which, according to him, are bacteria.

These various results have, moreover, given rise to rather lively controversies sustained by several Italian workers (Puntoni, Mortara⁵⁰¹, Skowron) who dispute the reality of the bacterial character of the corpuscles in the luminous organs,

but Pierantoni's conclusions have been confirmed through independent research by other authors, notably G. Meissner⁴⁹³, who obtained cultures of *Vibrio pierantonii* (starting with the light organ of *Sepiola intermedia*) and *Coccobacillus pierantonii* (from that of *Rondeletia minor*); moreover, she bases her own conclusions on serological data (the finding of antibodies, etc.). Let us also briefly note the researches carried out in Japan on *Watasesia scintillans* by Shima⁵³⁸, who obtained cultures of vibrios. These results have, however, been disputed by Hayashi⁴⁶¹.

We cannot enter here into further details on luminous organs of cephalopods and the discussions which have arisen on the subject of the reality of symbiotic bacteria. Let us mention that Buchner gives his support to Pierantoni's conclusions.

LUMINESCENCE IN PYROSOMA. Problems similar to those in cephalopods arise in connection with other types of luminous animals; let us first examine the case of *Pyrosoma*. The members of this genus are pelagic tunicates whose transparent colonies, in the form of hollow, cylindrical masses, intermittently give out a brilliant light, which has long been known. As early as 1804, Fr. Péron⁵⁰⁷ described the impressive spectacle of this phosphorescence of the sea in the Australian Pacific. In each member, or blastozoid, of the colony the light organs form a paired mass on either side of the entrance to the branchial cavity. The structure and origin of these organs has been thoroughly investigated by Julin⁴⁷³⁻⁴⁷⁴, beginning with the egg. The point of origin is in the "test cells" which, in all the tunicates, form a special envelope round the egg. These are the cells which give rise to the light organs of the first individuals of the colony, budded off by the embryo (*cyathozoid*). The egg itself is luminous and it is the test cells that shine. Within these cells are numerous sausage-shaped bodies that Julin interpreted as mitochondria or chromidia. The study of this material was repeated by Pierantoni⁵¹⁸, who confirmed Julin's descriptions, but who regards the intracellular elements noted above as symbiotic light-producing bacteria. The test cells are mycetocytes which go to form the light organs of the first individuals of the colony. Pierantoni saw corpuscles within these cells forming spores, which are passed out and go to contaminate other mesenchymatous cells; these new mycetocytes, carried by

the circulating blood, will constitute, step by step, the light organs of the various blastozoids as they are formed by budding. Moreover, in collaboration with Zirpolo and by taking the most careful precautions against contamination, Pierantoni was able to obtain agar cultures of bacterial colonies from the myctocytes. Here, again, there is the obvious objection that it is very difficult to guarantee the perfect sterility of extracts from

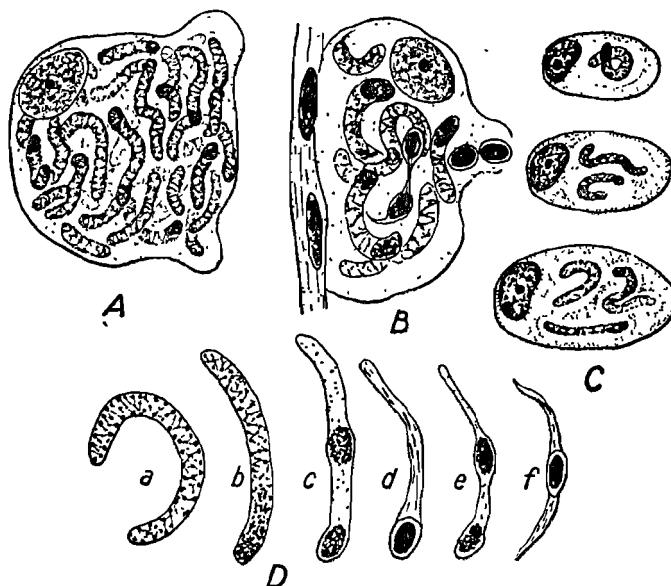


Figure 74. Cells of luminous tissue from *Pyrosoma giganteum* with photogenic bacteria (after Pierantoni).

A, luminous cell free in the peripharyngeal sinus, $\times 1,500$. *B*, the same in the light organs with spores being formed, $\times 1,500$. *C*, embryonic luminous cells with corpuscles undergoing multiplication, $\times 1,500$. *D*, formation of spores in the corpuscles, $\times 2,000$.

the light organs, when the cultures are started. When this possibility is taken into account, the conclusions of Pierantoni and Zirpolo still remain very plausible and they are supported by Buchner.

The salps are equally luminescent. Buchner has found that in this group there are symbionts in the cells of the young embryo.

LUMINESCENCE IN FISHES. We know of many cases of luminescence in fish where the light organs are very varied and

often highly differentiated, involving reflectors and lenses, and localized in very different regions of the body. Many of these luminous fishes are abyssal and accordingly remain practically outside the possibility of bacterial study. But it has been possible to deal with these problems in some more accessible species, for instance, in the Anomalopidae (*Anomalops*, *Photoblepharon*) living in the waters of Pacific atolls, where they have been the subject of research by Newton Harvey⁴⁶⁰. The light organs in these forms are at the periphery of the eyes. Illumination is continuous but can be masked by a palpebral fold. The structure of the organ shows a system of glandular ducts whose cavities are crammed with luminous bacteria arranged in chains, which can be cultured on peptone agar.

In Java, Harms⁴⁵⁸ found similar structures in a fish, *Equula splendens*. Here the luminescent organ forms a ring in the oesophagus at the entrance to the stomach, and it is furnished with a reflector; the glandular ducts are crammed with bacilliform bacteria.

Finally, the luminescent organs in a fish, *Monocentrus japonicus*, of the Japanese coasts, have been described by Yo K. Okada⁵⁰⁵; they are continuously luminescent, are situated in the anterior region of the mandibles and are analogous in structure to that found in the Anomalopidae: a tubular gland with an external opening whose cavities are crammed with highly mobile bacteria (1.5 to 3 μ) possessing flagella (vibrios). If the organ is squeezed, a luminous liquid is squirted out. Yasaki⁵⁵⁰ was able to obtain cultures of these bacteria.

So far, it has not been possible to study the luminous abyssal fishes when they are alive. From the structures seen in preserved material it seems clear that many of them have their own source of light, independent of symbiotic bacteria.

LUMINOUS TERRESTRIAL ANIMALS. In addition to the work of R. Dubois, mentioned earlier, we should cite that of Pierantoni who, in his research on the glow-worm, *Lampyris noctiluca*, has shown clearly that there are corpuscles shaped like rods or cocci, which he interprets as luminous symbionts. These bodies occur again in the eggs, which are also luminous, indicating a regular transmission of symbionts from one generation to the next. Dubois, it is true, considers these structures as being not autonomous organisms but intracellular particles

(*vacuolides*). Pierantoni obtained cultures on peptone agar, but they were not luminescent. Pierantoni's interpretation has excited contradiction (Vogel⁵⁴⁴, Vonwiller), and Buchner remains uncertain of the nature of the particles in question, whose culture leaves room for doubt.

Discussions of the same nature were aroused over the phenomenon of an oligochæte, *Microscolex phosphoreus*, emitting a luminous mucus, whose very body becomes luminescent under the influence of various stimuli. Pierantoni described symbiotic bacteria in the tissues, which Cuénot had already observed in *Eisenia rosea* and interpreted similarly, while Willem and Minne considered them to be products of cellular activity. Some researches by Knop in Buchner's laboratory have led to similar conclusions. Finally, Skowron, who took the matter up again in *Microscolex phosphoreus*, was able to induce luminescence in these particles, but he did not consider them to be bacteria and thought that their luminescence resulted from the luciferin-luciferase reaction of Dubois.

In short, the question remains unanswered, at least in its general form, and we do not know whether luminescence in animal tissues is due to the properties of particles actually belonging to the cell and setting up reactions that bring into play both an oxydizable substance and an enzyme, or whether it is a property of symbiotic bacteria.

EXPERIMENTAL RESEARCH ON SYMBIOSIS. It has been apparent from the mass of data presented in the preceding pages, very much abbreviated in form and by no means exhaustive, that symbiosis between the Metazoa and the lower plants, fungi or bacteria, extends over a very vast field and often raises very complex experimental problems. In a general way, this symbiosis exists under conditions that are strictly limited. In numerous cases it occurs in a specialized organ, the mycetome, formed from particular cells, the mycetocytes, and this organ develops by a series of equally well-defined processes. There, we find adaptations whose origin poses, as is always the case, problems of extreme difficulty. What has brought about the establishment and permanence of these associations which have become characteristic of the organism concerned, and are as precise and stable in their final structure and morphogenesis as the other elements concerned in the structure of the species?

The symbionts in each species are clearly defined; even the number of mycetocytes is fixed. There are some insects, as Buchner recognized, which possess two or even several species of symbionts. The respective proportions of these species are constant, the numbers of mycetocytes corresponding to each of them being fixed. The host organism appears as a precise regulating mechanism of symbiosis, capable in certain cases of eliminating the symbionts at a definite time by expulsion or by lysis.

After a purely descriptive period of researches into these symbioses we now come to an experimental phase. A series of investigations of this kind has been undertaken in recent years.

