C H A P T E R   T W O

Mollusca

It seems unusual that a phylum so highly organized as that of mollusks should contain several parasitic species and that morphologically specialized forms should be able to adapt themselves to parasitism.

We find evidence that different groups of mollusks have become parasitic and that distinct types of adaptation to parasitism have arisen. Ectoparasitic forms have evolved in a way different from endoparasites. In all of these, it is possible to observe regression of certain organs and the appearance and growth of new structures that have not existed previously.

Mollusks present two distinct types of parasitic adaptations. In the first, parasitism is resorted to by larval forms only, the corresponding adults being free-living whereas in the second, the adults only are parasitic and the larval forms free-living.

To illustrate the diversification of host relations and morphological adaptations of mollusks to parasitism, conditions in the *Unionidae* and in a series of peculiarly modified gastropods will be discussed. A series of genera will be compared, some of which are only commensals or predators while others show varied morphological and biological adaptations to specialized forms of parasitism.

Parasitism among larvae, sometimes called protelian parasitism, is found only in bivalve mollusks and constitutes a normal stage in the life cycle of fresh-water unionids. Consequently, parasitism in larval unionids is neither accidental nor occasional but represents an important stage in the life history of the species.

Female unionids incubate their eggs in brood pouches that are formed in the gills. On hatching the larvae are expelled through the excurrent siphon. The number of eggs produced by a single fresh-water clam is something remarkable; several hundred thousand to over a million larvae may be thrown out by a single mussel.

The larval unionids, known as *glochidia*, possess a characteristic morphology. A single glochidium has two small, hornlike shells or valves that protect the so-called embryonic mantle. The valves are mobile around their base and can be applied against one another by the contraction of a small transverse muscle that unites them. A gland located between the two valves, near their base in the region of the hinge, secretes a viscous fluid that hardens on contact with the water and emerges as a long thread from between the valves. The embryonic mantle bears sensory organs along its free edge. The shape of the valves is usually more or less triangular or heart-shaped, although in some species the valves are shaped somewhat like the head of an axe (*Proptera*). In several species, the apex of each valve bears on its inner margin an articulated hook or spine that folds back when the two valves are apposed. Smaller fixed spines are also found on either side of the hinged spine (*Anodonta, Unio, Strophitus*). In other species the valves are spineless (*Margaritana, Lampretes, Proptera*).

The glochidia are expelled in large masses from the clam and in some species remain attached to one another by their threads, forming small bunches that fall to the bottom. Their specific weight is so close to that of water that the slightest disturbance of the water throws up clouds of glochidia. The turmoil caused by the fins of passing fishes is sufficient to create a veritable tempest of glochidia that brings them into contact with their host. Most of the larvae are drawn in by respiratory movements of the fish and distributed over the gills or other parts of the body. Glochidia with articulated spines usually attach themselves to the fins and sometimes to the epidermis, whereas unarmed larvae (Fig. 15A) fix themselves onto gill filaments.[1]

In both cases the tissues of the host are imprisoned between the valves. When articulated spines are

[1] Hookless glochidia of *Quadrula heros* have been found on the fins of the sheepshead *Aplodinotus grunniens* Rafin. (Surber).

present, these first pierce the tissues and then fold back, so that the larval bivalves are literally clipped onto their host. The host's epidermis reacts strongly

