

THE NATURAL HISTORY OF SLAPTON LEY NATURE RESERVE: VI STUDIES ON THE PARASITES

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MANY protozoan and helminth parasites are encountered during the examination of laboratory and field animals. Their complex life cycles and the problems of their identification often deter the non-specialist from investigating them further.

From 1966 to 1971 a field course was conducted annually for a fortnight in September, the selected results of which, we are encouraged, will be of interest to specialists and to more general field biologists alike. Without being primarily didactic, as teachers we have permitted ourselves to discuss those aspects of our observations which we know are poorly treated elsewhere, and have emphasized features of the parasites in the Ley which are noteworthy and require future examination.

We are aware that our findings are highly selected, for although many parasites show seasonality, our records represent parasites of hosts sampled regularly only in September. Furthermore, absence from our lists might well mean only that parasites were overlooked.

NOTES ON THE PARASITES OF FISH

Fish were trapped in the open water and reeds around the bridge and boat house. They were also caught in seine nets at E₂ and E (Mercer, 1966, Fig. 6). Pike were occasionally provided by fishermen; these may have been caught anywhere.

Table 1. *Parasites of the fish in Slapton Ley*

Parasite	Site in host	Host
Ectoparasites—		
ANNELIDA, HIRUDINEA		
(a) <i>Piscicola geometra</i> (leeches)	Skin	<i>Esox lucius</i>
CRUSTACEA, BRANCHIURA		
(b) <i>Argulus foliaceus</i> (fish louse)	Skin	<i>E. lucius</i> , <i>Perca fluviatilis</i> , <i>Rutilus rutilus</i> , <i>Scardinius erythrophthalmus</i>
CRUSTACEA, COPEPODA		
(c) <i>Ergasilus gibbus</i>	Gills	<i>Anguilla anguilla</i>
PLATYHELMINTHES, MONOGENEA		
(d) <i>Dactylogyrus</i> spp.	Gills	<i>R. rutilus</i> , <i>S. erythrophthalmus</i>
(e) <i>Neodactylogyrus</i> spp.	Gills	<i>R. rutilus</i> , <i>S. erythrophthalmus</i>
(f) <i>Tetraonchus monenteron</i>	Gills	<i>E. lucius</i>
PROTOZOA, CILIATA		
(g) <i>Trichodina</i> sp.	Skin	<i>P. fluviatilis</i> , <i>R. rutilus</i>
Endoparasites—		
PLATYHELMINTHES, CESTODA		
(h) <i>Caryophyllaeides femica</i>	Intestine	<i>R. rutilus</i> , <i>S. erythrophthalmus</i>
PLATYHELMINTHES, DIGENEA		
(i) <i>Crepidostomum metoecus</i>	Pyloric caeca, intestine	<i>Salmo trutta</i>
(j) <i>Diplostomum spathaceum</i>	Lens and humour of eye	<i>A. anguilla</i> , <i>E. lucius</i> , <i>P. fluviatilis</i> , <i>R. rutilus</i> , <i>S. erythrophthalmus</i>
ACANTHOCEPHALA		
(k) <i>Acanthocephalus clavula</i>	Intestine	<i>P. fluviatilis</i> , <i>R. rutilus</i>
(l) <i>Acanthocephalus luci</i>	Intestine	<i>A. anguilla</i>
PROTOZOA, MASTIGOPHORA		
(m) <i>Trypanosoma remaki</i>	Blood	<i>E. lucius</i>
(n) <i>Trypanosoma percae</i>	Blood	<i>P. fluviatilis</i>
(o) <i>Trypanosoma granulolum</i>	Blood	<i>A. anguilla</i>
(p) <i>Cryptobia borelli</i>	Blood	<i>R. rutilus</i>
PROTOZOA, MYXOSPORIDA		
(q) <i>Myxobolus</i> spp.	Swim-bladder Gills	<i>S. erythrophthalmus</i> <i>R. rutilus</i>

(a) *Piscicola geometra* is a blood-sucking leech commonly attached to fish. It has a cylindrical green and cream body, is about 2.5 cm. long and has well marked segments, with the head region distinct from the body.

(b) *Argulus foliaceus*, the fish louse, is a temporary ectoparasite with a wide host range, found in the plankton and on the skin of fish. There are two suckers for holding the host and a poison spine and long proboscis for feeding. "Blooms" occasionally occur; in 1970 for instance very large numbers were recovered in a plankton trawl.

(c) *Ergasilus gibbus* (original record to be published by R. Wootton (personal communication)).

(d) and (e) *Dactylogyrus* spp. and *Neodactylogyrus* spp. are small (0.4 mm. long) flat, strap-shaped worms which are transparent except for four small black eyespots. These dactylogyrid gill parasites are, like most monogeneans, highly host specific. Precise identifications of the dactylogyrids on rudd and roach from the Ley have not been made; Yamaguti (1963) lists hosts and species of these two genera. Dactylogyrids have a single pair of large recurved hooks (hamuli) on the posterior attachment organ and these are joined either by a single connecting bar (*Dactylogyrus*) or by two connecting bars (*Neodactylogyrus*). Fourteen small larval hooks assist in attachment to the gill tissue and there are well developed sticky glands on the head region which are used during a leech-like looping locomotion and during feeding. The bi-limbed gut often appears reddish due to contained host blood on which the worm feeds together with gill epithelium of the host. The fish are infected directly by a ciliated oncomiracidium larva which hatches from eggs laid by the adult parasites.

(f) *Tetraonchus monenteron* is specific to pike gills; it is small and almost transparent and has four eyespots. The generic name of this parasite derives from the fact that these worms have four hamuli on the attachment organ and the specific name refers to the possession of a single-limbed, centrally situated gut. *T. monenteron* usually occurs in fairly large numbers on pike gills (100–200) and may show a slight preference for the first gill. Adult worms on the gills of the pike produce eggs which drop to the bottom of the water and eventually hatch, releasing a ciliated dispersive larva, the oncomiracidium, which infects a new pike.

(g) *Trichodina* sp. As with most trichodinids those found were ectozoic on the skin and gills of fish. Specific diagnosis is very complex and those found on perch in the Ley have not been fully identified. They are all drum-shaped, peritrichous ciliates measuring 50–100 $\mu\text{m.}$, with the aboral end developed into an elaborate disc bearing a cirlet of locomotory cilia, and an inner ring of articulated hooks which impart a radial symmetry (Plate I, Fig. 4). The ciliates skim over the epithelial surface of the host, attaching with the flexible disc. The oral surface, directed away from the host, bears a double row of peristomal cilia which create a feeding current. The ciliates swim freely for short periods holding the attachment disc in front. Reproduction is by binary fission and by conjugation, in which the conjugants may be of different sizes. Infection probably occurs when the ciliates swim from one fish to another. An account of the structure, habits and reproduction of trichodinids of fish is given by Davis (1947).

(h) *Caryophyllaeides fennica*, is astrobilate, i.e. the body is not divided into proglottids, and there is a single set of reproductive organs situated at the posterior end of the body. The worms measure about 1.0–3.0 cm. long and the anterior holdfast is unarmed and undifferentiated. *C. fennica*, like the related form *Caryophyllaeus laticeps*, is primarily a parasite of cyprinid fishes (chubb, dace, roach, rudd and bleak). These two genera are easily distinguished in that the uterus and lateral ovaries extend anteriorly to the male genital pore in *Caryophyllaeides*, whereas in *Caryophyllaeus* the ovary does not extend as far as, and the uterus only reaches the level of the male genital pore. It has been suggested by Borgström and Halvorsen (1968) that *Caryophyllaeides* may be a parasite of female roach and that some physiological barrier exists to infection of male hosts. Although fishes were sexed prior to examination at Slapton the records are not complete enough to permit speculation on this point. Kennedy (personal communication) does not believe that *C. fennica* has a

higher incidence in female fishes but this situation seems to differ for *C. laticeps* since Kennedy (1968, 1969) working on this parasite finds a higher incidence in female dace. He suggests this could be associated with a lowered resistance to infection due to stress or a hormone-linked phenomenon, or a change in the feeding habits of spawning females. The occurrence of *C. laticeps* from dace in the Hampshire Avon has been reported to be highly seasonal, being maximal from January to February, then declining until August when the infection may disappear altogether until December, when a new infection occurs (Kennedy, 1968). In fact, *Caryophyllaeus* seems to live for only a short time in the fish (3 months) and there is some evidence that some kind of host reaction may curtail the infection (Kennedy and Walker, 1969). The situation is probably different for *C. fennica* since Borgström and Halvorsen (1968) found *C. fennica* in roach throughout the year in Lake Bokstad, Norway and at Slapton *Caryophyllaeides* has been found at the end of September.

The adult worms in the gut produce eggs which are eaten by naidid worms. *Nais proboscidea* has been suggested as a host for *C. fennica* but *C. laticeps* uses a tubificid. The larvae hatching from the egg in the gut of the naidid uses its six hooks to bore through the gut wall of the annelid and reaches the body cavity where it develops to an infective proceroid. The proceroid probably lives in the annelid for up to two months. *C. laticeps* is infective after four months and may live for up to two years in its tubificid host.

(i) *Crepidostomum metoecus* was found in trout recovered from the Ley, but probably came from nearby streams. *C. metoecus* is about 0.9–3.0 mm. long and has an oral sucker surrounded by six papillae. The first intermediate host of *C. metoecus* is *Lymnaea pereger* in which stylet-bearing, xiphid cercariae are produced which bore out, damaging the snail and locate a water shrimp, *Gammarus pulex*. The xiphid cercariae penetrate the gammarid and encyst, remaining dormant until eaten by a trout.

C. metoecus is not strictly host specific to trout and has also been recorded from, for example, *Cottus*, *C. metoecus* may be found with a related form, *C. faronis*, which occurs in the posterior regions of the intestine of brown trout. *C. faronis* uses the bivalve *Pisidium* as the first intermediate host but the stylet cercariae penetrate *G. pulex* in the same way as *C. metoecus* before infecting the final fish host (see Awachie, 1968).