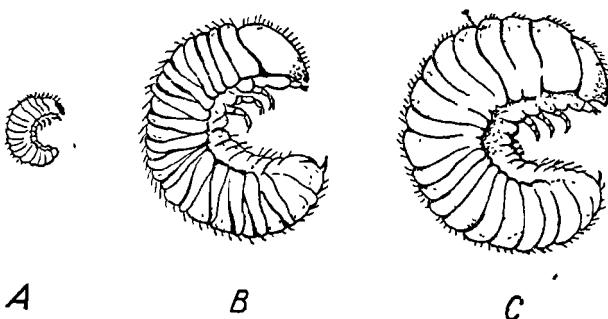


Figure 75. Larvæ of *Sitodrepa panicea* ten weeks old.

A, without symbionts. *B*, without symbionts but fed on dried yeast.
C, control of the same age provided with symbionts (after Koch, taken from Buchner).

We have already seen a brilliant example in the experiments carried out by Cleveland and Hungate on flagellates in termites. To close the present chapter I shall briefly indicate some very suggestive results.

The type of experiments which is enjoined is to bring about the suppression of the symbionts and see the consequences which arise therefrom. This has been done with the larva of a weevil, *Sitodrepa panicea*, living on flour; its symbionts are yeasts localized in intestinal cæca and the larva becomes infected at hatching by ingesting the symbionts deposited on the external surface of the egg when it is laid. It is thus sufficient to sterilize this surface before the larva hatches, for instance by immersing

it for some moments in a solution of sublimate. By doing this, A. Koch⁴⁸¹ obtained sterile larvæ, which he reared on an equally sterile food. The consequence was that the growth of the larvæ was almost totally checked. Fig. 75A shows such a larva at the age of ten weeks, C being a control larva hatched and reared under normal conditions, and B another sterilized larva, but one which has been fed on dried yeast; this food is physiologically equivalent to the symbionts and larvæ reared on it develop in a way that is comparable to that of normal larvæ, undergoing pupation and developing into a reproducing adult. The yeast provided as food contains B vitamins, which must normally be provided by the symbionts. The positive role of the latter is thus clearly shown. It must be the same in the Anobiidæ, the Cerambycidæ and other families of beetles.

It would, however, be dangerous to generalize too rapidly, as witness the case of the cucujid beetle, *Oryzæphilus surinamensis*, in which the symbionts are localized in cells enclosed in the general body cavity. Koch⁴⁸² succeeded in suppressing the symbionts in the egg, in the young larva, or even in the adult females, simply by keeping the insects at a temperature of 36° C. Animals sterilized in this way remained able to reproduce and Koch was able to obtain a series of generations in which typical mycetocytes occurred in their normal position, but were of smaller size and empty. This example explains how it is that one occasionally finds, in nature, individuals, or even races, in which the mycetome is empty. This was observed in an Egyptian race of the beetle *Calandra granaria* (Curculionidæ) which had become used to it. Similarly, in an ant, *Formica rufa*, individuals born parthenogenetically of workers, ordinarily sterile, possess a mycetome but no symbionts. In this case the existence of the mycetome shows that its formation is a process impressed by heredity on the morphogenesis of the species and not suppressed by the absence of symbionts.

I shall also mention the very elegant experiments made by Aschner and Ries⁴²³ on the body louse, *Pediculus humanus corporis*. In lice the mycetome is localized in a dorsal diverticulum of the foregut. One of these insects is placed on a slide and compressed very lightly with a mica coverslip pierced with a tiny hole, the insect being placed so that the mycetome lies exactly under the hole in the mica. The skin is then pierced

with a fine needle and, by pressure, the diverticulum containing the mycetome is forced outside and can be cut off. Lice so treated and deprived of the mycetome no longer feed, and ovary and eggs degenerate. If blood is injected into them by the anus it is still impossible to save them, although they recover if they are similarly injected with yeast extracts or bacterial filtrates. The results of these experiments show that under normal conditions the symbionts must provide the insect with vitamins that are

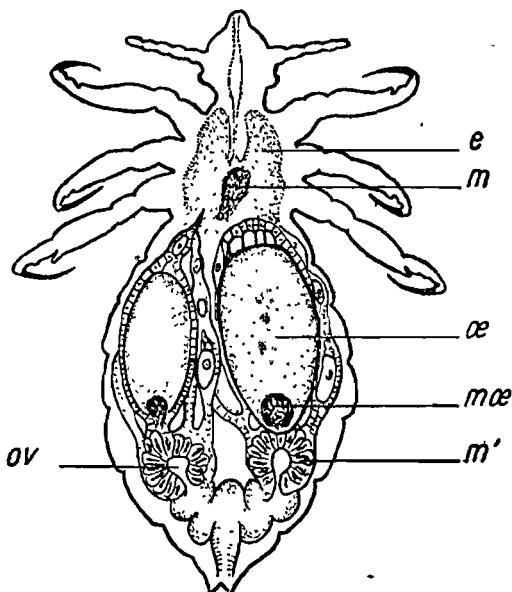


Figure 76. Louse, *Pediculus humanus capitatus*, ♀.

e, stomach; *m*, area of the stomach where the primary mycetome (here removed) is situated; *m'*, epithelium of the ovarian ampulla containing the secondary mycetome; *mae*, ovular mycetome (at the base of the egg, *ae*).

not present in the blood and it is possible that here is the determining cause of the general presence of a mycetome in various types of haematophagous animals. The blood that they absorb does not provide all the substances that are necessary to them, particularly vitamins.

These few indications suffice to show how fruitful experimental researches, such as have begun to be developed in the course of recent years, may become in the realm of symbiosis,

CHAPTER XII

SYMBIOSIS AMONG PLANTS

THE LICHENS. We now come to symbiosis in plants. The most classical case is that of the lichens. It is so complete that it has produced plants with a characteristic and well-defined appearance, from which it was possible to make a coherent classification and structural study without the dual nature of the plants being suspected, so much so that this last idea was vigorously opposed for a long time.

All lichens result from the association of a fungus and alga. The mycelium (*hyphae*) of the former forms the colourless part; it is generally an ascomycete, rarely a basidiomycete. The exact origin of these fungi is most often still unknown: with a certain number it has been possible to recognize the family to which they belong (Xylariaceæ, Hysteriaceæ, Patellariaceæ). The algæ, or *gonidia*, are most often Protococcaceæ, sometimes Chroolepidaceæ; often there is association with Cyanophyceæ. On the vegetative portion the reproductive organs are differentiated, which are either pure fructifications of Discomycetes and Pyrenomycetes, or similar fructifications into which the alga has penetrated and which are then termed *apothecia*. The spores of the fungus can begin to germinate alone, but the young thallus very quickly ceases to develop if it does not meet with the suitable alga.

In addition, many lichens propagate by special organs called *soredia*. These are little spherical masses composed of the alga surrounded by some hyphæ. Thus, the association is complete from the start. The soredia are formed in special organs.

Lichen associations, like all those already discussed, bring to mind the question of specificity. This is generally strict. It happens, nevertheless, that the same fungus can accommodate itself to several very different algæ. With each one it then gives a distinct lichen. Thus Möller⁵⁷¹ showed that a fungus belonging to the Basidiomycetes produced a lichen, *Cora*, with an alga of

the genus *Chroococcus*, and a *Dictyonema* with an alga of the genus *Scytonema*. Both lichens can even develop side by side in the same thallus by *parabiosis*. Conversely, the same alga can form different lichens with various fungi; a lichen can even transform itself into another by the progressive substitution of the fungus, a process which has received the name of *allelotropism*. These heterogeneous associations may be localized at limited places on the same lichen. They then form what are called *cephalodia*. Thus, on the lower surface of *Solorina saccata*, a lichen with green gonidia, one sees rounded structures, visible to the naked eye, which are associations of hyphæ and Cyanophyceæ.

The dualism of lichens was discovered in 1867 by Schwendener⁵⁷⁸. Bornet⁵⁶¹ established the precise anatomical relationships of the gonidia and hyphæ. It remained to constitute a lichen by culturing both components separately and then uniting them. But isolated cultures of the alga or fungus are very difficult to make and at that time culture methods were inadequate. Reess, Stahl and Möller made contributions to this synthesis, which was achieved in 1889 by G. Bonnier⁵⁶⁰ from pure cultures of both elements; fructifications were obtained on the resulting lichen. It would be interesting to repeat this demonstration today with the purity of culture that we can now attain.

The dualism of lichens is now universally recognized. Nevertheless, even in 1913, the Finnish botanist Elfving⁵⁶⁵ sought to show that the hyphæ were capable, on their own account, of producing gonidia and that these, when once formed, could live isolated in the algal condition. But if dualism is no longer seriously in question, the relations between the two components are still subject to discussion. The basic fact is that there is a permanent union between them and that from this there results an individualized organism with its characteristic and well-defined morphology and physiology, and that the two constituents have great difficulty in living in isolation. Thus we have a collection of data that clearly corresponds to the idea of symbiosis.

But is it necessary to see in it a perfectly mutualistic symbiosis, as is generally believed, each of the components being a source of balanced and reciprocal advantages for the other? To affirm this it is essential to know thoroughly the nutrition of the two plants both in an isolated state and in their

common life. Now, this knowledge is still very incomplete and the association has so far been regarded in very diverse ways, which can be summarized under the three following headings:

1. The fungus lives as a parasite at the expense of the alga.
2. The alga is a parasite of the fungus.
3. The association is a mutualistic symbiosis.