that the glochidium derives its necessary metabolites from disintegration products of its own body. The adductor muscle is the first organ to be digested
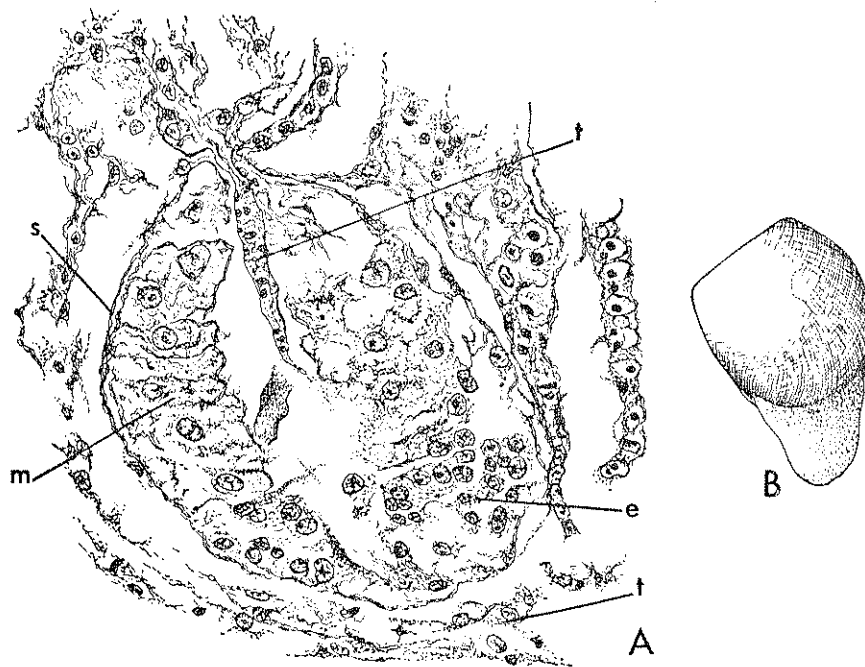

FIG. 15. A. Section through a gill to which a glochidium of *Elliptio complanatus* (Dillwyn) is attached. B. Young clam freshly detached from the fish. e.—embryonic cells. m. larval mantle. s.—larval shell. t.—gill tissue from the host (from an original slide presented by Dr. M. Matteson).

to the presence of the parasites and in a short time covers them completely. This host reaction is not accompanied by any local multiplication of the cells. The epidermis grows over the parasite much in the same way that it would cover a small wound (Arey). Neighboring cells migrate to the site of the lesion at a much faster rate than they would if it were an ordinary wound. When it is entirely enclosed within the epidermis of its host, the glochidium undergoes complete metamorphosis which is seldom accompanied by an increase in size except perhaps in the case of *Proptera laevissima* Lea. The colder the water, the longer the duration of metamorphosis and the easier it is to follow all the successive steps. The host tissues, enclosed within the valves, are gradually liquefied by a secretion arising from cells located in the embryonic mantle. The liquefied tissues are absorbed by the mantle and serve as nourishment. When all the host tissues are digested, it is found

and it is followed soon after by the larval mantle. During this time new structures are being formed. Definite organs, such as an intestine, heart, liver, gills, foot, and mantle, replace the embryonic organs. Metamorphosis is now terminated and the tiny mussel is seen to move around within its cyst, the walls of which become gradually thinner. Finally, thrusting out its foot, the young mussel breaks through the epidermis and falls to the bottom where it burrows in the mud and grows into an adult clam (Fig. 15B). All the energy necessary to accomplish larval metamorphosis is not derived entirely from the tissues of the host. The glochidium does not need to be in contact with the host's blood, for its cyst wall is not abnormally vascular. It is, however, probable that the glochidium benefits from its respiratory exchanges from the immediate vicinity of capillary vessels. Part of the materials used for building up the young mussel are derived from the disintegrated tissues of the glochidium. This metamorphosis is comparable to the nymphal stage in insects.

Protelian parasitism (Tucker) appears to be a necessary stage in the life history of all unionids

even in *Anodonta imbecilis* Say where it had been considered optional (Lefevre & Curtis). These authors also assume that metamorphosis of *Strophitus edentulus* Say occurs within mucus threads containing the glochidia which are formed in the body of the female, and later are expelled into the surrounding water. This observation is questioned by Arey.

Experimentally, glochidia may be made to attach themselves to many kinds of fishes and even to tadpoles and axolotls, yet it appears that complete larval development can be obtained only when the glochidia affix themselves to particular species of fish which seem to be fairly specific for a given mussel. In fish other than these, natural resistance to the glochidia seems to exist, although these attach themselves to the fish they are sloughed off before metamorphosis is completed.