(j) *Diplostomum spathaceum* occurred as the metacercaria or diplostomula stage of the strigeid digenean in the lens and humour of eels, perch, roach, rudd and pike from the Ley. Although equivalent to a metacercarial stage, diplostomuli are unusual in lacking a cyst wall and in moving actively, at least when the lens is dissected. There may be over thirty diplostomuli in each eye, so it is not surprising that infections of *Diplostomulum* have been reported to cause blindness in fishes, due to opacity and changes in shape of the lens (Erasmus, 1958). This may in turn affect the feeding behaviour of infected fishes so that, for instance, they may cease feeding in illuminated surface waters and resort to a benthic diet (Wooten, personal communication). The infected fish forms the second intermediate host in a life cycle that involves a lymnaeid snail, generally assumed to be *Lymnaea pereger*, the fish and finally a herring gull, *Larus argentatus*. Baylis (1939) recorded *D. spathaceum* from the eyes of rainbow trout as causing blindness in both eyes; he suggested that this might make the fish easier prey to the birds.

The adult strigeid lives in the small intestine of the bird, feeding on host epithelium

and secretions and the host's food. Strigeid digeneans have accessory holdfast organs in addition to the oral and ventral suckers typical of the Digenea, and the whole forebody is usually modified, being flattened and spoon-shaped in *D. spathaceum* (see Ohman, 1965). The eggs hatch to produce miracidia which infect *Lymnaea pereger* and subsequently develop into sporocysts producing fork-tailed cercariae or furcocercariae termed *Cercaria diplostomi spathacei* (or *C. diplostomum spathaceum* syn. *Cercaria* C. Szidat). These furcocercariae have two pairs of "penetration" glands posterior to the ventral sucker but these appear to produce lubricants or adhesive secretions rather than lytic secretions. The body of the cercaria, including the oral and ventral suckers, is spined (Wesenburg-Lund, 1934; Iles, 1959), and the spines on the oral sucker are thought to be important in assisting penetration through the skin of the fish and subsequent tissue migration. Erasmus (1959), working with a related form (*Cercaria* X Baylis) studied the penetration of the larvae into sticklebacks and noted that cercariae penetrated mainly in the head region, either via the skin or through the gills and pharynx.

Once inside the fish the diplostomuli may actively locate and migrate into the lens and Erasmus (1959) shows that most of the migrating larvae bore through the muscle and connective tissue rather than use a blood route. Larvae that don't reach the lens are destroyed by host phagocytes. The lens is an "immunologically privileged site" in the host, as its lack of blood supply minimizes the immunological response to parasites.

There is still confusion over the precise identity of diplostomulids found in the lenses of fish eyes generally. The situation regarding the identity of the stages in the lens is reviewed in Rees (1955) and in Ohman (1965); a real identification should be based on knowledge of all stages in the life cycles. The complete life history of the diplostomuli from fish in Slapton Ley has not, in fact, been studied by experimental infections, so that the identification given here cannot be definitive. Following detailed examination of over 100 fish aged 0+ to 5+ in 1972 it was found that perch were infected with diplostomuli only in the humour and roach only in the lens.

Lymnaea pereger is, as mentioned, most commonly implicated as the first host of *D. spathaceum* but other species of lymnaeid have been suggested (see Iles, 1959; Williams, 1966a).

Other kinds of strigeid flukes commonly found in eyes of fishes in the British Isles include:

Tyrodelpys clavata in the vitreous humour (only) of various fishes (trout, roach, perch, etc.).

Tyrodelpys podicipina (much larger than *T. clavata*) in the vitreous humour of perch (Wooten, personal communication) (see Kozicka and Niewiadomska, 1960).

Diplostomum gasterostei in the retina of sticklebacks (Williams, 1966a).

Diplostomum palmatoides in the eyes, spinal cord and brain of minnows (see Rees, 1955, 1957).

(k) and (l) *Acanthocephalus clavula* (syn. *Echinorhynchus clavula*) and *A. lucii*. Acanthocephalans are easily recognized by their cylindrical bodies and evaginable anterior proboscides armed with backwardly pointed spines. They live in the anterior intestine absorbing food through their body walls; like cestodes these parasites have no gut. Acanthocephalans have separate sexes, the males are slightly smaller than the females and have, in addition to testes, cement glands and at the end of the body a sack-like bursa which is used during pairing. The larger females can be distinguished

as their body cavities are packed with elongate, oval to lemon-shaped eggs. Female worms were found more often than males possibly because the males are shorter-lived after copulating whereas females persist to lay their eggs. *A. clavula* can be separated from *A. lucii* as it has approximately 17 longitudinal rows of proboscis spines, whereas *A. lucii* has only about 8 longitudinal rows.

Life cycle

The life cycle of these acanthocephalans involves aquatic crustaceans. The eggs pass into the water and are eaten by asellid crustaceans. A hooked acanthor larva hatches from the eggs, bores through the gut wall into the haemocoel and here develops in about 50 days through an acanthella stage into an encapsulated cystacanth with a fully formed invaginated proboscis. Cystacanth of *A. clavula* have been found in *Proasellus meridianus* in the Ley and the incidence of infection ranged from 0 to 0.7 per cent in different regions of the Ley sampled. Chubb (1964) has stated that *P. meridianus* appears to be the only intermediate host of *A. clavula* in Llyn Tegid and that *Asellus aquaticus* appears to be the only host of *A. lucii* in Rostherne Mere. *A. aquaticus* was not found in the Ley, however, so that if this is the only intermediate host of *A. lucii* the eels may have acquired the infection in fast-flowing streams, where *A. aquaticus* is more likely to occur, before moving into the Ley. Data collected over six years suggests that the incidence of acanthocephalans in fish from the Ley is declining, but the reasons for this are not clear.

Trypanosoma spp.

Trypanosomes have been found in pike (*Trypanosoma remaki*), perch (*Trypanosoma percae*) and eels (*Trypanosoma granulorum*) recovered from the Ley. Roach, rudd, trout and the 3-spined stickleback from the Ley were not found infected, though trypanosomes have been described from these fish. Trypanosomes are slender protozoans with a single flagellum, arising posteriorly near a kinetoplast and passing forward along the body on the edge of an undulating membrane.

Trypanosomes are highly host specific and can be identified by characters of the form in the blood. *T. percae* (Plate I, Fig. 1) measures 19.0–52.0 μm . in length and is characterized by a prominent undulating membrane, lateral kinetoplast and crook-like posterior end. *T. granulorum* (Plate I, Fig. 2) is an impressive trypanosome with its body thrown into many tight folds bearing a narrow, undulating membrane almost invisible in life, and a long free flagellum. Commonly occurring short forms (40.0–62.0 μm .) and rare large forms (66.0–80.0 μm .) are often distinguished. Similar small and large forms are recorded for *T. remaki* from pike with measurements from 15 μm . to 57 μm .

Trypanosomes move actively in the plasma, weaving between the blood cells. Most fish harbour low-level infections which are difficult to detect. Blood is best examined fresh after allowing a clot to form: removal of the clot leaves a drop of serum on the slide containing a concentration of trypanosomes.

In experimental infections peak numbers of trypanosomes have been recorded about 2 weeks after infection, followed by chronic low-level infections for many weeks. Dividing forms have only rarely been recorded from blood, suggesting that in many species the increase in numbers during the early stages of infection is brought about by division stages located in the tissues.

Trypanosomes of fish are transmitted by the blood-sucking leech *Hemiclepsis*

marginata. The infective metacyclic forms develop in the gut or proboscis sheath and are inoculated into the fish blood.

(p) *Cryptobia borelli*

Species of this genus have been recovered from the seminal vesicles and spermatophores of land snails, from the gut of marine fish and from the blood (but not the gut) of fresh-water fish. Transmission of the intestinal forms is believed to occur directly from fish to fish though cysts are unknown. Species inhabiting the blood of fresh-water fish are transmitted by the leeches *Hemiclepsis marginata* and *Piscicola geometra*.

Cryptobias resemble trypanosomes in possessing a kinetoplast but differ in having two flagella, both arising anteriorly: one is directed forwards, the other trails on the edge of an undulating membrane. The elongate kinetoplast occupies a lateral position at the anterior end and the nucleus lies further back in the posterior third of the body (Plate I, Fig. 3).

Forms of *Cryptobia* measuring 10–20 μm . recorded from numerous different fish all resemble each other closely and, as thought by Keysellitz (1906), may belong to a single species *Cryptobia borelli* (Plate I), which was originally described from rudd. Other specific names have been given to species from fish, including *Cryptobia gurneyorum* from pike and *Cryptobia truttae* from trout.

As division forms have been reported only rarely from the blood of fish, it is possible, as in the case of trypanosomes, that division occurs mostly in the tissues. Heavy infections can occur but low-level infections are more common.

(g) *Myxobolus* sp.

Myxosporida are common parasites of freshwater fish, often occurring as well-defined cysts in skin or internal organs. Many species are pathogenic, as abundant cysts on the gills may impair respiration and internal cysts may be so large that they cause necrosis of surrounding tissues. Their incidence at Slapton was low: cysts were found on the gills of two rudd and in the connective tissue of the swim-bladder of a single roach. The parasites were identified in both cases as belonging to the genus *Myxobolus* but the species were not identified from the dozen or so which are known to occur in these hosts.

The spores are characteristic: the spore wall, composed of two valves encloses a complex of two polar capsules containing eversible filaments and a binucleate infective agent or sporoplasm, often with an iodophilous vacuole in the cytoplasm. Infections are initiated by ingestion of spores, the sporoplasm emerges when the valves open and is thought to penetrate the intestinal epithelium and be carried in the blood to its site of infection, to form cysts or diffuse infiltrations. Amoeboid trophozoites give rise to spores.

If the site of infection is near the external surface as on the gills of roach, mature spores are liberated by rupture of the cysts into the water. In the case of species inhabiting internal organs, as that in the swim-bladder of rudd, spores are liberated only on the death of the host.