1. Schwendener was a partisan of the first theory, which he developed on lines of imagery. The fungus is the master, the green algae are the slaves: he goes on to say that it envelops them as the spider envelops its prey, with a close network of threads which is gradually transformed into an impenetrable sheath. But while the spider sucks the blood of its victim and only abandons it when it is dead, the fungus excites the algae taken in its web to greater activity and even to more intense reproduction; it thus makes more vigorous growth possible and the whole colony develops well. The algae kept in slavery are transformed in a few generations to such a point that they are no longer recognizable. But in fact these opinions are not justified by precise physiological studies made on the isolated members of the association. According to Schwendener, the alga brings about syntheses starting from the carbon dioxide of the air, the fungus brings to the alga water and the mineral salts of the soil.

Many authors have shared the view of Schwendener; for instance, Bornet, G. Bonnier and Warming. The last-named considers that the alga can live alone, although the fungus needs the alga and the latter is prevented by the fungus from reproducing by zoospores. The alga is thus parasitized, and Warming gives the name of *helotism* to this special type of parasitism, in which the parasite (the fungus) provides its host (the alga) with some of its food.

A Russian worker, Daniloff, goes so far as to maintain that the fungus kills the gonia by means of a network of hyphae which penetrate them and absorb their contents, and which he compares to the mycoplasma of Erickson.

2. The converse theory—that the alga is parasitic on the fungus—was formulated by Beijerinck⁵⁵⁶. This worker did not succeed in culturing the alga (*Cystococcus*) of *Physcia parietina* when he provided it with nitrogen in the form of nitrate or ammonia, to which sugar had been added, but he succeeded with

nitrogen in the form of peptone, and here is, according to him, the link between the alga and fungus: the fungus feeds on ammoniacal nitrogen and sugar; the peptones it produces diffuse through its cytoplasm and ensure the nutrition of *Cystococcus*. Thus the alga actually feeds at the expense of the fungus, at least as far as nitrogenous substances are concerned. This opinion has found confirmation in the work of Artari. According to Tobler, the alga also receives some of its carbon from the fungus, which is saprophytic, and this must make good a deficiency in its photosynthesis hindered by its difficult situation in the thallus of the fungus.

3. Between these two conceptions stands the idea of mutualistic symbiosis, the principal supporters of which are de Bary, Reinke and van Tieghem. According to Reinke⁵⁷⁶, the relationship of the alga to the fungus is that of the leaves and roots of a green plant. The alga (autrophic) synthesizes carbohydrates and borrows from the fungus (heterotrophic) the nitrogenous and albuminoid material that the latter builds up with the help of the carbohydrates furnished by the alga; besides this, the fungus draws up water and mineral substances.

Symbiosis appears in yet a different light from the work of Monsieur and Madame Moreau⁵⁷², namely as an *antagonistic symbiosis*, reflecting the ideas of Noël Bernard on orchids, which we are going to study later, and linked up with the idea of the parasitism of the alga on the fungus. The aerial thallus of one of the Peltigeraceæ—a group specially studied by the authors—is, according to them, the equivalent of an organ deformed by a parasite, such as a gall. This idea must be extended to all the lichens, whose thalli are equivalent to *algocecidis*, or algal galls. The lichens would be diseased fungi injured by a chronic infection, of a specific nature, which has become necessary to the species, the infecting agent being an alga.

On ridding ourselves of verbal phantoms we find that the question is really one of analyzing, by precise experiments, the relations of the alga and fungus, and of careful comparison of their behaviour in an isolated state and in association.

As far as the fungus is concerned, these studies are still but slightly advanced. It has rarely been cultivated successfully in a pure state. Möller obtained mycelia without gonidia, but they did not develop reproductive bodies. The germinating spore

must quickly find the right gonidia. On contact with them, as if by virtue of a special tropism or taxis, the mycelium forms swellings which fix the gonidia, surround them and enclose them. The gonidia seem to be, at least under normal conditions, the necessary condition for the development of the mycelium. The fungi of lichens have certainly become closely adapted to the gonidia and have more or less lost the faculty of living alone.

As for the alga, it lives in isolation more readily, and the study of it in a solitary state has received considerable stimulus thanks to the important researches of R. Chodat⁵⁶³ into the methods of culturing these organisms in a pure state. But even these researches emphasize the difficulty of drawing clear conclusions as far as lichens are concerned. Chodat, indeed, observed that most of the lower algae that he cultured, and not only the gonidia extracted from lichens, are more vigorous if they are provided with an organic food and not only nitrate or ammoniacal nitrogen. The preference of the gonidia for nitrogen supplied in the form of peptone is not then a certain sign of the parasitism of the alga.

An interesting contribution to this problem is furnished by work by A. Letellier⁵⁶⁷, a pupil of Chodat, and I shall briefly summarize his essential results by way of an example. He studied in pure culture the nutrition of *Nostoc peltigeræ* extracted from *Peltigera*, that of *Cystococcus* extracted from *Xanthoria parietina*, of various kinds of *Stichococcus* (some free-living and another from *Conioxybe furfuracea*), and that of *Coccomyxa* (free-living or coming from a species of *Solorina*). Letellier observed, thus, that *Nostoc peltigeræ* is distinct from free-living Cyanophyceæ, studied earlier, in its great ability to assimilate different sugars and in its proteolytic enzymes. In species of *Cystococcus* the gonidia have a preference for assimilating organic food. Some of the free-living members of the genus *Cystococcus* behave in the same way, others prefer an inorganic nitrogenous food. Gonidia of *Stichococcus*, from the point of view of nitrogenous food, seem to be less parasitic in character than those of certain free-living members of this genus. In the *Coccomyxa* group the gonidia prefer an inorganic food, as regards nitrogen as well as carbon.

There is not, therefore, any fundamental distinction between the gonidia and their free-living algal congeners. Sometimes the

former and sometimes the latter are better adapted to an organic diet. The food relations between the algæ and fungi must thus be very varied. These results indicate the complexity of the problem and show that it demands numerous and extremely precise studies.

In reality, the lichens result from a long reciprocal adaptation of fungi and gonidia. Both organisms are modified in this association and no longer possess their initial characteristics.

MYXOMYCETES. The Myxomycetes provide us with an example of symbiosis that can be compared with that of lichens. To tell the truth, although Myxomycetes are generally regarded as fungi, their fundamental element is amœbæ, in reality rhizopods; that is to say, they are a part of the animal kingdom, or at the most they are on the borders of both kingdoms. The analysis of symbiosis in the Myxomycetes is principally due to Pinoy⁵⁷³. The Myxomycetes are, in reality, accumulations of amœbæ, the myxamœbæ, associated with bacteria. Nadson (1899) and Potts (1902) had already formulated the opinion that there was symbiosis between these two elements. Using culture methods of great precision, Pinoy worked on *Dictyostelium mucoroides* and was able to isolate the bacteria on one hand and the spores on the other and show that the spores would not germinate in the absence of bacteria. This myxomycete can only live when the myxamœbæ associate with living bacteria. The myxamœbæ engulf bacteria and digest them in their vacuoles by secreting an intracellular enzyme (*acrasiae*) which liquefies gelatin, acting only in an alkaline medium or a feebly acid one, and resembles trypsin; its properties recall those of the enzyme isolated by Mouton from ordinary amoebæ. In short, *Dictyostelium mucoroides* is parasitic on colonies of micro-organisms (generally of *Bacillus fluorescens* var. *fluorescens*).

Pinoy extended these findings to other Myxomycetes of the same group as the Acrasieæ and to those with endospores (*Didymium difforme*, *D. diffusum*), where he recognized that the sporangia were always contaminated by numerous bacteria of various kinds. He was successful in culturing them with a single type of bacterium.

He also extended these findings to the case of *Plasmodiophora brassicae*, which produces cabbage rot. This disease is actually caused by the bacteria introduced with the myxamœbæ. The

bacteria, finding an extremely favourable medium for development in the cells of the cabbage, destroy the roots of the plant and thus set at liberty the spores of the parasite within the cells. The bacteria are necessary to the extracellular life of the parasite and no one has succeeded in making the myxamœbæ live alone.

MYXOBACTERIA. Here I am going to compare the preceding results with those that Pinoy⁵⁷⁴ obtained from the Myxobacteria. In pure culture, these organisms behave like common bacteria; in other conditions they build up complex structures: in *Chondromyces crocatus* there is a branched foot which, towards its extremity, carries projections terminated by spherical heads in which ovoid spores are inserted. These structures are composed of strings of bacterial elements ensheathed in a hard substance of a bright orange-yellow colour. The condition necessary for the formation of these structures, called *fructifications*, is that *Chondromyces* be associated with a bacterium related to *Micrococcus luteus*. On culturing both species together one sees that *Micrococcus* is lysed by *Chondromyces* and the fructifications form in contact with the area where lysis has occurred. With other bacteria (*B. fluorescens*, *B. pyocyaneus*) abnormal forms are obtained, one of which closely resembles *Chondromyces catenulatus*. It is as though one species were transformed into another.