The European species of mussels, *Anodonta cygnaea* (L.), *Unio batavus* Lam., and *Margaritana margaritifera* (L.), are always found on cyprinids, the first species attached to the gills and the last two to the fins. Complete larval development of *A. cygnaea* has been obtained on axolotls (Fausseck). In this country, the glochidia of *Lampsilis anodontoides* Lea attach themselves to the gar pike, *Lepisosteus osseus* L.; those of *Lampsilis luteola* Lam. to the large mouth bass *Huro salmoides* (Lacep.), and those of *Hemistema ambigua* Say to the gills of mud puppies, *Necturus maculatus* Rafin. Even normal hosts acquire some kind of immunity that appears after the third consecutive infestation. The skin of the fish becomes unsuitable for further glochidial development in exactly the same way as that of an unfavorable host (Arey). An antagonism between glochidia and parasitic copepods also seems to exist. Twenty specimens of the latter on a short-nosed gar, *Lepisosteus platostomus* Rafin., are sufficient to cause a skin reaction that will prevent the glochidia from attaching themselves (Wilson).

The enormous number of glochidia produced by a single female mussel might appear as a physiological adaptation, somewhat teleological in nature, to a parasitic mode of life. Yet other bivalves, oysters for example, produce enormous numbers of young. These, however, do not have a parasitic existence but become sedentary as soon as they are expelled into the sea. Incubation in the gill pouches is found only in fresh-water bivalves. In all cases where the number of eggs is small, as in *Sphaerium*, incubation proceeds until metamorphosis is terminated. In *Mus-*

culium partumeium (Say) eighteen to twenty-four eggs may be incubated simultaneously. But there is evidence that these small fresh-water bivalves do not live longer than one year. The length of life of unionids is much greater than this and during this time growth continues. This might account for the larval mussels being expelled before attaining their complete development, since the female utilizes part of its food requirements for growth. Yet no explanation can be found as to why the incompletely formed clams attach themselves to fishes.

Parasitic adult snails do not form a homogeneous group although there is evidence of their possessing converging anatomical characters. Curiously enough, all the known parasitic snails belong to the prosobranchiate gastropods and are usually placed with the *Aglossa*, i.e., they are deprived of a radula.

Snails are recognized as predators or commensals of other snails, tunicates, and echinoderms, but all the parasitic species are associated with echinoderms only. This is all the more interesting since both prosobranch mollusks and echinoderms are among the most ancient invertebrates and their fossils are found together in early Paleozoic beds. A fossil commensal, *Platyceras spiralis* Hall, has been found at Crawfordsville, Indiana, on the arm of an early Triassic crinoid and another species has been reported from a crinoid recovered from Devonian beds in the Eifel (Germany).

Although our knowledge of parasitic gastropods has increased greatly in recent years, the nature of their association with the hosts is not always clear and it is probable that further research will reveal that a number of species recorded as parasitic are sedentary predators.

Species of the pyramellid genus *Odostomia* are found free in the sea, under stones, and associated with bivalve mollusks. *O. scalaris* Macg. introduces its proboscis in between the two valves of a mussel, feeding on the organisms in the branchial chamber (Fig. 16). This species is apparently a very specialized feeder and may also thrust its proboscis into the mouth of tubicolous annelids. A false foot that surrounds the proboscis appears to exist. The eggs are deposited upon the host and the snails are found to be protandrous hermaphrodites (Fretter & Graham). *O. tellinae* Pelseneer lives within the mantle cavity of

[2] *Entovalva mirabilis* (Voeltzkow) is a lamellibranch mollusk that has been recovered from the intestine of a *Synapta*. It does not appear to be a true parasite.

a much greater egg production has become possible by a modification of existing organs. The vagina and oviduct become enormously dilated and function both as a receptacle for the eggs and as a brood pouch.

In *Paedophoropus*, the foot is transformed and is adapted as a brood pouch but this genus shows evolutionary trends distinct from the previous types.