NOTES ON THE PARASITES OF AMPHIBIANS

Almost all of the toads were collected from under logs and stones at South Grounds and G₁ and E₃ on the Causeway (Mercer, 1966, fig. 6).

Table 2. *Parasites of the amphibians of Slapton Ley*

Parasites	Site	Host
Endoparasites— ACANTHOCEPHALA (a) <i>Acanthocephalus ranae</i>	Small intestine	<i>Bufo bufo</i> , <i>Triturus vulgaris</i>
NEMATODA, RHABDIASOIDEA (b) <i>Rhabdias bufonis</i>	Lungs	<i>B. bufo</i> , <i>T. vulgaris</i>
NEMATODA, TRICHOSTRONGYLOIDEA (c) <i>Oswaldocruzia filiformis</i>	Small intestine	<i>B. bufo</i>
NEMATODA, OXYUROIDEA (d) <i>Cosmocerca</i> (e) <i>Aplectana</i>	Large intestine Large intestine	<i>B. bufo</i> <i>B. bufo</i>
PROTOZOA SARCODINA (f) <i>Entamoeba ranarum</i>	Rectum	<i>B. bufo</i>
PROTOZOA MASTIGOPHORA (g) <i>Trichomonas batrachorum</i> (h) <i>Monocercomonas bufonis</i> (i) <i>Hexamita intestinalis</i> (j) <i>Opalina ranarum</i>	Intestine and rectum Rectum Rectum Rectum	<i>B. bufo</i> , <i>T. vulgaris</i> <i>B. bufo</i> , <i>T. vulgaris</i> <i>B. bufo</i> , <i>T. vulgaris</i> <i>B. bufo</i>
PROTOZOA, CILIATA (k) <i>Balanitidium elongatum</i> (l) <i>Balanitidium entozoon</i> (m) <i>Balanitidium duodeni</i> (n) <i>Nyctotherus cordiformis</i>	Intestine and rectum Rectum Rectum Rectum	<i>B. bufo</i> , <i>T. vulgaris</i> <i>B. bufo</i> <i>B. bufo</i> <i>B. bufo</i>
PROTOZOA, SPOROZOA (o) <i>Eimeria</i> sp.	Rectum	<i>B. bufo</i>

(a) *Acanthocephalus ranae*

Acanthocephalus ranae was found in 60–100 per cent of toads in September. Up to 60 individuals were found in a single toad, but the average number of worms per host was 16 in 35 toads studied. Slightly lower infections were found in newts (*Triturus vulgaris*) at the same time of year. Male and female worms showed a clumped distribution within the gut of the toads at the pyloric end of the intestine. Female worms measure about 4.0 mm., the males being slightly smaller. Fewer males than females are usually present so that one or both sexes must have to move around for mating. The proboscis of *A. ranae* is an active structure and the fact that this is invaginable means that the spines it bears can be lifted easily from the host gut mucosa with minimum tearing. The mechanism of attachment in *A. ranae* has been studied by Hammond (1967). The life cycle is typical and involves eggs, acanthor, acanthella and cystacanth stages but the identity of the first intermediate host is still uncertain. Both *Asellus aquaticus* and *Gammarus pulex* have been cited as possible first intermediate hosts and during a student project what was identified as the cystacanth of *A. ranae* was found in *Proasellus meridianus* from the Ley. If these aquatic crustaceans are the only intermediate hosts of *A. ranae* the parasitaemia might be expected to show a seasonal occurrence as toads and newts are terrestrial and would only be exposed to infection during spawning. Crompton (1970) states, however, that *A. ranae* can persist in frogs that have not fed for four months, so possibly the infection could be acquired whilst the frogs or toads were in the water and then

persist. It may be that *A. ranae* is specific to only one species of intermediate host, though cystacanths of acanthocephalans have the ability to re-encyst following development in a paratenic host until eaten by the correct definitive host. Possibly, then, the life cycle of *A. ranae* could involve one true intermediate host and one or several paratenic hosts before amphibians are infected. A search for the intermediate host of *A. ranae* coupled with an investigation of the feeding habits of newts and toads might prove quite rewarding.

(b) *Rhabdias bufonis* occurred in 60 per cent of the toads examined, with a mean of 6.2 parasites per host. There was no significant preference for the right or left lung. This high parasitaemia may be related to the entire absence of lung flukes from the Ley, which are normally common and may compete with *R. bufonis* (Lees, 1962). The adults, which are protandrous hermaphrodites live in the lungs, having a conspicuous black intestine pigmented with haematin and haemosiderin from the host blood (Colam, 1971). Eggs laid in the lungs hatch quickly and first stage larvae are found throughout the lungs and gut, passing out with the faeces. Infective larvae then develop which are said to penetrate the skin of new hosts, or there may be one or more totally free-living generations with separate males and females (a heterogonic cycle). The original descriptions of the life cycle are over 100 years old (Leuckart, 1865; Metschnikov, 1865) and although some biological studies have been made on members of the genus this century (Goodey, 1924) this common host/parasite system provides many intriguing problems and its re-examination would be most interesting.

(c) *Oswaldocruzia filiformis* was found in about 20 per cent of toads examined. It is a very easily diagnosed nematode, being long and thin and the only bursate nematode encountered in these toads. The male has an umbrella-shaped "bursa" at the tail end, with two dark, conspicuous male accessory copulatory organs. The head in both male and female is enlarged into an inflated bula. The life cycle is direct, the first two larval stages are passed in the egg. Little experimental or ecological work has been done on this species.

(d) and (e) *Aplectana* sp., *Cosmocerca* sp. Oxyurid nematodes are very commonly encountered in the rectum and posterior intestine of toads. They feed on bacteria and tend to be non-pathogenic. They are short and fat, with pointed tails and a conspicuous bulb at the base of the oesophagus. Males are very rare, and the specific identification of the two genera on female characters is very difficult (Cox, 1971).

A number of Protozoa are commonly found parasitizing the rectum and, to a lesser extent, the intestine of amphibians. They are often found in large numbers but apparently cause little harm to the hosts. Infections are usually acquired by tadpoles and persist in the adult. A good account of their structure and general biology is given by Dobell (1908), and a checklist is given by Cox (1971).

(f) *Entamoeba ranarum*

The trophozoite inhabits the intestine and rectum and the cysts, formed in the rectum, are passed in the faeces. *E. ranarum* is of particular interest because of its close resemblance to *Entamoeba histolytica*, a parasite of the large intestine causing amoebic dysentery in man. The cysts of *E. histolytica*, however, do not hatch and produce infections in amphibians.

The development of *E. ranarum* in culture has been described by Sandars (1931). The trophozoites which measure 10.0–19.0 μm . give rise to uninucleate cysts measuring 9.0–14.0 μm . The glycogen mass and chromatoid bodies are used up as the 4-nucleate stage is produced. In excystation, the tetranucleate amoeba emerges, the nuclei divide once and cytoplasmic division gives rise to eight uninucleate amoebae.

An amoeba resembling *E. ranarum* has been reported as trophozoites and cysts from the cytoplasm of opalinid flagellates, also parasitizing the rectum of amphibians. Although as many as 100 amoebae were present in a single opalinid host they apparently had no effect on its activity. Most have been reported from *Zelleriella* spp. but all four genera of Opalinata have been found parasitized, including *Opalina* (Chen and Stabler, 1936; Stabler and Chen, 1936).

(g) *Trichomonas* spp.

The species present in *B. bufo* and *T. vulgaris* collected near Slapton Ley have not been identified but the commonly occurring *T. batrachorum* is almost certainly represented. This is a pyriform flagellate, 8–12 \times 4–8 μm . The trichomonads are easily recognized by their jerky rotating movement brought about by the rippling of the prominent undulating membrane, which bears a trailing flagellum on its outer margin. The three anterior flagella and the axostyle protruding from the posterior end are also visible in the living organism. The flagellates divide by transverse symmetrogenic fission (producing mirror images) and large numbers are often present. No cysts are formed and infection is believed to occur directly to tadpoles by means of trophozoites which survive in pond water for long periods.

(h) *Monocercomonas bufonis*

This parasite is similar in size and structure to *Trichomonas* except that the trailing flagellum is free. Movement is jerky and in the absence of the undulating membrane the rotating component is not well marked.

(i) *Hexamita intestinalis*

Hexamita is easily distinguished from the trichomonads by its narrower body (10.0 \times 3.0 μm .) and very rapid, jerky movement. The organism is bilaterally symmetrical with paired oval nuclei, three pairs of anterior flagella and a pair of flagella emerging posteriorly: the latter are often seen clearly because of adherent particles of debris. Transmission is by means of cysts which are tetranucleate.

(j) *Opalina ranarum*

These are large oval flattened "ciliated" organisms almost universally present in the rectum of toads collected at Slapton. The entire body is up to 700 μm . long, uniformly covered with short cilia in oblique rows, but other ciliate characters are absent. There are numerous nuclei all of one type, fission is usually with the plane of fission between the ciliary rows and sexual reproduction is by syngamy.

Sexual reproduction is linked to the reproductive cycle of the host and can be induced experimentally by sex hormones. The sexual cycle has been described by Metcalf (1909) and others. Asexual forms are found throughout the year but as spawning approaches, a more rapid fission results in the production of smaller daughters with about six nuclei. These encyst and are passed out with the faeces

into the water. In tadpoles acquiring the infection the encysted organisms emerge and give rise to anisogamous gametes, which fuse by syngamy to produce zygotes. These either give rise to infections directly or encyst to produce infections in other tadpoles.

El Mofty and Smyth (1960) investigated the effect of hormonal treatment on sexual reproduction of opalinids, concluding that reproduction was related to levels of gonadal hormones in the host.

(k), (l) and (m) *Balantidium* spp.

These trichostomatid ciliates are characterized by the possession of an anterior vestibulum, an ectoplasmic depression leading to the cytostome. The body surface is uniformly covered with short cilia in rows and these are continuous with short rows of enlarged feeding cilia lining the vestibulum. Several species are known from the gut of amphibians of which *Balantidium entozoon*, *Balantidium elongatum* and *Balantidium duodeni* have been found at Slapton.