NODULES IN THE LEGUMINOSÆ. Another example of symbiosis in the plant kingdom, equally classical today, is that of the nodules on the roots of leguminous plants, which cannot be more than mentioned here; the soil bacteria, which assimilate atmospheric nitrogen, are incorporated into nodules on the rootlets and modified into bacteroids whose substance is finally assimilated by the plant. The benefit which the Leguminosæ exert on the soil has been known from remote times and Liebig showed that it is based on an increase of nitrogen. Hellriegel and Willfahrt, in 1888, demonstrated that this is due to symbiosis of the plant with soil bacteria which extract nitrogen from the atmosphere, as Schlöesing and Laurent proved. The bacteria (*Bacterium radicicola*) were isolated by Beijerinck and the nodules were produced synthetically by culturing first the bacteria and secondly the plant in sterilized soil, and then seeding the former into the soil.

An analogous symbiosis exists in the alder tree whose roots also show nodules, produced by Streptomycetaceæ, and in various Eleagnaceæ (*Eleagnus*, *Hippophaë*).

We also know of nodules produced by symbiotic bacteria on the leaves of Rubiaceæ and tropical Myrsinaceæ under conditions similar to those shown by the Leguminosæ. All these structures are basically very similar to galls and could be considered as bacteriocecidis.

MYCORRHIZA. I shall dwell in greater detail on those extremely widespread associations called mycorrhiza between fungi and the roots of arboreal and herbaceous plants.

As early as the middle of the 19th century they were pointed out and today they are known in a large number of cases: in the prothallus of certain Hepaticæ, in the mosses, in various groups of vascular cryptograms (prothallus and sporophyte of Lycopodiaceæ—*Lycopodium*, *Psilotum*, *Phylloglossum*—amongst the ferns—*Ophioglossum*), in most perennial plants and trees. In 1881 Kamienski put forward the hypothesis of a symbiosis between the fungus and its host. This theory was developed principally after 1885 by Frank ⁴⁴⁸, who at the same time showed the great extent and regular occurrence of mycorrhizas. He distinguished between ectotrophic mycorrhizas which remain external to the roots, around which they form a mycelial sleeve, and are found principally on forest trees (Coniferæ, Amentaceæ), and endotrophic mycorrhizas which penetrate into the cells of the root.

According to Frank, there is a mutualistic symbiosis between ectotrophic mycorrhizal fungi and plants bearing them. The fungus is said to be a functional substitute for the root hairs: it must imbibe from the soil and bring to the plant both mineral salts and organic nitrogenous food from humus; the plant, for its part, must yield carbohydrates, which it has built up, to the fungus. The endotrophic fungus would, in addition, make a final contribution to the nutrition of the plant in being digested by it and thus providing it with nitrogenous matter.

Frank's original conception has since been considerably modified. It is in connection with orchids that these researches have been most precise in character, and we shall examine them separately. As far as forest trees are concerned the role of mycorrhiza does not appear to be as precise a symbiosis as Frank

suggested. The root hairs are by no means suppressed and remain functional. The fungus appears to be a parasite, little harmful and tolerated. A historical survey of research on endotrophic forms up to 1904 is given by Gallaud⁵⁶⁶ in a thesis which contains a profound morphological study of these fungi.

Endotrophic mycorrhizal fungi (from what is known of orchids) appear, according to the characters of their vegetative parts, to constitute a natural enough group but one whose affinities remain obscure. On the tip of the mycelial filaments there are often extra- or intracellular vesicles and, above all, strongly branched bushy growths or arbuscles, which are specially characteristic of them and were demonstrated by Gallaud (Fig. 77). These arbuscles undergo a characteristic type of degeneration in which the tips of the main growths end in a kind

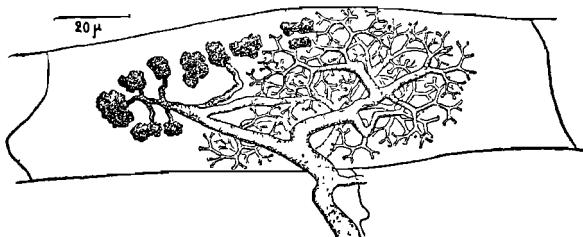


Figure 77. Intracellular termination (arbuscle and sporangioles) of an endotrophic mycorrhiza in *Allium sphærocephalum*.

of ball or sporangiole. Arbuscles and sporangioles occur in mycorrhizas of the most varied plants and they are not known elsewhere. So far, it has not been possible to isolate this mycorrhizal fungus and culture it; the systematic position is therefore unknown. The fungi have certainly been much modified by their adaptation to a life in association with the tissues of roots.

As for reciprocal reactions of the plant and fungus, we find that the cells containing the arbuscles, and those in their neighbourhood, do not contain starch grains. It appears that the fungus consumes the sugars from which this starch would be formed. In the arbúscular cells the nucleus swells up, assumes amœboid contours, shows excess chromatin and sometimes divides amitotically. As a rule the cell ends by digesting the fungus. Endotrophic mycorrhizal fungi, in short, take carbo-

hydrates from their host. Their external communications are, on the other hand, quite insufficient for one to be able to admit that they draw an appreciable amount of material from the soil and bring it to the plant. They feed, then, at the expense of the plant and behave as parasites. But their effect appears to be confined to inert organic substances elaborated by the plant, and not to affect the living substance of the latter, as is the case with truly parasitic fungi (Uredineæ, Peronosporeæ, etc.). They end by being phagocytes. Gallaud considers that endotrophic mycorrhizal fungi are saprophytes, which vegetate in plant tissues without causing serious damage, but also without assisting the assimilation of the host. It does not seem, then, at least in our present state of knowledge, that we should regard these associations between plants and mycorrhizal fungi as a symbiosis.

These conclusions are, however, not likely to be valid for all mycorrhizas, an opinion to which one is led by facts concerning those of the orchids and probably also of the lycopods and *Ophioglossum*.*

MYCORRHIZA OF ORCHIDS. The existence of endotrophic mycorrhizas is general in the orchids and they were pointed out as early as the middle of the 19th century. In 1846 Reissek saw the mycelium and tried to culture it. In the course of the next twenty-five years a series of observers, such as Irmisch, Schacht, Prillieux, Fabre, Drude, etc., saw them without recognizing their nature, and it was Kamienski who, in 1881, interpreted their presence as a symbiosis with the orchid. Wahrlich, in 1889, showed how widespread they were by finding them in the roots of all the orchids he examined, approximately 500 species. But it was Noël Bernard²¹⁷ who showed their importance and their exact role in the life of the plant.

He proved, indeed, that it was the presence of the fungus that makes it possible for the seed of the orchid to develop. It is well known that these plants, the flower of which is so specialized, produce very tiny seeds, rudimentary in structure, in enormous numbers (more than one million per capsule in certain tropical orchids). They have no albumen and the embryo in them is undifferentiated, reduced to a mass of cells with a suspensor. The germination of orchids was unsuccessful during the

* Additional references on mycorrhizas in general are given at the end of the bibliography.

19th century, save in an irregular and empirical manner, and by methods kept secret. Bernard, who had tried in vain to germinate the seeds of *Neottia nidus-avis*, an indigenous orchid lacking chlorophyll, completely resolved the problem by discovering a plant of *Neottia* in which the flower stalk was curved towards the soil and whose seeds had spontaneously germinated on contact with the earth, even in the capsule of the fruit. By observing the young seedlings under the microscope he saw that they had been invaded by a fungal mycelium and that this extremely precocious infection occurred at the point of attachment of the suspensor. The penetration of the fungus thus appeared as the first phenomenon of germination; in it he saw the determining cause of the latter and this hypothesis was amply verified.

Thus, the empirical successes and failures of workers were easily explained. It was, indeed, known that to get the seed to germinate it was necessary to sow it on the ground of the pot in which the parent plant had been grown, that is to say, in soil containing the fungus. With time the germination of orchids in greenhouses became gradually easier, because the soil there had gradually become richer in fungi as a result of prolonged culture. In natural conditions the immense number of seeds compensates, as far as the perpetuation of the species is concerned, for the loss of numerous embryos which do not meet the fungus necessary for their development. This is a mechanism parallel to that shown by animal parasites and one that has the same consequences.

Bernard also saw the influence that the fungus exercised over tuber development and even believed that, generally speaking, the latter was the result of infestation of a subterranean organ by symbiotic fungi; he showed the coexistence of both facts in a number of plants. One can, it is true, bring about tuber formation apart from the presence of fungi. Molliard, for example, obtained it in radishes by cultivating them in a solution of glucose in an aseptic medium, but this is not incompatible with Bernard's explanation.

As far as the role of fungi in orchid germination is concerned, Bernard⁵⁵⁸ demonstrated it experimentally by most careful methods. He succeeded in isolating and cultivating the fungus *in vitro*, an achievement which has not yet been successful with other mycorrhizas.

Here, in a few words, is his method. He dissected, under a binocular microscope and in rigorously aseptic conditions, an infected seedling or root cultured in a sterile tube; and isolated from the fungus the intracellular mycelial coils (pelotons) which constitute one of its essential characteristics. It is thus protected from all the common moulds or bacteria which would otherwise smother the mycorrhizal fungus in culture. These coils are then placed, one by one, by means of a sterile platinum loop, on a culture medium, where they develop into a sheet, whose characteristics we shall consider later.

The seeds, gathered aseptically by flaming the capsules and rapidly plunging them into alcohol before opening them, are sown in sterile culture tubes of a type customary in bacteriology, on agar or absorbent cotton wool, to which a decoction of



Figure 78. Seedling of *Phalaenopsis* (at 18 months) grown in a sterile tube by being sown on cotton wool steeped in a decoction of salep with *Rhizoctonia mucoroides* (after Noël Bernard).

salep* has been added. In these conditions they remain for months at a time without undergoing modification; or else they become green and acquire the first stage of differentiation, which varies according to the species, but always remain rudimentary. They do not germinate.