The intimacy of parasitic adaptation in mollusks may be judged by the gradual regression of the digestive organs. These adapt themselves to liquid food of high nutrient content. The disappearance of the
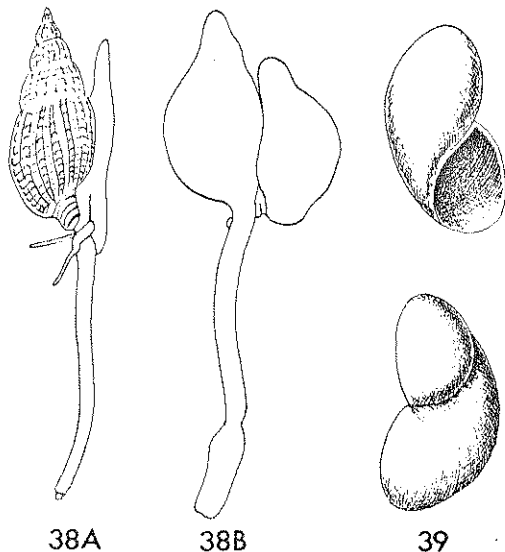

38A   38B   39

FIG. 38.   FIG. 39

FIG. 38. A. *Nassa*. B. *Paedophoropus*. Showing the comparative development of the foot. (Iwanow).

FIG. 39. Larval shells of *Paedophoropus* showing the tendency to wind spirally. Compare with Figure 30 (Iwanow).

stomach, intestine, and anus implies that all of the food is resorbed and consequently that it is entirely liquid and predigested before being taken in by the parasite. Finally all traces of digestive organs have disappeared and the parasites assimilate their food directly from the surrounding tissues of the host with which they are practically incorporated.

The distribution of sexes in mollusks is highly variable; in a given genus some species are hermaphroditic and others bisexual. This condition is so labile that in many instances there may be seasonal alternation of sex in the same individual and in extreme instances, males have entirely disappeared leaving only parthenogenetic females. It is, there-

fore, not surprising to find the same conditions among the parasitic species. Sexual dimorphism cannot be attributed to parasitism, since it is constantly found in the free-living species. However, dwarf males, probably neotenic larvae, have never to our knowledge been reported from free-living snails. Their appearance in *Entoconcha* and *Entocolax* has no doubt enabled these parasites to become highly specialized, since the hazards for successful fertilization would otherwise be far too great for their survival.

Finally, the foot that represents such an important organ in free-living forms has evolved, in parasitic species, along different lines. It is enormous in the females of *Paedophoropus* and has entirely disappeared in *Entoconcha*, *Entocolax*, *Enteroxenos*, and *Thyonicola*, while in the other genera its reduction is variable. The false foot is an entirely new adaptation.

It is clear that mollusks have been able to adapt themselves to parasitism with the remarkable plasticity of their organs. Different organs independently at different times and in different groups have become specialized. The trend toward specialization is still visible and has enabled the parasitic species to adapt themselves successfully to their hosts. Although our present knowledge is too scanty to determine the host-parasite relationship, it is probable that we are dealing with very old associations. It should be remembered, however, that echinoderms are about the only potential hosts that are sluggish enough to allow snails to climb over them and that perhaps the host-parasite relationship that we observe today is only the result of natural selection, involving failure of the snails to attach themselves to other hosts.

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From data available, it is clear that specific glochidia occur on fishes that inhabit the same biotope as the adult clams, and that both the speed of the fish and the levels at which it swims influence the fixation of the larval clams. Consequently, ecological segregation appears to be the principal cause of this form of ectoparasitism. It should, however, be borne in mind that results obtained experimentally are not always comparable with conditions as found in the field. Usually, experimental infestation of aquarium fishes with glochidia are far more intense than in nature, since the fishes cannot escape from the parasites. On the other hand, from experimental evidence it appears that the fish reacts to the presence of the parasites in such a way that subsequent infestations become lighter and finally that no more infestation occurs. This would indicate that the fish can acquire some kind of immunity toward successive infestations by the same parasites. A tissue reaction has been found in the host and has been studied by various authors, although its nature has not yet been discovered (Reuling). Since this reaction is correlative with the intensity of the infestation, it is probable that it hardly ever occurs naturally since most hosts are able to escape from massive infestations such as would occur in the laboratory.