B. entozoon, for example, is an ovoid ciliate, 50–80 μm . long with a conical vestibulum extending posteriorly to the mid-line. The macronucleus is kidney-shaped and there are four large contractile vacuoles.

In division the plane of fission cuts across the rows of cilia (perkinetal) in a manner that produces daughters in tandem (homothetogenic fission). Conjugation is unknown in the species in amphibians but has been studied in *Balantidium coli* from the large intestine of man and pigs.

(n) *Nyctotherus cordiformis*

This ciliate measuring up to 200 μm . in length is larger than *Balantidium* and is further distinguished from it by the presence of a prominent S-shaped buccal cavity lined by fused cilia or membranelles. The body is flattened and kidney-shaped, pointed at both ends and uniformly ciliated with short cilia. The peristome, bearing the adoral zone of membranelles begins anteriorly and follows a ventral course to the mid-line where the membranelles turn inwards into the buccal cavity. Oval uninucleate cysts are passed in the faeces. Binary fission occurs throughout the life cycle but conjugation only occurs in tadpoles. According to Wichterman (1937) conjugants are found mainly in tadpoles developing their hind legs. He suggested that the physiological state of the tadpole gut at metamorphosis is unsuitable for survival of the ciliates and provides the stimulus for conjugation. Young tadpoles are infected by the ingestion of cysts. Small individuals (preconjugants) are produced by fission and adhere as conjugants along their oral surfaces. After exchange and reorganization of nuclei the conjugants separate. Exconjugants found in adult frogs are large individuals which give rise to normal vegetative forms by binary fission.

(o) *Eimeria* sp. Oocysts of *Eimeria* have been found in the rectum of *B. bufo*. Endogenous development in the gut epithelium has not been observed but oocysts, allowed to sporulate showed two sporocysts each with four sporozoites.

NOTES ON THE PARASITES OF AQUATIC BIRDS

From time to time birds from the Ley became available for parasitological examination because they had become damaged in some way; the cygnet, for instance,

had swallowed a fishing hook a few days before it died. As the number of birds sampled was extremely limited, the list of parasites found cannot be comprehensive and only includes helminths.

Table 3. *Parasites of aquatic birds of Slapton Ley*

Parasite	Site in host	Host
Endoparasites—		
ANNELIDA, HIRUDINEA		
(a) <i>Theromyzon tessulatum</i>	Nasal passages	<i>Cygnus olor</i>
PLATYHELMINTHES, CESTODA		
(b) <i>Diorchis inflata</i>	Small intestine	<i>Fulica atra</i>
(c) <i>Nematoparataenia southwelli</i>	Small intestine	<i>C. olor</i>
PLATYHELMINTHES, DIGENEA		
(d) <i>Cotylurus cornutus</i>	Small intestine	<i>Anas platyrhynchos</i> , <i>C. olor</i>
(e) <i>Cyclocoelum mutabile</i>	Lungs	<i>F. atra</i>
(f) <i>Cyclocoelum</i> sp.	Lungs	<i>Gallinula chloropus</i>
(g) <i>Cryptocotyle lingua</i>	Small intestine	<i>Larus argentatus</i>
(h) <i>Dendritobilharzia pulverulenta</i>	Renal vein	<i>F. atra</i>
(i) <i>Diplostomum spathaceum</i>	Small intestine	<i>L. argentatus</i>
(j) <i>Echinoparyphium recurvatum</i>	Small intestine	<i>G. chloropus</i>
(k) <i>Eucotyle</i> sp.	Kidney	<i>F. atra</i>
(l) <i>Notocotylus gibbus</i>	Caecum	<i>F. atra</i>
(m) <i>Spelotrema excellens</i>	Small intestine	<i>L. argentatus</i>
(n) <i>Typhlocoelum sisowi</i>	Trachea	<i>C. olor</i>
ACANTHOCEPHALA		
(o) <i>Filicollis anatis</i>	Small intestine	<i>C. olor</i> , <i>F. atra</i>
(p) <i>Polymorphus minutus</i>	Small intestine	<i>C. olor</i>

(b) *Diorchis inflata*. These small hymenolepids measuring only 9 mm. long and 0.4–0.5 mm. in width (though sexually mature), were found high in the small intestine in numbers often over 30 per individual. The scolex which measures 290–350 μm . across, bears a rostellum (20–25 μm . extended) armed with 10 hooks (63–75 μm . long). There is a prominent rostellar sac behind the four suckers, measuring 240–250 μm . in depth. The scolex suckers bear a pile of fine spines on their inner surfaces and measure 100 μm . across. This genus derives its name from the possession of two testes lying side by side in the narrow proglottids.

(Identification of this species was made by Dr. J. D. McLoughlin of the British Museum.)

The life cycle of *Diorchis* from coots is thought to be a typical aquatic hymenolepid cycle. Eggs containing oncospheres are eaten by fresh-water crustaceans and hatch in the gut to release the hexacanth which then bore into the haemocoel where they become infective cysticeroids. The crustaceans involved are thought to be the ostracods *Cypris* and *Cypridopsis* spp.

(c) *Nematoparataenia southwelli*. We were fortunate to find this unusual cestode in the single swan examined. It is a small worm measuring only 1.6–3.5 mm. long and was present in quite large numbers (30+). The body is not divided into proglottides and there is no separate vitelline system since yolk is produced by the ovary. The scolex is characteristic and beautiful to watch in action. It bears four large suckers and these surround the rostellum which is armed with an undulating

array of over a thousand tiny spines, each about 6 μm . long. This spreads out in a petalloid fashion to grapple with the host mucosa. A mass of gland cells is present at the base of the rostellum. The life cycle is not known.

(d) *Cotylurus cornutus*. As in most strigeid digeneans the anterior region of the body of *Cotylurus* is specially developed into a forebody cup which is pulled up in a kind of collar around the oral and ventral suckers. In addition to these suckers are the two lappets which lie on each side of the oral sucker and the "adhesive organ" which lies behind the ventral sucker. The total length of these worms is about 1.5 mm. Adult *Cotylurus cornutus* live only about 12–18 days in ducks (Nasir, 1960) and there is some evidence that the infection may be highly seasonal with its greatest incidence in summer and autumn. Eggs laid by the adult worms hatch in water, liberating miracidia which penetrate the first intermediate snail host. The snail host of *C. cornutus* in Slapton Ley has not been identified, but it has been proposed that various snails may serve as first intermediate hosts for this parasite including *Lymnaea pereger* and *Physa fontinalis* (N. Fifeshire, Harper, 1931), *L. stagnalis*, *L. auricularia*, *L. palustris*, *Planorbis corneus* and others. The first intermediate host produces furcocercariae which have been variously referred to as *Cercaria A. Szidat* or *Cercaria strigea tardae* Steenstrup. *Cercaria A. Szidat* has been redescribed by Iles (1959); it is distinguished by possession of 20 flame cells and two pairs of penetration glands located anterior to the ventral sucker. Cercariae liberated from snails may either penetrate another snail or into leeches (Plate II, Fig. 2), where they develop into tetracotyle larvae called "*Tetracotyle typica*" which are specialized forms of metacercariae and owe their name to the four-lobed shape of the body. In Slapton Ley 72 per cent of 241 *Erpobdella octoculata* were found to contain tetracotyle cysts; there were much lower infections in other leeches (see p. 704). It is not certain, however, that all the cysts found were those of *Cotylurus cornutus*, since *Apatemon gracilis* also uses leeches as intermediate hosts and the tetracotyle larvae of these two genera are not easy to tell apart. In general tetracotyle larvae of *Apatemon* have a thicker cyst wall (37.0–60.0 μm .) than those of *Cotylurus* (21.0–23.0 μm .) but this character is only of relative value in distinguishing the two kinds of cysts since it takes both genera several weeks to encyst (depending on the temperature). Another difference is that the posterior end of the cyst of *Cotylurus* is penetrated by an excretory channel whilst that of *Apatemon* is not. When excysted, either naturally or artificially using 1 per cent trypsin + 0.6 per cent sodium taurochlorate in Earl's salt solution at 40 °C., the juveniles of the two genera were seen to differ. Excysted *Apatemon* has the forebody clearly constricted from the hindbody whilst that of *Cotylurus* is scarcely delimited in this way (McCaul, personal communication). The site where cysts occur in the leech may also be characteristic and tetracotyle cysts of *Cotylurus cornutus* have been found in the sex glands and blood vascular system of leeches; *Apatemon gracilis gracilis* also occurs in the blood vascular system but *Apatemon gracilis minor* occurs in the general leech tissue and is not found in the blood system (see Iles, 1960). Using some of these characters as a guide it was suggested that about 12 per cent in March and 20–30 per cent in September, of cysts found in leeches at Slapton were those of *Cotylurus cornutus*; the remainder were probably *Apatemon*.

(e), (f) *Cyclocoelid digeneans*. The cyclocoelids are fairly large reddish digeneans (those collected from coots and swan were about 10 mm. long when fixed and flattened). Adults have no obvious suckers but there is a suctorial pharynx; the gut is "circular" since the two caeca are confluent posteriorly. Within the loop of the

gut caecum the body is filled with coils of the uterus and this is packed with eggs containing fully developed miracidia each with a conspicuous eyespot. The miracidia of *Typhlocoelum* are said to contain at the time of hatching a single mother redia, an unusual feature which, as far as is known, is shared only with *Parorchis acanthus*. Rails and anatids have different genera of cyclocoelid parasites. The cyclocoelids from the lungs of coots and moorhens are *Cyclocoelum*, whilst those from the trachea of swans are *Typhlocoelum*; the two genera are easily distinguished since *Typhlocoelum* has 20–22 diverticula on the inside of the gut caecum whilst *Cyclocoelum* lacks these. Lapage (1961, in his checklist of parasites of anatids) cites *Typhlocoelum sisowi* as a parasite of the mallard but does not list it with the parasites of swans so this may possibly be a first record for this host. Beverley-Burton (1961) gives a description of *T. sisowi* in her paper on the trematodes of British fresh-water birds. The miracidia of *T. sisowi* are said to infect planorbid snails, e.g. *Planorbis corneus*, and these give rise to monostome cercariae which encyst in the same snail. Water birds become infected when they consume planorbids containing cyclocoelid metacercariae.