But if the mycelium of the fungus which has been cultured separately is gradually sown into the tubes where the seeds have remained dormant, the latter develop in a short time. At first they generally assume the aspect of a small tubercle in the shape of a spinning top, only producing leaves and roots later, and comparable to what Treub observed in the lycopods (which also possess a mycorrhiza) and called a *protocorm*.

The protocorm then gradually gives rise to the leafy plant. In this way Bernard regularly obtained the germination of very many orchids in culture tubes. Fig. 78 shows a specimen of *Phalaenopsis*—an epiphytic orchid whose germination was particularly difficult to obtain—which sprouted under these

* Salep is a powder obtained by grinding up dried tubers of Orchidaceæ.

conditions and which, having been entrusted to an expert and finally cultivated in soil by ordinary methods, flowered normally.* Fig. 79 shows seeds and numerous young plants undergoing differentiation.†

Let us return to the fungi themselves. Their growth in the plant is characterized by the formation, in the cells, of compact coils of filaments. These formations reappear, although rather rarely, in cultures *in vitro*. It is not mechanical compression that determines their formation in the cell. They are just the type of intracellular growth characteristic of a mycorrhiza, and Bernard considers that this is determined by a humoral effect; he compares the latter to the agglutination of a bacterium by the serum of a vaccinated animal. No success has been achieved in obtaining the perfect form of the mycorrhizal fungus, but only the mycelium. Bernard thinks that all the mycorrhizas of orchids belong to the same natural group which is adapted to these plants and which he places in the genus *Rhizoctonia*. One species of this genus is common on the potato and forms greenish sclerotia there. It is considered to be identical with *R. violacea* of Tulasne, found on the roots of lucerne and saffron. This fungus forms intracellular coils, like the endophytes of orchids.

The numerous fungi extracted by Bernard from orchids were considered by him to constitute three species:

1. *Rhizoctonia repens*, the most widespread, taken from numerous genera and species, which is said to be the most primitive form.

2. *R. mucoroides*, extracted only from the roots of *Phalaenopsis* and *Vanda*, but always found in the plants of these genera, whatever their origin.‡

3. *R. lanuginosa*, obtained only from *Odontoglossum grande*.

Burgeff⁵⁶², who repeated Bernard's researches and verified and confirmed all his principal results, believes in a much greater specific variety in the fungi. He makes a new group for these

* Towards the bottom of the figure the dots that one sees on the surface of the agar are the sclerotia of the fungus.

† Quite recent researches by F. Mariat⁵⁷⁰ have shown that the addition of vitamin B to the culture media used by N. Bernard and his followers encourage the growth and differentiation of embryos of *Cattleya*. Pyrimidine alone and a mixture of pyrimidine and thiazole act in the same way. It is possible that in the orchid-fungus association the fungus contributes biological factors of the nature of vitamins, capable of acting on the growth and differentiation of the embryos.

‡ Bernard obtained the same fungus from the roots of *Ophioglossum*, but it was without effect on the orchids.

fungi, the Orcheomycetes, and described 15 species in it. He considers that each species of orchid has its own endophyte.*

Bernard's work is not limited to these results of considerable practical and theoretical importance. Making use of *Rhizoctonia*, he was able to analyze thoroughly its role in symbiosis and establish facts or make suggestions of the greatest interest.

The relationships of the orchids with their mycorrhiza are far from being constant and uniform. It is quite clear that the rudimentary structure of the seeds is a secondary state, resulting from an evolution which has gradually made symbiosis necessary and which must be represented by various stages.

And, indeed, amongst the orchids studied by Bernard there is a species, *Bletilla hyacintha*, of the Far East, that specialists (Pfitzer) consider to be primitive from its characters taken as a whole, and here symbiosis with the fungus is not necessary for the germination of the seed. Bernard was able to get the seedlings to develop aseptically; but then they germinate differently, without developing the protocorm, and a comparison of both types in the same plant allows us to see what the actual influence of the fungus is on the form of growth. In the grown plant *symbiosis is very intermittent*. The rhizome to which the plant is periodically reduced is free from mycorrhiza; each year there is a fresh growth of roots, which become infested on their own account. The mycorrhiza then appears as an intermittent and usual infection.

But *Bletilla* constitutes an exception and in the great majority of terrestrial and epiphytic orchids the embryo only develops under the influence of the fungus. In its absence only an outline of germination is produced; in its presence the latter goes ahead without delay. In most forms (*Cattleya*, *Cypripedium*, *Ophrydium*) *symbiosis remains intermittent* in the adult state; it is renewed each year with the growth of the roots and disappears when they do.

In the Sarcanthineæ (*Phalaenopsis*, *Vanda*), epiphytes which Pfitzer considered the most highly evolved of the orchids,

* Burgeff made an extensive study of the properties of these fungi in culture. They transform sugars (with the help of invertase and maltase), break down glucosides (by emulsine), produce tyrosinase, do not assimilate free nitrogen but freely take up organic nitrogen (of salep), produce proteolytic enzymes, etc. Bernard recognized that species of *Rhizoctonia* digest cellulose. Indeed, they disintegrate the absorbent cotton wool on which they are often cultured.

germination occurs only with *Rhizoctonia mucoroides*, and *symbiosis becomes continuous*, the roots here being persistent. This character attains its maximum in *Tæniophyllum*.

The terrestrial orchids show the same degrees of symbiosis as the epiphytes and it is in *Neottia nidus-avis* that this type of growth is carried to its greatest extent. Here, indeed, *symbiosis is absolutely continuous* during the whole life of the plant and, instead of being limited to the roots as in the preceding cases, it extends to the rhizome. Further, it is directly transmitted from one generation to the next. When, as frequently happens, *Neottia* flowers and fruits underground, the fungi in the rhizome spread directly into the fruit and infest the seeds, which germinate *in situ*. At this level, as Bernard remarks, fungus and orchid practically achieve a new and permanent individuality, comparable with that of a lichen.

Thus, in the orchids there are found certain stages of an evolution in symbiosis reached by several series of forms which are independent of each other, and Bernard remarks that this same evolution very probably occurs in other groups, notably in *Ophioglossum* and the lycopods, where symbiosis presents similar characteristics but where it has not yet been studied as in the orchids.

We find again, indeed, in these plants, either in the gametophyte (prothallus) or in the sporophyte, the same strange facies of the vegetative parts (tuberization in the prothallus, spinning-top form of seedlings, analogous localization of the fungi) as in the orchids. So that symbiosis must have been an important evolutionary factor in groups which are quite independent and separate from one another. It would obviously be most interesting to verify Bernard's ideas on the Ophioglossaceæ and the Lycopodinae.*

* Bernard even goes so far as to ask whether symbiosis has not been a major factor in plant evolution, one to which is due the appearance, deriving from primitive mosses, of plants with perennial arborescent sporophytes, almost all infested with mycorrhiza. Annual plants would have returned to this state by eliminating their symbiotic fungi. This evolution may have been able to recur several times. The orchids would represent one of these secondary evolutions. These are at present only purely speculative conceptions.

Magrou⁵⁶⁹, in a quite recent article, found some confirmation of Bernard's ideas in observations made on *Rhynia*, fossil plants in the red sandstone of the Scottish Devonian, which have been compared with Hepaticæ but which show in their axis, thought to be a stem, some differentiation of vascular tissue, and can therefore be considered as one of the possible initial forms of vascular plants. These erect axes of *Rhynia* and *Hornea*, borne on an underground rhizome which,

One of the most interesting aspects of Bernard's researches, from the point of view which occupies us here, is the physiological analysis of the relationships of *Rhizoctonia* and orchids. Under the conditions in which he cultured the fungi, it happened, indeed, quite generally that after a long period of culture *in vitro*, *Rhizoctonia* gradually became powerless to make the seeds germinate. It had become inactive and was totally so after two or three years of tube culture. But it can be made active again by being passed through seedlings or seeds. Here we have a phenomenon that Bernard compares very suggestively, and it seems very justly, with variations in virulence (attenuation and augmentation) in bacterial infections.

That led him to study the way in which the fungus grows and propagates in the orchid, making this investigation either with the fungus normal to the species, or by bringing about abnormal associations, for instance, by inoculating *Rhizoctonia mucoroides* or *R. lanuginosa* into species which harbour *R. repens*, or vice versa.

The fungus penetrates at definite points of entry, for instance, the place of attachment of the suspensor, or the base of the absorbing hairs of the roots. These points are those where the plant shows the maximum permeability and which play the principal role in exchanges with the environment. It must be supposed that these zones excrete soluble substances which, in culture, attract the fungus and which offer the minimum resistance to its penetration. *Rhizoctonia* digests pure cellulose. It only traverses the epidermal cells without forming coils in them. Each area of penetration, once this has been effected, acquires an immunity which is opposed to all fresh infection. Thus the suspensor is only invaded once. Successive infestations must be made at distinct points of entry.

The appearance of *Rhizoctonia* in the tissues depends on the degree of its activity and it is only at a suitable degree that symbiosis is established. Thus, either in nature or in cultures, all the seeds are far from germinating, even when they meet the fungus, in *Hornea lignieri*, is formed from segments of a tubercular shape, recall those described by Treub in certain lycopods. Now, in these tubercles structures have been seen which have been attributed to a fungus (mycelium without cell walls, insinuated between the cells and swelling into vesicles recalling those that one sees in mycorrhizas). Magrou saw in this a confirmation of the views of Treub on the role of the embryonic tubercles in the genesis of vascular plants and of those of Bernard on the symbiotic origin of these organs.

as the seedlings in the tube show (Fig. 79). *Symbiosis*, to use Bernard's expression, *is on the frontiers of disease*.