b. *Adults parasitic; larval stages free-living.*

The nature of the relationship between parasitic prosobranchs and their hosts has not been sufficiently investigated to support any evidence of host specificity. Moreover, the data available as to the rate of infestation are far too scanty to be of any statistical value. It should be noted, however, that in all cases where parasitic prosobranchs have been reported, the hosts are always echinoderms and no species of parasitic snail is known from any other group of hosts. Since both gastropods and echinoderms are exceedingly old forms of animal life, it seems likely that the association that has sprung up between them must have arisen sometime in the late Paleozoic or in early Mesozoic times.

Most of the parasitic copepods can be included under this heading, although in several cases their free-living larval existence is shortened through metamorphosis occurring while the young is still within the egg membranes.

In many cases there exists a very distinct host specificity visible in that certain genera and species always occur upon the same hosts. Many genera are specific for ascidians, others for annelids. Fishes belonging to the same family harbor identical genera of copepods that are sometimes different from those harbored by other fish families. Unfortunately, here also, statistical evidence is insufficient to warrant definite results. Parasitic copepods are obviously ecologically segregated upon their hosts; and the more specialized modes of feeding, with the morphological adaptations that appear subsequently, have certainly caused the association to become very intimate. This is particularly well marked in blood feeders of which each genus and often even each species is adapted to a definite species of host.

The majority of fleas have free-living larvae that occur either in the nests or in the dens of their hosts where they feed on organic detritus. Consequently, the relationship of the parasite and the host acquires a definite degree of permanence. On the other hand, as everybody knows, fleas are apt to abandon one host to pass onto another. Such exchanges occur even when both of the hosts are living. The ecological isolating factor, however, still occurs and in certain cases this has given rise to new species of parasites.

Fleas occur exclusively on mammals and on birds, the mammalian species being the more primitive. *Palaeopsylla*, a genus found on present-day shrews and moles, occurred in the Oligocene where it has been reported from Baltic amber.

Ecological segregation of adult fleas upon their hosts is very clearly marked when the hosts themselves occupy a specialized biotope. For instance, ischnopsyllines have been reported only from bats, and coptophyllines from jerboas, a group of Old World jumping mice. Such instances of isolation upon hosts living in colonies from specialized biotopes may even lead to supporting evidence of phylogenetical relationship between hosts.

European ground squirrels harbor a series of genera and species that are included in the citellophyllinines. One species of ground squirrel, *Citellus fulvus* (Licht.), from Southern Russia occasionally harbors only fleas belonging to the oropsyllines, a group that occurs exclusively on American ground squirrels and prairie dogs. Since both prairie dogs and ground squirrels are known to have arisen from common ancestors, it can be assumed that the latter already harbored fleas. This situation must have existed before Eurasia became separated from America, or in other words, during the Miocene. It is also possible to assume that the species of fleas from the Russian ground squirrel has retained ancestral characters

The ecological approach to the study of parasitism clearly shows that many organisms appear to have been predisposed to becoming parasitic, and that they were preadapted to a different mode of life that has enabled them to establish themselves successfully in a new ecological niche.

The idea of preadaptation, as conceived by modern biologists, in no way implies the existence of a preconceived plan, of a directed form of evolution outside the scope of human discernment. Preadaptation means that organisms living in a given environment may possess, besides their normal adaptive characteristics, other potentialities that may never, normally, become manifest. If, however, for some accidental cause the environment be modified, fresh water becoming brackish or drying up for instance, the organisms that possessed such potentialities are able to survive in the new environment and would, therefore, be considered as preadapted. Preadaptation may be either physiological or morphological, and it also implies that such organisms are able to pass from a generalized type of environment to a more specialized one.