(g) *Cryptocotyle lingua*. This fluke is a fairly common intestinal parasite of piscivorous birds (gulls, terns, etc.). The life cycle is marine and involves the winkle *Littorina littorea* and shore feeding herrings which become infected when cercariae liberated from the winkles bore into the skin causing pigment deposition at these sites. Birds become infected by eating fish containing metacercariae.

(h) *Dendritobilharzia pulverulenta*. This worm is listed as a parasite of the mallard by Lapage (1961). Like all schistosomatid digeneans these blood flukes have separate sexes. The genus *Dendritobilharzia* is characterized by the absence of suckers, spines and tubercles from the body. The gut caeca join about one-third of the way down the body to form a common caecum which zig-zags down the rest of the body, giving off side branches. The female of *D. pulverulenta* is characterized by a short uterus usually containing only a single egg (see Cheatum, 1941).

(i) *Diplostomum spathaceum*. A description of this parasite and its life history has already been given, pp. 684–685.

(j) *Echinoparyphium recurvatum*

Echinoparyphium is an echinostome digenean and the cercaria, metacercaria and adult can all be recognized by the possession of 43–45 collar spines, the oral or ventral being slightly smaller than the dorsal. A fairly common, related form, *Echinostoma revolutum*, has only 37 collar spines. *E. recurvatum* does not appear to be very specific to its final vertebrate host, as it has been recorded from *Nyroca* spp., *Gallus domesticus* and *Columba* sp. (Rašín, 1933). Some related echinostomes of the genus *Echinostomum* sp. have been recorded from man and in Formosa 3–6 per cent of the population may be infected with *Echinostoma revolutum* from eating raw fresh-water mussels. In the Ley the cercariae of *E. recurvatum* were found in *Lymnaea pereger* and metacercarial cysts of this parasite were found in *Sphaerium corneum*. *Sphaerium*, a bivalve, has a very localized distribution in the Ley, being found only in the soft mud of the reed beds of Ireland Bay (Station E₂), but 98 *Sphaerium* examined were found to be 100 per cent infected. Up to 320 metacercariae were found in one bivalve and when these were fed, experimentally, to commercially reared ducklings they excysted in the duck gut. Encysted metacercariae of an (unidentified) echinostome were also found in the digestive gland of the snail *Physa fontinalis*. Previous reports suggest that the metacercariae of echinostomes are not confined to bivalve

second intermediate hosts but occur in planarians and amphibians; they may also encyst in the first snail host.

(k) *Eucotyle*, like *Notocotylus*, is a monostome and lacks a ventral sucker. The anteriormost region of the body is delimited from the remainder by means of an annular thickening.

(l) *Notocotylus gibbus*. This digenean is a parasite of water rails and a description is given in Beverley-Burton (1961) who found this species in the moorhen, *Gallinula chloropus*. These monostome digeneans are identified to species level by the number and arrangement of the ventral gland openings. There are three rows of ventral glands down the body, two lateral and one median; these may form an adhesive organ. They open to the outside via transverse slits surrounded by thick muscular lips. The gland openings, of which there are eleven in the lateral series in *N. gibbus* and five in the median row, are probably most easily seen in fixed specimens which have not been flattened and mounted. The ovary which is flanked by a testis on each side is situated at the posterior end of the body. The overall length of *N. gibbus* was found to range from 0.8–1.5 mm.

Notocotyloid cercariae, recognized by their possession of an oral sucker only (monostome condition) and three pigment eyespots, were found in *Limnaea pereger* from the Ley and may have been the cercariae of *N. gibbus*, although this was not confirmed experimentally. Notocotyloid cercariae encyst readily under the microscope. As a rule they encyst on either the same snail in which they developed or on other snails, or pond weed, after a brief free swimming dispersal phase. The metacercariae infect such birds as coots that feed on the snails and plants bearing them.

(m) *Spelotrema excellens*. Adult *Spelotrema* and related forms can be identified by the gut caeca which terminate level with the ventral sucker.

(o) *Filicollis anatis*. These acanthocephalans were attached deeply into the gut wall of the small intestine (Plate II, Fig. 1). Pieces of gut with worms still attached were sectioned and it could be seen that the proboscis which is almost globular was buried deep in the muscles of the gut wall, forming a powerful ball anchor. A slender neck with powerfully developed longitudinal muscle connects the proboscis with the cylindrical main body region. Whole mounts of these worms showed that the tip of the proboscis was armed with 7–9 rows of spines. Cystacanths of *Filicollis anatis* occur in *Asellus aquaticus* and ducks, geese, swans and coots become infected with this parasite when they feed on infected *Asellus*. As *Asellus* was not, in fact, found in the Ley, birds may have become infected in neighbouring bodies of water.

(p) *Polymorphus minutus*. Typically a parasite of mallards but capable of infecting a range of water fowl, this species has been the subject of comprehensive biological investigations of late (see Crompton, 1970, for review). The adults found in the small intestine of the swan measured about 5 mm. in length and were distinguished by their bright orange colour when living, caused by the presence of carotenoids in the tissues.

The life cycle involves the water shrimp *Gammarus pulex* which consumes the lemon-shaped eggs laid by female worms when they sink to the bottom of the water. The tough egg shell of the parasite is ruptured by the chewing action of the water shrimp and within the gut of this intermediate host an acanthor larva (with no gut) and bearing blade-like spines on the head and smaller body spines, hatches and bores through the gut wall into the haemocoel. After a brief acanthella stage a cystacanth develops, with a fully formed, armed, invaginated proboscis and this is surrounded

by a cyst of orange carotenoid-containing substances. Infected gammarids can be easily picked out with the naked eye by the orange spot visible through the transparent dorsal body wall.

NOTES ON THE PARASITES OF STARLINGS

One starling was recovered and a few helminths were positively identified from it.

Table 4. *Parasites of starlings around Slapton Ley*
(see Plate IV, Fig. 1)

Parasites	Site in host	Host
Endoparasites— ACANTHOCEPHALA (a) <i>Prosthorhynchus cylindraceus</i>	Small intestine	<i>Sturnus vulgaris</i>
NEMATODA, STRONGYLOIDEA (b) <i>Syngamus trachea</i>	Trachea	<i>S. vulgaris</i>
PLATYHELMINTHES, DIGENEA (c) <i>Brachylaimus (fuscatus)</i> (d) Dicrocoelid	Small intestine Gall bladder	<i>S. vulgaris</i> <i>S. vulgaris</i>

(a) *Prosthorhynchus cylindraceus*. This paleoacanthocephalan has been reported to be present in the middle third of the small intestine of starlings (Plate IV, Fig. 1). It also occurs in other British birds such as the blackbird, song thrush, etc. A related form, *Prosthorhynchus formosus*, uses the terrestrial arthropods *Armadillidium vulgare* and *Porcellio* spp. as intermediate hosts.

(b) *Syngamus trachea*. Living in the trachea of many wild and domesticated birds is *S. trachea*, known as "gapeworm" as it causes asphyxiation and death in young fowl. It is unmistakable, being bright red from its blood diet (Rose and Hwang, 1967), and the small male is permanently attached to the female, forming one arm of a "Y" structure. *S. trachea* produces eggs which pass into the host faeces and can be directly infective following development to the infective stage, or they may pass into an earthworm (Clapham, 1934).

(c) *Brachylaimus* sp. (*fuscatus*?). A brachylaimid, probably *B. fuscatus*, was found in the small intestine of starlings at Slapton. Owen and Pemberton (1962) noted that *B. fuscatus* tends to occur in the first third of the small intestine and uses terrestrial snails as intermediate hosts, metacercarial cysts occurring in these snails.

(d) *Dicrocoelid*. A dicrocoelid was found in the gall bladder of starlings, but was not identified. This may have been *Platynosomum petiolatum* (see Owen and Pemberton, 1962).

NOTES ON THE PARASITES OF SMALL MAMMALS

Small mammals were trapped in Longworth traps for the whole period of each course. Traps were pre-baited for two nights and thereafter set and visited morning and evening. All mammals caught were taken back to the laboratory, caged singly in plastic cages and examined for ectoparasites. A blood film was taken from each and some were killed, but the majority were released in the areas in which they had been captured. Three trapping areas were used, Slapton Wood, the hedges along

Wood Lane and the seaward side of the Higher Ley. Slapton Wood was the most satisfactory site.

Apodemus sylvaticus was the most common mammal trapped, *Clethrionomys glareolus* the next and *Microtus agrestis* the rarest. Over the period of this survey 58 *A. sylvaticus*, 57 *C. glareolus* and 5 *M. agrestis* were killed and examined for parasites. Occasionally shrews, *Sorex araneus*, were found in the traps, but they were invariably dead. A single mole was examined in 1972 and although no notes are given its protozoal parasites are listed.