As we have said, *Rhizoctonia* only traverses the epidermal cells and it is in the subjacent parenchyma that it grows with the very characteristic form of filamentous pelotons in the cells. But in cases where the seed germinates well, the invasion remains limited. There is always some kind of barrier which prevents the mycelium from developing at the growing point and which checks it as growth advances. At the point where the invasion is checked a proportion of the cells of the orchid's

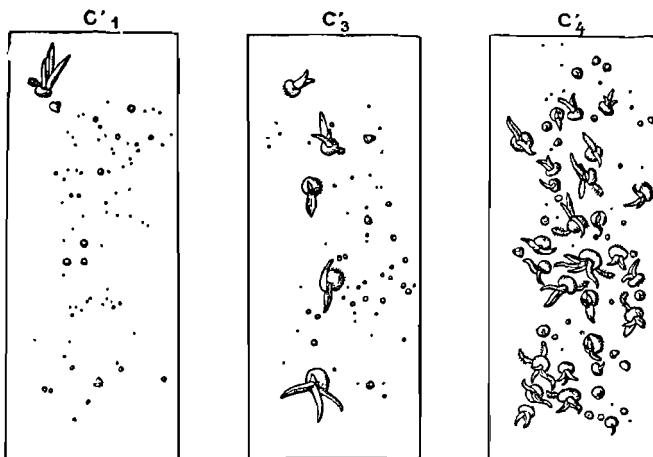


Fig. 79. *Lelio-Cattleya* sown in sterile tubes inoculated with *Rhizoctonia* of increasing activity, C'1, C'3, C'4 (after Noël Bernard).

parenchyma play the part of phagocytes (Fig. 80); their nucleus becomes enlarged (it attains up to 60 times its original volume, according to Burgeff) and lobed, and the mycelial coils contained in its cells are digested, leaving a residue.* This occurrence was, moreover, seen by the first observers of mycorrhiza, such as Prillieux in 1856, but was not interpreted. Magnus in 1900 and Shibata in 1902 described this process of digestion. It is, says Bernard, a true phagocytosis which governs the extent of infection in symbiosis. The differentiation of the nucleus of the

* The formation of sporangioles at the expense of the arbuscles of the endotrophic type of mycorrhiza studied by Gallaud, is a similar type of phenomenon.

phagocytes even precedes the penetration of the fungus into them and must result from a distance reaction caused by soluble products or by an enzyme from the mycorrhiza.

Most of the workers, particularly Frank, who observed this process of digestion before Bernard, considered it to be a matter of nutrition, essential to the life of plants with endotrophic

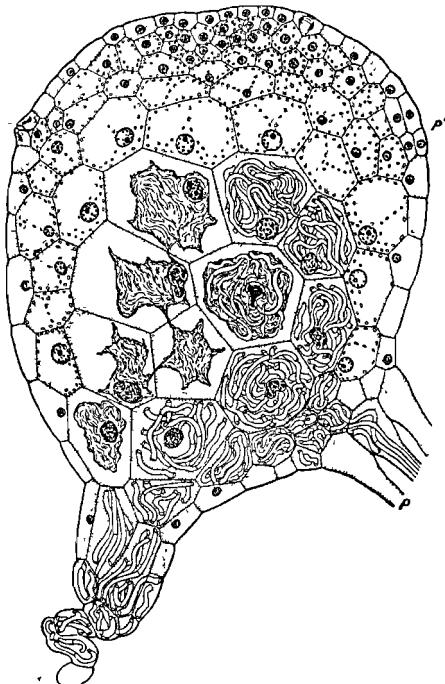


Figure 80. Section of a germinating *Odontoglossum*, showing the penetration of the suspensor after one month, and the intracellular coiling of *Rhizoctonia lanuginosa*, as well as its destruction by phagocytosis; *s*, stoma; *p*, absorbing hairs (after Noël Bernard).

mycorrhizas. According to them the plants were *fungivorous* as some are insectivorous, and this digestion was a proof of mutualistic symbiosis, a compensation for the loss of the carbohydrates consumed by the fungus at the host's expense. But Bernard clearly established that it has no connection with the development of the plant. *Rhizoctonia* does not play a direct part in the nutrition of orchids.

Phagocytosis is the organism's defensive reaction. If orchids are infested with abnormal *Rhizoctonia*, as we have said, or with inactive *Rhizoctonia*, either the infestation is rapidly checked by phagocytes, symbiosis is not established and the seed fails, or else the plant dies from a generalized invasion of its tissues and its growing point, without the phagocytic reaction being observed or at least without its playing a very effective part. Between the benign infestation, rapidly checked by an almost immediate phagocytosis, and a rapidly fatal infestation in which phagocytosis is insignificant or non-existent, occurs the intermediate case of symbiosis in which phagocytosis is exercised without, however, arresting the propagation of the fungus, and in which, nevertheless, the plant does not succumb. This symbiosis can last throughout life, as in *Neottia nidus-avis*, or else be intermittent.

Since the fungus never attains the growing point, the plant achieves a certain immunity which is the condition of its development. The intracellular coiling of *Rhizoctonia* must, then, be a phenomenon connected with this immunity; for, in cases of fatal infection, studied by Bernard, the fungus abandons this type of growth and from that time the mycelial filaments run in a straight line, invading all the tissues. The humoral action to which we have already alluded must be lacking.

Bernard finally sought to understand the way in which mycorrhizas act, without invoking either the word or the mystical conception of symbiosis. He asked himself whether the effective role of mycorrhizas might not be due to a favourable modification that they produce in the intracellular environment. Now, he was successful in obtaining the germination of certain orchids without fungi, by sowing seeds on concentrated solutions (agar-agar or absorbent cotton wool impregnated with a decoction of strong salep and often with saccharose added). He noted, moreover, that *Rhizoctonia* cultured on salep-saccharose caused an increase in the molecular concentration of the solution employed (which can be determined by variation in freezing point). It is possible that their enzymes break up complex molecules into a larger number of simpler molecules. One can then imagine that they act in the same way in their intracellular growth and that they increase the degree of molecular concentration in the sap of the seedlings into which they penetrate; this condition would

permit germination. Bernard compares this suggestion with the production of experimental parthenogenesis in animals by the use of hypertonic solutions. Although this is hypothetical, the fact remains that a stronger concentration of solutions allows the fungus to be dispensed with in the germination of a certain number of orchid species.

Symbiosis between orchid and mycorrhizal fungus is by no means a fixed entity, nor a mutualistic association for assisting both parties. It is a phenomenon of parasitism, an infection, a constant disease become essential but one which, according to its degree or its appearance, ensures the development of the plant, stops it, or even kills the plant. In general biology it is a chapter of pathology parallel to that of bacterial infections and not to be distinguished from parasitism.

With this in mind, there is obviously reason to investigate plants with a similar aspect—Hepaticæ (*Fegatella*), Lycopodiaceæ (*Lycopodium*, *Psilotum*, *Phylloglossum*), Ophioglossaceæ.

The generalizations to which N. Bernard has been led from his magnificent researches on the orchids have given rise to numerous discussions. This is, after all, the common lot with all new ideas. We must greatly regret the premature loss of this investigator, at once a precise experimentalist and a man of great vision, who had not time to explore the horizons he opened up. Recent research tends to determine the physico-chemical mechanisms which operate in symbiosis, the association of two organisms providing one of them with elements, notably vitamins, that it cannot produce itself. For this aspect, reference should be made to the works of Magrou and of his pupil Mariat⁵⁶⁸⁻⁵⁷⁰. As an example, I shall cite here the fact that the fungus *Sphaerocybe concentrica* (Stelbaceæ) when cultured alone only fructifies on media containing a B vitamin, thiazole, but when in association with a red yeast, *Rhodotorula rubra*, which builds up thiazole, the fructifications are obtained without thiazole being added to the culture medium. It is the same when *Sphaerocybe* is associated with *Sordaria finicola* (Sphaeriaceæ).

CONCLUSION. We have thus finished reviewing the principal groups of facts which are connected with the idea of symbiosis. The conclusion emerges that they do not constitute a clearly distinct category but are related to parasitism and to

commensalism by an intermediate series without showing a distinct contrast to either.

In classical examples, such as those of the lichens, it is necessary to abandon the idea of a purely mutualistic association with equivalent reciprocal benefits. It is a conflict between alga and fungus, habitually and intimately associated, in which the two organisms have reacted on each other. That is, after all, the conclusion formulated in 1906 by the Russian botanist Elenkine. He stated that the mutualistic conception of symbiosis would have to be replaced by that of an unstable state of equilibrium: the two associated organisms react differently to the conditions in the external environment and to their variations. These were not equally favourable to both; and according to the case in question, the one or the other would dominate. These variations must remain within the limits in which neither of the two organisms succumbs, a conception which is equivalent to that of N. Bernard: "*La symbiose est à la frontière de la maladie.*"

In this association the two organisms react on each other; there is *evolution within the symbiosis*, evolution both morphological and functional, leading finally to new requirements as in the germination of orchids, or to absolutely new functions as in the case of yeasts in insects, or luminous bacteria in cephalopods. These last cases, which Pierantoni called hereditary physiological symbioses, do not appear at first sight to fit in with the idea of conflict or instability. There is, nevertheless, no doubt that in the first place they were infections of insects or cephalopods by alien organisms, but the conflict was terminated by the dominance of one of the organisms over the other and by a stable equilibrium exactly corresponding to a novel function. These are the cases which, in the present state of our knowledge, represent the most complete evolution.