Cave-dwelling arthropods (mites, dipterans, and other insects) have passed secondarily onto bats. From leading a purely guanophilic existence they were prepared to become blood feeders, since they were accustomed to a high nitrogen content in their diet. Richer food was advantageous for the species, whose reproduction rate increased in consequence. Once arthropods were established physiologically, morphological changes could be evolved and, naturally, those that were best adapted for the particular type of existence stood the greatest chance of surviving. It is obvious that the individuals that were physiologically adapted, but not morphologically, were gradually eliminated by selection.

The origin of lice, and probably also of fleas, can be explained in similar manner although here the free-living ancestors were no doubt insects dwelling in the bark of trees. Subsequently, as in lice, the entire life cycle occurred upon the host.

Two very good instances of constitutional preadaptation are that of fly larvae and of worms like nematodes that normally feed upon decaying organic matter, and, in this case, physiological adaptation appears to have been more important than the subsequent morphological adaptation. The latter does not even appear to have occurred in fly larvae and exists, moreover, in only a few groups of parasitic nematodes.

It has been demonstrated that adult flies lay their eggs in certain places or upon certain animals to which they are attracted by odor, and also that the nature of this attraction is liable to be conditioned. Consequently, maggots will grow in different hosts but the selective influence that will eliminate unfavorable hosts will also, but inversely, affect conditioning of the adult flies to the most favorable hosts.

Since free-living nematodes and scavenger beetles both feed upon decaying organic material, it is easy to understand in what way the former have become established in the latter species. It is probable that nematodes became established in the intestine of vertebrates either directly or via insects, but, in any case, they were physiologically preadapted to living in an atmosphere with a low oxygen tension. Many of the present-day species of nematodes that live in the cloaca of reptiles, and that reproduce continuously without leaving their hosts, should be considered as illustrating one of the stages through which the free-living forms passed before becoming parasitic.

All the known ecological niches have been populated accidentally and this is especially true for parasites. The number of unsuccessful attempts must have been enormous and were doubtless due, primarily, to the inability of the species to become physiologically adapted, since among parasites there does not appear to be any evidence of competition for survival as the food supply is generally plentiful.

From the outset, parasitism benefits the species that has adopted this mode of life, boosts its fertility, and thus increases the chances for the invasion of new hosts. Parasitism also exerts a conservative influence on the species because lack of competition is particularly favorable for the survival of a much

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larger proportion of mutations than would persist among free-living organisms.

Life cycles involving intermediate hosts have no doubt arisen secondarily, since they are corollary to an increased fertility; but here, of course, ecological factors are of primary importance in establishing the nature of the intermediate hosts.

The distribution of parasites, as found today, is clearly the outcome of hundreds and thousands of unsuccessful experiments, in the course of which species or individuals have been eliminated. There is no evidence of ectoparasites being older than entoparasites; both types have evolved independently and sometimes side by side. Ectoparasites are frequently a cause of irritation to their hosts, that scratch and bite themselves to get rid of these undesirable animals and, in so doing, swallow their parasites. Yet this has never led to the parasites becoming established in the intestine of the host.

All turbellarians are hermaphroditic and from this stock have arisen some of the most successful lines of parasites, such as monogenetic trematodes, digenetic trematodes, cestodarians, and cestodes, although some of these have become secondarily dioecious. It can be easily understood to what extent hermaphroditism is able to benefit a species, since it increases its chances of invading new niches. For each freshly established bisexual parasite, the corresponding number of hermaphrodites is many times greater.

One of the most evident consequences of the parasitic mode of living is the appearance of neoteny that mostly affects the male sex only or, more rarely, both sexes as in certain mites. Neoteny has also been reported from free-living organisms although much less frequently. The cause for neoteny is undetermined, but its relative frequency among parasites might indicate that it is in some way related to the quality of the food available and to the presence, in the latter, of certain essential substances.

As previously stated, physiological adaptation has been a condition *sine qua non* for organisms to be able to become parasitic, and even more so for entoparasites than for ectoparasites. Parasitism affects an organism in two totally different ways, physiologically, through causing it to lose the power to synthesize part or all of its essential nutritional requirements, and morphologically, through the loss of all superfluous organs. The greater the effect of either one or of both of these factors, the more

highly specialized and therefore the more intimately adapted to its host will the parasite be.