Table 5. Parasites of small mammals around Slapton Ley

Parasite	Site in host	Host
Ectoparasites—		
ACARINA		
(a) <i>Ixodes trianguliceps</i>	Skin	<i>Apodemus sylvaticus</i> , <i>Clethrionomys glareolus</i>
(b) <i>Ixodes ricinus</i>	Skin	<i>A. sylvaticus</i>
ARTHROPODA, SIPHONAPTERA		
(c) <i>Ctenophthalmus nobilis</i>	Skin	<i>A. sylvaticus</i>
(d) <i>Histrichopsylla talpae</i>	Skin	<i>A. sylvaticus</i>
Endoparasites—		
ACANTHOCEPHALA		
(e) <i>Centrorhynchus aluconis</i>	Encapsulated in mesentery	<i>Sorex araneus</i>
NEMATODA, OXYUROIDEA		
(f) <i>Syphacia stroma</i>	Caecum, posterior intestine	<i>A. sylvaticus</i>
(g) <i>Syphacia obvelata</i>	Caecum, intestine	<i>C. glareolus</i>
NEMATODA, RHABDITOIDEA		
(h) <i>Pelodera strongyloides</i>	Lachrymal fluid	<i>C. glareolus</i>
NEMATODA, TRICHOSTRONGYLOIDEA		
(i) <i>Nematospiroides dubius</i>	Duodenum, small intestine	<i>A. sylvaticus</i> , <i>C. glareolus</i>
NEMATODA, TRICHOSYRINGIDA		
(j) <i>Capillaria muris sylvatici</i>	Intestine	<i>A. sylvaticus</i> , <i>C. glareolus</i>
(k) <i>Capillaria hepatica</i>	Liver tissue	<i>A. sylvaticus</i> , <i>C. glareolus</i>
PLATYHELMINTHES, CESTODA		
(l) <i>Catenotaenia</i> sp.	Small intestine	<i>A. sylvaticus</i> , <i>S. araneus</i>
(m) <i>Choanotaenia crassicolex</i>	Small intestine	<i>S. araneus</i>
(n) <i>Cysticercus taeniae-taeniaeformis</i>	Liver	<i>C. glareolus</i>
(o) <i>Hymenolepis</i> spp.	Small intestine	<i>S. araneus</i>
PLATYHELMINTHES DIGENEA		
(p) <i>Brachylaimus oesophagei</i>	Oesophagus and stomach	<i>S. araneus</i>
(q) <i>Brachylaimus</i> sp.	Small intestine	<i>A. sylvaticus</i>
(r) <i>Corrigia vitta</i>	Interlobary canals of pancreas	<i>A. sylvaticus</i> , <i>C. glareolus</i> , <i>Microtus agrestis</i>
PROTOZOA, SARCODINA		
(s) <i>Entamoeba muris</i>	Large intestine	<i>C. glareolus</i>
PROTOZOA, MASTIGOPHORA		
(t) <i>Trichomonas muris</i>	Large intestine and caecum	<i>A. sylvaticus</i> , <i>C. glareolus</i> , <i>M. agrestis</i>
(u) <i>Chilomastix bettencourti</i>	Large intestine and caecum	<i>A. sylvaticus</i>
(v) <i>Hexamita muris</i>	Large intestine and caecum	<i>A. sylvaticus</i> , <i>C. glareolus</i>

Table 5—continued

Parasite	Site in host	Host
PROTOZOA, MASTIGOPHORA—contd.		
(w) <i>Giardia muris</i>	Small intestine	<i>A. sylvaticus</i>
(x) <i>Giardia microti</i>	Small intestine	<i>C. glareolus</i> , <i>M. agrestis</i>
(y) <i>Trypanosoma evotomys</i>	Plasma of blood	<i>C. glareolus</i>
(z) <i>Trypanosoma grossi</i>	Plasma of blood	<i>A. sylvaticus</i>
(a ₁) <i>Trypanosoma talpae</i>	Plasma of blood	<i>Talpa europaea</i>
PROTOZOA, SPOROZOA		
(b ₁) <i>Hepatozoon erhardovae</i>	White blood cells	<i>C. glareolus</i>
(c ₁) <i>Frenkelia glareoli</i>	Brain	<i>C. glareolus</i>
(d ₁) <i>Eimeria</i> sp.	Caecum and rectum	<i>C. glareolus</i>
(e ₁) <i>Cyclospora caryolytica</i>	Intestine and rectum	<i>T. europaea</i>
(f ₁) <i>Babesia microti</i>	Red blood cells	<i>C. glareolus</i>
PROTOZOA (UNCERTAIN TAXONOMIC POSITION)		
(g ₁) <i>Eperythrozoon</i>	Red blood cells	<i>A. sylvaticus</i>
(h ₁) <i>Haemobartonella</i>	Red blood cells	<i>A. sylvaticus</i>
(i ₁) <i>Grahamella</i>	Red blood cells	<i>A. sylvaticus</i>
(j ₁) <i>Elleipsisoma talpae</i>	Red blood cells	<i>T. europaea</i>

(a) *Ixodes trianguliceps* is the most common tick on British small mammals and were on *A. sylvaticus* and *C. glareolus* at Slapton.

(b) *Ixodes ricinus* is the sheep tick. A single adult was found on *A. sylvaticus*. For a detailed account of ticks on British animals see Arthur (1963).

(c) *Ctenophthalmus nobilis*. Fleas are common on British small mammals and were found on *A. sylvaticus* and *C. glareolus* as well as in traps from which shrews had been taken. Fleas tend to leave their hosts in traps or in cages and this makes quantitative studies difficult. About eight species of fleas occur on British small mammals, of which five were on rodents. Only one species, *Ctenophthalmus nobilis*, was positively identified from *A. sylvaticus*.

(d) *Histrichopsylla talpae* is a very large flea, called the mole flea, with a relatively wide host range.

(e) *Centrorhynchus aluconis*. Several cystacanths of *C. aluconis* were found encapsulated in the mesenteries of one shrew examined having bored out of the intestine. *Centrorhynchus* is paratenic in shrews, i.e. the shrew becomes infected by consuming, presumably, some kind of terrestrial crustacean containing cystacanths. The shrew does not harbour the adult parasite but only a resting stage which serves to distribute the parasite into its final host, the owl, *Strix aluco sylvatica*, which preys on shrews. *Centrorhynchus* is not highly specific to its paratenic hosts and occurs in the body cavity of amphibians (frogs and toads) as well as shrews. Other acanthocephalans also have the ability to bore out of the gut of various paratenic hosts and survive in an encapsulated form until they are carried via a food chain to the appropriate final host.

(f), (g) *Syphacia stroma*. Pinworms are very common in small mammals, living in the caecum and posterior intestine. They feed on bacteria and are largely non-pathogenic. *S. stroma* predominates in *A. sylvaticus* and *S. obvelata* is commonest in *C. glareolus*. Distinguishing between these has been made much clearer in a comprehensive review by Ogden (1971). Ogden says (p. 265) that *S. obvelata* occurs in the

house-mouse, bank-vole and field vole, while *S. stroma* parasitizes the field mouse. Males may be distinguished by the arrangement of mamelons on the tail and the males of the closely related *Aspiculuris tetraptera* has no spicules.

(h) *Pelodera strongyloides*. A common, but little-known nematode, occurs in the lachrymal fluid of small rodents, being found in up to 90 per cent of *C. glareolus*, and less frequently in *A. sylvaticus* (Plate IV, Figs. 2–4). Only third-stage larvae and preadults are found in the orbits, and they have not been reported from anywhere else in the hosts, nor do they have any pathological effects. The same species lives free in the soil. Infection rates in voles and mice increase in drought and it is possible that the nematode in response to desiccation produces a stage which sojourns for some weeks in the lachrymal fluid. Up to 1,293 individuals were counted in the eyes of one vole (Poinar, 1965), and we often encountered 20–40 larvae. Larvae can be removed by carefully flushing the surface of the eye with water in a pipette. A particularly notable feature of the stage in the rodent is the easily visible “phasmids”, structures often difficult to discern in nematodes (Plate IV, Figs. 2–4).

(i) *Nematospiroides dubius*. *N. dubius* is a frequent parasite of the duodenum and small intestine of *A. sylvaticus* and *C. glareolus*, regularly infesting up to 60 per cent of hosts. The life cycle is direct with free-living bacteriophagous larvae, moulting to form infective ensheathed larvae which enter as contaminants of food (Ehrenford, 1954). Rainbow (1971) has demonstrated a competitive exclusion between *N. dubius* and *Syphacia stroma*. The adults are tightly coiled (hence the generic name) and reddish in colour due to nematode haemoglobin.

(j) *Capillaria muris sylvatici*. This “whipworm” with a long tapering oesophagus consisting of a series of cells called a stichosome, is common in the intestine of *A. sylvaticus* and *C. glareolus*. The adult oesophagus is deeply embedded in the intestinal mucosa where they probably feed on blood. The life cycle is direct, the infective larvae developing inside the egg which is then infective.

(k) *Capillaria hepatica*. The livers of *A. sylvaticus* and *C. glareolus* were frequently covered in yellow patches. In 1970, when careful records were attempted, 75 per cent of rodents were found infected. The patches may be squashed under a microscope to reveal the adult female and many rows of eggs. The eggs are released into the field by predators such as foxes or owls. The eggs pass unchanged through the predator’s gut, and after a period of development enter rodents as contaminants of food (Shorb, 1931).

(l) *Catenotaenia* sp. This anoplocephaline cyclophyllidean cestode belongs to a group that lacks rostellar hooks; the scolex of the adult is armed with four suckers and traces of an apical sucker can sometimes be seen. *Apodemus* and *Clethrionomys* become infected with *Catenotaenia* by consuming as a contaminant of their food tyroglyphid mites which contain the infective merocercoid larvae in their haemocoel. *Glyciphagus domestica* transmits *C. pusilla*; no precise information seems to be available for *C. lobata*. Tapeworms are usually highly specific to their final vertebrate hosts, but *C. pusilla* and *C. lobata* infect both *Apodemus* and *Clethrionomys* and may infect shrews, although Lewis (1968b) did not find this genus in shrews in Wales. The species of *Catenotaenia* from shrews at Slapton were not identified.

(m) *Choanotaenia crassiscolex*. This dilepid tapeworm can be easily separated from *Catenotaenia* with which it competes for a feeding site in the small intestine of shrews by the presence of 10 rostellar hooks; these literally being crochet-hook shaped. The rostellum retracts into a copious rostellar sac and in addition the scolex bears

four suckers. *Choanotaenia* occurs only in the intestine of the insectivorous shrews and does not occur in rodents. Lewis (1968*b*) reports that the cysticercoids of *C. crassiscolex* occur in a land snail, the glossy snail *Oxychilus helveticus* so that shrews become infected on eating infected snails. A description of this tapeworm is given in Rawson and Rigby (1960).