CHAPTER XIII

IS SYMBIOSIS A PRIMORDIAL CHARACTERISTIC OF THE CELL?

THE facts of symbiosis, such as those we have just examined, form a continuous series and are fairly widespread in nature. It is sufficient to think of zooxanthellæ and zoothiorellæ, of lichens, mycorrhizas, of bacteroids in nodules on roots, of yeasts in insects, and of luminous bacteria, to the extent in which their role is definitely recognized. Nevertheless, these facts remain exceptions in organic life taken as a whole. Normal life does not necessarily involve these internal associations. They are a deviation from the normal.

Now, some years ago a certain number of biologists showed an inclination to see them in a contrary light, as a fundamental form of vital functioning. The cases recalled above would only be gross and macroscopic examples, in some sense, of what is the life of the cell; the latter would always be a symbiosis. The cell, indeed, would swarm with symbiotic micro-organisms to which would belong the essential metabolic powers.

The idea is not new. It followed an already long series of hypotheses in which attempts were made to explain heredity and life by the conception of particles endowed with special properties. These ideas are to be found methodically set out in the book by Y. Delage on heredity. Most were purely speculative; others tended more or less to acquire an objective reality. Amongst them some, such as the *micella* of Nägeli, the *pangenes* of de Vries, the *biophores* of Weismann, with which were finally connected the *genes* of Johannsen, have played an important role in contemporary biology because they were conceived in terms of cellular structure, as revealed by the microscope. They provided, just at that time, a solid material basis for studies in mendelian heredity. Others, on the contrary, were conceived in an entirely speculative fashion; such were the *microzymas* of Béchamp. Others, finally, derived from pure

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observation, such as the *granules* of Altmann⁴¹², which ultimately became mitochondria; today, these last hold a place of the first rank in cytological research as well as in the domain of physiology. For the conception of the cell as the ultimate morphological unit, Altmann wished to substitute that of the granule. The granule is an entity which is continuous and reproduces itself. The aphorism, *omnis cellula e cellula*, gives way to *omne granulum e granulo*. For Altmann the granules are the intrinsic elements of the organism.

Some years ago another conception was opposed to this one, that of seeing in the cell primitively distinct organisms and intra-cellular symbionts which were the substratum of the principal cellular functions, though originally alien to the cell.

Conceptions of this kind suggested themselves incidentally to certain biologists. Raphael Dubois, in his work on animal light and on colour-producing organs, thought that the seat of these functions lay in the intracellular corpuscles, *vacuolides*, to which he ascribed a great degree of autonomy; he claimed, by reviving various theories, the paternity of ideas to which systematic studies on cellular structure had led, and which resembled his own.

More recently a series of methodical observations and experiments by Pierantoni and Portier* has led to conclusions which have been set out in a particularly precise fashion. In the theories formulated it is necessary to distinguish exactly between what is definite knowledge and what remains debatable or even ill-founded.

Let us first examine the ideas of Pierantoni, who, in any case, slightly preceded Portier. They are concerned with researches into the symbiotic yeasts of insects, the results of which were indisputable, and which led him to study the light organs in cephalopods. The first of his conclusions is that luminescence in *Rondeletia* and *Sepiola* is due to symbiotic bacteria, swarming in the lumen of the glandular ducts of the light organ, occasionally passing outside, and being regularly inoculated into successive

* Galipe⁴¹⁵ arrived at the same conclusions through his conception of *normal parasitism*. According to him, there are infinitely small bodies which are normally essential for the regulation of cellular activity. They are characteristic of the cell's functioning and are to some extent the simplest representation of life in organized beings.

Galipe himself stressed the affinity of these ideas with Béchamp's speculations on microzymas.

generations by way of the egg. It is obviously very tempting to try to include in such an explanation the production of light in the other cephalopods, in *Pyrosoma*, and in animals in general. In abyssal cephalopods the light organs are closed; the photogenic region is a cell complex, more or less syncytial in nature, in which the granulations swarm that are the seat of the light phenomena. According to Pierantoni⁵¹⁶, these granules are bacteria adapted to intracellular life. In researches on *Charybditeuthis* he says that he saw "à la partie la plus externe de la masse de l'organe lumineux anal (qui est clos) une couche où, avec corpuscules extrêmement petits, se trouvent aussi des formes bacillaires (de vrais bactéries) en voie de fragmentation en grains minuscules; *des bactéries qui, en somme, evoluent de la forme bacillaire à la forme granulaire.*" But one sees how difficult it is to give irrefutable proof of such an affirmation which, nevertheless, is necessary. According to Pierantoni's idea, the intracellular granulations which seem to be the seat of light in all luminous animals, and which correspond to the vacuolids of Dubois, would then be bacteria become intracellular and changed into the form of simple granules. Similarly, according to the researches of Dubois on the formation of the purple in *Murex trunculus*, this is formed by "des corpuscules très petits" that Dubois calls *vacuolides zymasiques* or *sphérules élémentaires*, and "Comment ne pas penser—sur la base de ce qui a été exposé de la transformation et de l'adaptation des bactéries photogènes à la constitution de la substance photogène des organes lumineux—à une adaptation analogue possible de bactéries chromogènes à la fonction de la production des couleurs?" Pierantoni has undertaken experimental research in order to prove by means of cultures that the pigmentary granulations are also symbiotic bacteria. All this "place sous un nouveau jour l'activité des plasmes cellulaires et assignerait aux inclusions cytoplasmiques et peut-être à beaucoup des constituants du protoplasme une vie autonome et une activité spécifique, au bénéfice des organismes dans lesquels ils vivent."

Such are the theories of Pierantoni which clearly tend to attach to symbiotic organisms adapted to intracellular life a large number of special functions that occur in animals: functions of luminescence, colour production, pigmentation, etc. It remains a purely theoretical idea as long as no irrefutable proof

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is given by the autonomous culture of the granulations in question. This has by no means been provided for us at the present time.

Portier⁴¹⁹ was led to analogous views by researches into xylophagous insects and he formulated them in a much more general and rigid fashion in his book, *Les Symbiotes*, published in 1918. The facts and ideas set out in that book gave rise to very lively controversy at the time when the first French edition of this present book appeared. Today, one can consider this question as settled; the ideas upheld by Portier have been abandoned completely. I have nevertheless thought it necessary to retain the following pages, because they appear to me to illustrate a type of question which, in various forms, periodically recurs, and because the nature of the arguments produced gives rise to types of discussion whose interest survives the particular debate and can put our minds on guard against too hasty interpretations. The fundamental unity of the cell, without in any way being a dogma, is sufficiently established for it not to be contested without absolutely categorical proofs.

For Portier the cell was by no means the fundamental unit in organisms. It was essentially a symbiotic complex. It would always be crammed with symbionts indispensable for effecting organic syntheses, which are none other than mitochondria; these would be bacteria adapted to the symbiotic intracellular life. The bacteria alone would be autotrophic, that is, capable of feeding independently. All cells and, consequently, all animals and plants with a cellular constitution, would be heterotrophic and would only assimilate through the intermediary of symbiotic bacteria. There is obviously no *a priori* impossibility about such a conception; but, as it brings into question all the fundamental notions of biology, it must be based on irrefutable proofs. One can affirm without any hesitation that this is by no means the case.

The starting point of Portier's ideas is to be found in his *Recherches physiologiques sur les champignons entomophytes*⁵²⁷. He believed it established that there was a regular and general symbiosis between wood-eating insects and fungi of the genus *Isaria*. This symbiosis would manifest itself even after death, with particular distinctness in the Lepidoptera, which very frequently, according to entomologists' saying, *turn to fat*. This is

due to the invasion of the corpse by the mycelium of *Isaria*, whose conidia were present before this in the state of symbionts. The very frequent infection of insects by *Isaria* is well known, but it is considered simply as a phenomenon of parasitism. Metchnikoff, then Giard⁴⁵⁰, even tried to make use of these parasites to produce epizootics on a large scale in the larvæ of harmful insects, particularly in beetroot weevils and cockchafers.

Portier acquired the idea of a constant symbiosis of these fungi by studying the development of a caterpillar, *Nonagria typhæ*. That was his starting point. He believed that he found conidia in the digestive tube of this caterpillar. He found them again, and drew them, in the intestinal epithelium and in all the tissues of the adult, including the eggs by which they were said to be transmitted to the following generation. But the identification of the structures figured as conidia of *Isaria* remains more than arguable. Positive proof has not been given and one can even affirm that the bodies figured, principally on account of the way in which they stain (cf. *Les Symbiotes*, Fig. 9, p. 30; Fig. 26, p. 176), must be spores of Microsporidia whose presence in the various tissues is very simply explained. All the facts produced relative to the caterpillar of *Nonagria typhæ* appear as the simple result of an infestation by a microsporidian of the genus *Nosema*, like that of the silkworm by pebrine, and we know well enough that this last has nothing to do with symbiosis.* The presence of corpuscles in the oocytes is very natural; it takes one back to the work of Pasteur on pebrine. It would be very desirable, besides, that the preceding statement should be verified by work on *Nonagria typhæ* taken from the localities where Portier studied it.