It is certain that parasitism has appeared at frequent intervals in the course of the thousands of centuries during which plants and animals gradually occupied all the available niches. In several groups, such as arthropods, nematodes, and protozoans, parasitic forms arose from species that had already become differentiated, and consequently that had evolved along distinct lines. This is clearly evident in the actual parasitic mites and in the nematodes.

Indirect evidence, as stated previously, leads to the conclusion that flagellates have been associated with termites and other wood-eating insects ever since the Paleozoic, and that during the same period the crinoids harbored myzostomids and perhaps the echinoderms, parasitic snails. The ancestors of cestodes and acanthocephalans have disappeared, together with their primitive fish hosts but, unlike the latter, they unfortunately did not leave their impression in the stone.

Primitive, mid-Tertiary mammals harbored fleas that showed all the characteristics of the group as it is known today, and parasitic tachinid larvae developed from maggots that fed upon these same dead animals.

It is obvious that new ecological niches for parasites appeared as the vertebrates evolved into their ultimate orders and families, and that the parasites invaded these new territories, some successfully, others less so. Subsequent isolation of both the host population and the parasites led to speciation and also to segregation of the larval forms. In physiologically highly specialized parasites like tapeworms that also require metamorphosis of the infestive larvae, there is every evidence that parallel evolution of the hosts and the parasites has occurred and has been maintained in spite of different hosts occupying identical biotopes. This is primarily due to the peculiar nutritional requirements of the parasites. It is possible that a similar mechanism may have existed originally for all helminths, but, in the groups other than tapeworms, the infestive larval forms do not need to undergo metamorphosis in the final host, and also the parasites appear to be less specialized from a physiological standpoint. Consequently, ecologically similar hosts are apt to harbor the same species of parasites and the distribution of these parasites will also be ecological as opposed to the phylogenetic distribution of cestodes.

It has often been stated that groups of hosts or host species that are isolated geographically, or for other reasons, harbor parasites that tend to split into a great number of subspecies. Examples of such instances are the lice and tapeworms of hyraxes and the tapeworms of African green pigeons and also of guinea fowls. Inbreeding of isolated populations tends to preserve small genetic variabilities that disappear when random mating occurs. This is especially true for hyraxes and also for the two groups of birds mentioned previously, which tend to subspeciate to a degree that is alarming to taxonomists.

Lice that live upon these isolated populations inbreed freely and, consequently, small genetic variations are preserved and are considered by taxonomists as of sufficient importance for distinguishing species. Tapeworms are mostly self-fertilizing and, consequently, the conditions are particularly favorable for preserving all the genetic variations that may occur. Since the intermediate host is, necessarily, an arthropod that occurs in the same territory as the host, the chances of these genetic variations being preserved are considerable, much more so, in fact, than if the hosts were spread over entire continents.

This also shows that it is impossible to ignore the host when studying the parasites, and that slight variations from a given morphological type may lead to interesting conclusions. In the cestode genus *Hymenolepis* for example, the combination of mor-phological characters of the species is considerably smaller than in other genera, owing to the fact that there are only three testes and that the rostellum is usually armed with a small number of hooks, the shape of which varies slightly even within a given species. This genus contains a very great number of species, many of which occur exclusively in ducks and these hosts, although migratory, breed in ecologically similar surroundings. Moreover, during the breeding season they form distinct populations which explains also the extraordinary variations found in their parasites.

From the foregoing conclusions it is clear that parasites no longer appear as organisms that have escaped from the effects of selection and sought a secluded existence within another organism, the host. Parasites are probably as old, if not older, than most of their present hosts, and a definite physiological preadaptation has enabled them to invade such peculiar ecological niches as the digestive system, natural cavities, the skin, the gills, etc., of other animals where they have become successfully established. As new hosts appeared and new niches became available, the parasites also invaded them, yet in the process they have continually been subjected to the same laws as all other living organisms, except that the rather peculiar nature of their ecological niches excludes competition and, consequently, parasites would be the only animals that are spared the struggle for existence.