(n) *Cysticercus taeniae-taeniaeformis* (syn. *Cysticercus fasciolaris* Rud. 1808). This is the larval strobilocercus of *Hydatigera taeniaeformis* which has its adult stages in carnivores such as foxes or owls. It can also occur as a larva in the liver of rats and mice which can then infect dogs and cats. *Clethrionomys* is the intermediate host, becoming infected directly by eating eggs. The large cysticercus is contained within a fibrous cyst formed by a host reaction to the parasite. The scolex is invaginated at one end of the body and at the posterior end is a cyst-like development which can easily be mistaken for the head at first sight (see Rees, 1951).

(p) *Brachylaimus* sp. Only a single specimen of *Brachylaimus* sp. was recovered from the small intestine of *Apodemus* and this was almost certainly *B. recurvum*.

(q) *Brachylaimus oesophagei*. This fluke occupies the unusual site of oesophagus and stomach of *S. araneus*. Lewis (1968*b* and 1969) has described the life cycle of this digenean from a region around Aberystwyth. Eggs containing miracidia hatch in the gut of a land snail. The miracidium is unusual in having a stylet and cilia on stalks; it penetrates into the snail tissue and gives rise to microcercous cercariae. Lewis (1968*b*) found microcercous cercariae but no sporocysts in the kidney of the hollowed snail *Zonitoides excavatus* so it is possible that cercariae formed in one snail migrate up the ureter and into the kidney of *Zonitoides* (a similar phenomenon has been recorded for a different species of *Brachylaimus*). The cercariae considerably damage the kidney of the snail. In this context it is interesting that slugs infected with another brachylaimid, *B. fulvus*, can be killed by this parasite.

(r) *Corrigia vitta*. *Corrigia* is a dicrocoelid fluke related to *D. lanceolatum* of cattle and *D. soricis* of shrews. Dicrocoelid flukes are also common in British birds. The body of *Corrigia* is elongate 3–7 mm. Lewis (1968*a*) found a higher incidence of *Corrigia* in *Apodemus* from woodland than from rough grassland in Wales and noted that male long-tailed field mice harboured higher worm burdens and showed a greater intensity of infection than females. The life history of *Corrigia* is unknown, but is assumed to parallel the life history of other dicrocoelid digeneans. *Cepaea* has been suggested as a possible first intermediate host and the red wood ant as second intermediate host, but there is incomplete evidence for this. Ten *Corrigia* were found in a single *Clethrionomys* on one occasion at Slapton.

Trypanosomes are best seen in fresh blood but intracellular parasites are only recognized after staining of blood films. Gut contents should be examined in saline for trophozoites and faeces for cysts. Surveys of parasites in populations of wild mice in Britain have been conducted by Elton *et al.* (1931) and Ring (1959) and an illustrated account of the parasitic Protozoa of British small mammals is given by Cox (1970).

(s) *Entamoeba muris* is the only amoeba found in the intestines of small mammals. It has a characteristic cyst with eight nuclei and is morphologically indistinguishable from *E. coli* of man. It is a harmless commensal feeding on bacteria in the gut. *E. muris* has been found occasionally in *C. glareolus* at Slapton, although it has been recorded from *A. sylvaticus* and *M. agrestis* as well as in rats and house mice elsewhere.

This is a difficult parasite to find and this may account for its low incidence in this survey.

(t) *Trichomonas* spp. Trichomonads are small flagellates with a plastic body supported by a rigid rod or axostyle. One flagellum runs backwards and is associated with an undulating membrane, the flickering of which is diagnostic of these flagellates. *Trichomonas muris* is the largest of the trichomonads of small rodents and is common and occurs in large numbers in nearly all *A. sylvaticus*, *C. glareolus* and *M. agrestis* at Slapton. Two smaller species *T. microti* and *T. sylvaticus*, in *A. sylvaticus* (see Ring, 1959), have been recorded in Britain but have not been recognized during these field courses.

(u) *Chilomastix* spp. *Chilomastix* is a small flagellate with three free flagella and a conspicuous cytostome. *C. bettencourti* has been recorded occasionally in *A. sylvaticus* from Slapton. It is probably common but has not been recognized regularly because of its small size and its superficial similarity to the much more abundant *Trichomonas*. Ring (1959) considers that *Chilomastix* in voles belongs to a different species.

(v) *Hexamita muris* is common in *A. sylvaticus* and *C. glareolus* at Slapton. It is a small flagellate with all the organelles paired, with six free anterior flagella and two trailing flagella. The cysts are elongate with rounded ends. *Syndomita* and *Octomitus* are synonyms (see Ring, 1959).

(w), (x) *Giardia*. Small flagellates with bodies shaped like half a pear are commonly found in the small intestine and sometimes the caecum of *A. sylvaticus* and *C. glareolus* at Slapton. This is the only flagellate which occurs in the small intestine. The species are difficult to differentiate but *G. muris* occurs in *A. sylvaticus* and *G. microti* in *C. glareolus* and *M. agrestis*. The cysts contain four nuclei.

(y), (z) *Trypanosoma* spp. The trypanosomes in the blood of small mammals are host specific: *T. evotomys* (Plate III, Fig. 1) occurs in about 30 per cent of *C. glareolus* at Slapton. *T. grosi* was found in 5 out of 18 *A. sylvaticus* during one survey of blood parasites but not at any other time. *T. microti*, which occurs in *M. agrestis* has not been recorded at Slapton. They are transmitted by fleas.

These trypanosomes cannot be distinguished on the morphology of the adult trypomastigotes in the blood. They are typical of the sub-genus *Herpetosoma*: there is a pointed posterior end, a round or oval kinetoplast lying across the body some distance from the posterior end, a central nucleus, undulating membrane and free flagellum. They measure 25–30 μm . in length.

T. evotomys and *T. microti* reproduce as amastigotes by multiple or binary fission in lymphoid tissue and there are no dividing stages in the blood. In fleas reproducing epimastigotes are found in the pyloric region and intestine and the metacyclic trypomastigotes are passed in the faeces. *T. grosi* reproduces by unequal multiple fission as epimastigotes—the site of reproduction in the tissues is not known but dividing forms are found in the blood. In fleas reproducing epimastigotes as well as metacyclic forms are found in the rectum. Detailed accounts of the biology of *T. evotomys* and *T. microti* are given by Molyneux (1969a, b).

(b₁) *Hepatozoon* is a parasite of internal organs during the phase of schizogony and the gametocytes are found in leucocytes in peripheral blood. Species have been described from voles and field mice, which though resembling one another in the blood phase, undergo schizogony in different sites. A good account of the species in small mammals in Europe is given by Krampitz (1964). Schizonts of *H. sylvaticae* from *A. sylvaticus* are in the bone marrow, those of *H. microti* from *M. agrestis* are in

the lung and to a lesser extent in the liver, while those of *H. erhardovae* from *C. glareolus* occur only in the lung. Intermediate hosts of *H. erhardovae* are fleas but those of *H. sylvaticae* and *H. microti* are unknown.

H. erhardovae was occasionally found in *C. glareolus* at Slapton (Plate III, Fig. 3). The gametocytes are uninucleate, sausage-shaped bodies which lie in lymphocyte-like cells adjacent to the host cell nucleus.

(c₁) *Frenkelia glareoli* has been found in a single specimen of *C. glareolus* from Slapton (Toye and Tappin, 1972).

The type species, *F. microti*, was first found in *M. agrestis* in Wales (Findlay and Middleton, 1934) as large cysts in the brains of voles. Cysts from this host are 0.5–1.0 mm. and are rosette-like with short blunt lobes. Cysts of *F. glareoli* are smaller, up to 0.6 mm. and are rounded or oval without lobes (Plate III, Fig. 2).

Both species are known only as cysts embedded in nervous tissue. Large cysts can easily be seen as white spots through the thin skull bones. The cyst has a thin wall which is continuous with septa which project inward to divide the cyst into polygonal compartments packed with thousands of "zoites". Zoites of both species are uninucleate, elongate cells, pointed at one end, rounded at the other, measuring $7\text{--}9 \times 2\text{--}3 \mu\text{m}$.

The parasite bears a striking resemblance to *Toxoplasma* and *Sarcocystis*. A good account of the group of organisms is given by Frenkel (1956). *Toxoplasma* develops as a typical coccidium in the gut of the domestic cat, producing oocysts which are infective to a wide variety of hosts, including small rodents: in these hosts proliferative forms develop in macrophages and cystic forms in the brain. *Sarcocystis* occurs as cystic forms in striated muscle of many vertebrates: after feeding cysts from pig and ox to man, typical coccidial oocysts have been passed in the faeces (Rommel and Heydorn, 1972).

Unlike *Toxoplasma* and *Sarcocystis*, nothing is known of the development of *Frenkelia* or its mode of transmission.

(d₁) *Eimeria* spp. are mostly parasites of the gut wall of their hosts and are transmitted directly by resistant oocysts. Fully sporulated oocysts contain four sporocysts, each with two sporozoites.

Endogenous development, which is initiated by hatching of the sporozoites after ingestion of oocysts, involves one or more generations of schizogony and macro- and micro-gametocytes producing gametes. The zygote resulting from fertilization is passed in the faeces as a resistant oocyst to complete its sporulation outside the host.

Oocysts of *Eimeria* have been found in the caecum and rectum of *C. glareolus*. Several species have been recorded from voles and field mice (listed in Levine and Ivens, 1965) but the species found at Slapton was not identified. In view of the host specificity of most *Eimeria* species, it seems unlikely that the coccidians found by Elton *et al.* (1931) and Ring (1959) were correctly identified as *E. falciformis*, this species being a parasite of *Mus musculus*.

(f₁) *Babesia microti*. This small protozoan (Plate III, Fig. 4) which parasitizes red blood cells and is transmitted by ticks, has been recorded from all small mammals (rodents and insectivores) in Britain. The parasites show no differences in their behaviour in different hosts and can be passed by blood inoculation from one to another.