As for the other facts pertaining to xylophagous insects, they appear to me not to have sufficient validity as a basis for the conception of intracellular symbiosis. The only ones which can support it are those relating to the yeasts in the myctome of Hemiptera (aphids, coccids, etc.) which we have already reviewed: these are undoubtedly but their application is strictly limited.

* The regular presence of one organism within another is not a sufficient criterion for assuming that it is a matter of symbiosis. There are indisputable parasites which occur with absolute regularity. Such is, amongst other cases, the gregarine *Lithocystis schneideri* in *Echinocardium cordatum*, which was discussed earlier.

Another basis for Portier's theory—indirect in this case—would be the impossibility of aseptic life and the necessity for symbionts, asepsis being taken in the ordinary sense of the word. The intestine of animals usually contains a rich and varied flora, sometimes useful, sometimes harmful, and Pasteur considered it possible that the existence of such a flora was absolutely necessary. It is probable, as we have seen earlier, that in most animals the intestinal fauna or flora contributes to the transformation of food substances, and it is even possible that it plays a regular and important part in this! We are generally agreed today in attributing such a role to the ciliates in the paunch of ruminants, and to the trichonymphids of termites, and we have pointed out, too, the suggestions by Wigglesworth concerning the intestinal bacteria of *Rhodnius prolixus*. But the possibility of an aseptic life is fully established today. It was achieved under rigorous conditions in mammals by Nuttall and Thierfelder⁵⁰⁴, in spite of the technical difficulties of rearing them aseptically, and later by Cohendy⁴³⁸ in Metchnikoff's laboratory. Such an experiment is very complicated in practice, and it is clear that reasons of quite a secondary nature render it precarious. Mme Metchnikoff⁴⁹⁷ also reared some frog tadpoles aseptically, and Wollmann⁵⁴⁸ some flies (*Calliphora*). Portier⁵²⁷, too, observed that mining caterpillars—notably those of *Nepticula flosculatella*—on hazel trees, are naturally aseptic as long as they remain beneath the epidermis of the leaf. But the problem of the aseptic life has been solved practically and on a large scale by Delcourt and Guyénot⁴⁴¹ with *Drosophila*, and their results have been confirmed by such workers as J. Löeb. Delcourt and Guyénot developed an exact technique for this, thanks to which breeding could be carried out regularly—as with a pure culture of a species of bacterium—and infinitely better than under ordinary conditions. Guyénot⁴⁵⁶ pursued this aseptic breeding through nearly 50 successive generations, comprising thousands of individuals, without any adverse symptoms ever developing.

The interest of these researches is, moreover, not only in the demonstration of the possibility of the aseptic life. This method, as Guyénot showed, places the experimenter in possession of absolutely constant environmental conditions for precise investigation into fundamental problems of nutrition. Now, in the

flies raised in this way, none of the symbionts which Portier considered essential was found.

But, in reality, all that we have just considered deals only with secondary matters in the theory of symbionts as it was formulated by Portier. The essential point, really, is the dualism in the constitution of the cell, the existence—absolutely general—within it of autonomous organisms said to be the mitochondria. It would be necessary, then, by extracting mitochondria from the cell and culturing them, to prove that they are indeed autonomous organisms, bacteria adapted to intracellular life. Portier declared that this proof was indeed supplied by his work on various glandular organs of mammals, principally the testes, in which the mitochondrial apparatus has been much studied by the cytologists, in seminal lineage. But, in reality, Portier's experiments relate principally to the peri-testicular adipose tissue; from this tissue, he obtained—attempting to work in a stringently aseptic fashion—some cultures which were said to be those of intracellular symbionts, and he studied the physical and chemical properties of these organisms.

In point of fact, he did not obtain these cultures regularly, and the conditions in which they were produced were not sufficiently explained. But a first objection to his interpretation derives from the fact that the organisms cultured have properties which are irreconcilable with the hypothesis that they could be mitochondria.

They were first cultured with paradoxical facility on the ordinary broth of bacteriologists, to which had been added 5 per cent. glycerine and 1 per cent. potassium nitrate. Now, we know how difficult it is as a rule to find a medium suitable for bacteria adapted to conditions as special as those of intracellular life. It would, then, be at least surprising that mitochondria, highly modified forms if they are indeed bacteria, would let themselves be cultured so easily in an ordinary medium.

The characters of the culture were no less bizarre. The bacteria were extremely polymorphic. They were astonishingly resistant to heat, up to 115° in a moist atmosphere, to 145–150° in a dry one. The scum, immersed in absolute alcohol and chloroform, resisted for whole months; on dehydration it could be brought to boiling point in both these liquids, or heated in acetone to

120° in a sealed tube. Finally, these bacteria were motile and strictly aerobic.

Now, on the contrary, the precise observations of different workers, notably of Regaud⁵²⁸ and of Guilliermond⁴⁵⁵, have taught us that within cells the mitochondria that can be seen in living tissues without the action of any reagent are extremely fragile structures; a slight variation in osmotic pressure makes them swell up and disappear; they do not resist a temperature over 40°. They are also destroyed by alcohol and acids, even weak ones. To preserve them, special fixatives are needed, such as formol. They are homogeneous structures, semi-liquid bodies, malleable, structureless, whereas bacteria are rigid in form, with a definite structure and are resistant to the most varied reagents. When suitably fixed and stained, preparations of mitochondria show, it is true, an outline reminiscent of bacteria, but it is a chance resemblance and quite superficial.

Histologists, including Regaud, Guilliermond and Laguesse, relying on these considerations, have regarded Portier's identification as absolutely impossible. The mitochondria are intracellular bodies, being derived perhaps always from each other by division, certainly playing a considerable role in intracellular differentiation and synthesis, but with particular properties that are irreconcilable with those of the bacteria cultured by Portier and described by him under the name of symbionts.

These properties, as Portier recognized, recall to bacteriologists either those of *Bacillus subtilis*, which might have been introduced in the course of manipulation (the aseptic extraction of certain organs is extremely difficult to achieve), or those of common saprophytes, provided with spores, which occasionally break through the external or intestinal barriers of the organism and become immobilized in the form of spores in the organs or tissues. Control experiments made at the request of the *Société de Biologie* by Portier and Bierry on one side, and L. Martin and Marchoux on the other, led the four experimenters to the following conclusions:

1. The passage of pieces of the organs of an animal into a culture medium is always difficult to achieve with constant asepsis. It is one of the most difficult operations in bacteriology.
2. A successful culture is not generally obtained from healthy organs when the pulp of testes is used.

3. One may find micro-organisms in testes either when working with whole organs or with large fragments. The presence of these microbes in the testes is not constant, hence it is impossible to affirm that they exist normally (*C.R.Soc. Biologie*, vol. 83, p. 654, 8th May, 1920).

Consequently, it cannot be considered as established that normal intracellular micro-organisms have been cultured, still less mitochondria.

One is no more justified in saying, with Portier (*Les Symbiotes*, p. 79), that mitochondria have previously been cultured *in vitro*, and referring, as a proof of this, to the bacteroids of the Leguminosæ. These have, indeed, been cultured and are autonomous organisms, *Myxobacteria*. All that they have in common with mitochondria is that they are intracellular.

The hypothesis of normal and primordial intracellular symbiosis, such as Portier proposes, does not rest, then, on authentic facts established by experiment, and the classical cellular theory stands in its entirety. That does not dispel all possibility of reality for ideas of cellular dualism and the existence of autonomous intracellular organisms. But they still have to be demonstrated from start to finish, and, moreover, it is just as natural, if not more so, to attribute to the cell itself the faculty of accomplishing the essential functions of life, as to imagine it powerless and only able to assimilate through the intermediary of bacteria.

Symbiosis, then, remains for the present an exceptional phenomenon in multicellular organisms, or in the cell considered in isolation; we know, as we have had occasion to see, that it occurs over a very wide field, and it is possible that it will finally be found to be of even greater extent. In the present state of our knowledge it in no way represents the fundamental form of cell life.

CONCLUSION. If one seeks to extract a conclusion from the collection of facts analyzed in this volume, one comes to see that no natural distinction exists between them. Commensalism, parasitism and symbiosis are only categories created by us and as soon as they are thoroughly analyzed it is impossible to delimit them.

Under varied aspects they are only manifestations of the struggle for life, characterized by specialization in the way in

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which it is exerted, but deprived of all finality or pre-established harmony. Those associations survived which balanced their accounts in a fashion compatible with the existence and perpetuation of the associates; many others must have arisen from time to time but have not lasted through failing to satisfy this necessity.

Where organisms pass from the normal conditions of existence in free-living forms to those in which they are associates, they undergo very considerable structural changes sometimes of enormous extent, which are perhaps the most striking illustration of the reality of their evolution, and, above all, of the influence of the environment on the organisms; but the capricious diversity of these transformations indicates that the evolutionary changes are principally conditioned by the intrinsic properties of diverse living forms.

The associations which we find in the different forms of commensalism, parasitism and symbiosis involve in the participating organisms functional activities and special developments that we do not see in free-living forms. From this arise multiple problems, not only morphological in character but also, and perhaps principally, physiological, problems of extreme complexity that we are only beginning to perceive and touch upon, and of which the interest cannot be exaggerated. Although points of view will inevitably change, the subject of this book will long remain topical in biology.

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