The parasites are very variable in their appearance in erythrocytes (Shortt and

Blackie, 1965). Ring forms with a conspicuous vacuole and division forms of four individuals in Maltese-cross arrangement are commonest (Plate III, Fig. 4); uninucleate rods, amoeboid and band forms with two nuclei are rare. Only at the beginning of an infection are parasitaemias high; infections are usually difficult to detect and are found only after prolonged searching of stained blood films.

All known intermediate hosts of piroplasms are ticks. *B. microti* has been transmitted in the laboratory by *Ixodes trianguliceps*.

Three non-protozoan micro-organisms are commonly found in the blood of small mammals. These are *Eperythrozoon* which takes the form of small open rings often in the plasma as well as the red blood cells, *Haemobartonella*, which appears as round solid bodies in the corpuscles and *Grahamella* which takes the form of a large number of round solid bodies occupying almost the whole of a red cell. All have been found at Slapton, particularly in *A. sylvaticus*, but also in voles. Little is known of their nature or transmission.

NOTES ON THE PARASITES OF AQUATIC ANNELIDS AND ARTHROPODS

Almost all the invertebrates were collected under stones and in the reed beds at the northern end of the Ley, E₁, E₂ and E₄ (Mercer, 1966, fig. 6).

Table 6. *Parasites of aquatic annelids and arthropods in Slapton Ley*

Parasite	Site in host	Host
ACANTHOCEPHALA		
(a) <i>Acanthocephalus clavula</i>	Body cavity	<i>Proasellus meridianus</i>
(b) <i>Polymorphus minutus</i>	Body cavity	<i>Gammarus pulex</i>
PLATYHELMINTHES, CESTODA		
(c) <i>Hymenolepid cysticerci</i>	Body cavity	<i>Piscicola geometra</i>
(d) <i>Caryophyllaeus laticeps</i>	Body cavity	<i>Psammoryctides barbatus</i>
PLATYHELMINTHES, DIGENEA		
(e) <i>Apatemon gracilis</i>	Body tissues	Leeches, see text
(f) <i>Cotylurus cornutus</i>	Body tissues	Leeches, see text
PROTOZOA, MASTIGOPHORA		
(g) <i>Trypanosoma</i> sp.	Gut and proboscis	<i>Hemiclepsis marginata</i>
(h) <i>Crytobia borelli</i>	Proboscis sheath	<i>H. marginata</i> , <i>P. geometra</i>
PROTOZOA, CILIATA		
(i) <i>Mesnilella rostrata</i>	Gut lumen	<i>Pelosclex benedeni</i>
(j) <i>Radiophrya</i> sp.	Gut lumen	Tubificid worm
(k) <i>Collinia circulans</i>	Haemocoel	<i>P. meridianus</i>

(a) *Acanthocephalus clavula* cystacanths were found in *P. meridianus*, the normal intermediate host of this fish parasite (p. 685).

(b) *Polymorphus minutus* cystacanths were found in *G. pulex*, the intermediate host of this parasite (p. 695). Infected *G. pulex* may be readily identified by their bright orange colour.

(c) *Hymenolepid* cysticercoids. Tubificids in Ireland Bay showed 80 per cent infections with cysticercoids in the body cavity. There was a lighter (2 per cent) infection halfway down the Ley at station E₁.

(d) *Caryophyllaeus laticeps* (see p. 683).

(e), (f) *Apatemon gracilis*, *Cotylurus cornutus*. The leeches most commonly found in the Ley were *Helobdella stagnalis* and *Erpobdella octoculata*, both of which feed on invertebrates; *Theromyzon tessulatum* which feeds on the blood of water fowl (obtained from the buccal or nasal cavities) was next most common, then *Hemiclepsis marginata*, collected from the leaf blades of *Iris*, which, like *Piscicola geometra*, feeds on fish and amphibian blood. *Piscicola* (see p. 682), which is attached most of the time to fishes and *Glossiphonia complanata*, were encountered less frequently.

In addition to trypanosomes and *Cryptobia*, leeches were found to harbour encysted tetracotyle larvae of the strigeids *Cotylurus cornutus* and *Apatemon gracilis* (see p. 693). The infection rate for various species of leeches with both kinds of tetracotyle were as follows: *Erpobdella* 72 per cent (241 sampled), *Helobdella* 30 per cent (249 sampled), *Hemiclepsis* 27 per cent (29 sampled), *Glossiphonia* 18 per cent (17 sampled) and *Theromyzon* 0.6 per cent (158 sampled). These leeches were sampled in September when the infection is probably at its highest. *Theromyzon* is a much tougher leech than the others and it may be that the furcocercariae of *Cotylurus* and *Apatemon* have difficulty in penetrating into these leeches. On the other hand *Theromyzon*, being a successful parasite of the nasal passages of water birds (the final hosts of *Cotylurus* and *Apatemon*) is probably rarely consumed by them, so that infection of *Theromyzon* with larval stages of these strigeids would probably not contribute greatly to the success of the life cycle. The cysts are just visible with the naked eye and measure 0.30 mm. by 0.40 mm. The process of encystation has been reported to take 20–30 days for *Cotylurus* and 6 weeks for *Apatemon* so cysts will probably be found in different stages of development. Fully developed *Apatemon tetracotyle* larvae have a much thicker cyst wall than *Cotylurus* cysts (45.0 μm . and 20.0 μm . approximately respectively). In mature cysts the accessory holdfast organs, the lappets each side of the oral sucker and the adhesive organ lying behind the ventral sucker can be seen.

(g) *Trypanosoma* spp. from fresh-water fish are transmitted by *Hemiclepsis marginata*. The infected blood is taken into the crop where the trypomastigotes with posterior kinetoplasts, change to epimastigotes which have the kinetoplast just anterior to the nucleus. The epimastigotes undergo at least two divisions, eventually producing slender metacyclic forms which do not divide. The metacyclic trypanosomes of *T. granulorum* migrate to the proboscis sheath and are inoculated into the fish when the leech next takes a blood meal. Infective forms of *T. remaki* and *T. percae* remain in the crop and infect the fish by active migration forwards or by regurgitation while the leech feeds.

The leeches have been found only in the bases of iris growing at the margin of the Ley. Pike and eel habitually swim amongst the marginal vegetation and readily acquire infections. Perch swim as small shoals in middle water in their first and second years and have been found with a lower infection rate, but older fish feed from the bottom and amongst reeds and thus come into contact with the leeches and have shown a high incidence of infection. A decrease in the numbers of infected fish has been noted during the years of examination.

(h) *Cryptobia*. Forms of *C. borelli* were found in the proboscis sheath of *H. marginata* and *P. geometra*. These were small comma-shaped flagellates about 20 μm . long with a rounded anterior end and tapered posterior end. Unlike the fish-blood forms the nucleus lies in an anterior position level with the kinetoplast (Plate 1, Fig. 3). Robertson (1912) studied *Cryptobia* from goldfish in *H. marginata* and *Piscicola* sp. Multiplication occurred in the crop as comma-shaped forms. These gave rise to

elongate metacyclics which migrated to the proboscis sheath. The crop forms could divide repeatedly and provide a continuous supply of infective stages. The stages found in the leeches at Slapton resembled the crop stages described by Robertson (*loc. cit.*) but did not divide.

(i) *Mesnilella* spp. Astomatous ciliates of two types were present in the gut of the tubificid worm *Pelosclex benedeni*. Both were identified as species of *Mesnilella*. Cysts have not been seen.

Small forms measured 100–200 μm . (Plate V, Figs. 3, 4). Their bodies were uniformly covered with very long cilia, up to 15 μm . long, arranged in longitudinal rows. The anterior end was differentiated as a concave sucker angled between the dorsal and ventral surfaces: when viewed laterally, this appeared as a slanting, straight or slightly curved blade (Plate V, Fig. 3) but when viewed dorsally the body appeared to taper gradually to a point (Plate V, Fig. 4). A single long spicule arose in the cytoplasm at the dorsal point, passed along half the base of the sucker and turned backwards for two-thirds of the length of the body in a gentle curve. The ribbon-like macronucleus occupied most of the length of the body and tapered to a thin line anteriorly. The small, ovoid micronucleus lay about half-way along its length. There were three or four large contractile vacuoles in a row on one side of the macronucleus. Division was by binary fission into two equal daughters.

Large forms measured 1,000 μm . (1.0 mm.) or more (Plate V, Figs. 1, 2). The distinctly concave sucker lay on the ventral side overhung by an anterior lip. The margins of the sucker were prominent ectoplasmic flaps. The spicule arose dorsally to the sucker in the anterior lip, passed along the base of the sucker and extended through almost the entire length of the body. The body was widest posteriorly, measuring up to 30 μm . and was covered by cilia measuring about 10 μm . The nuclei were similar to those of the small forms but there were numerous contractile vacuoles, often more than 50 in a single row. Division was by unequal budding producing several individuals of varying size which remained in tandem.

The large and small forms have been ascribed to *Mesnilella rostrata* by Rossolimo (1926) and Cheissin (1930) as the small forms are said to be produced by division of the large forms. At Slapton the worms frequently contained the small forms alone but large forms were never seen without the small forms. Morphologically the two types differ in the form of the sucker, the alignment of the spicule and the number of contractile vacuoles. Budding of the small forms from the large was not seen, but both types divided by homothetogenic fission to give rise to individuals of their own size range. No evidence was provided that they were different forms of the same species.

Individuals of both forms were seen to attach to host cells by the sucker. As these ciliates have no cytostome the attachment is probably to maintain station against the peristaltic movements of the gut while feeding occurs by absorption through the pellicle. The function of the spicule is obscure: it does not prevent the bending of the body; as it is embedded deeply in the cytoplasm no anchoring function can be ascribed to it directly; as it follows the base of the sucker before running through the body cytoplasm, contraction of the cytoplasm may act on the spicule to depress the base of the sucker when the edges are clamped on to a cell, thus providing the suction force.

(j) *Radiophyra* sp. This ciliate was occasionally found in the gut of an unidentified tubificid worm. Individuals measure up to 1.0 mm. long and frequently have one

or more satellites. A refractile organelle in the form of a furcula is seen anteriorly but as in *Mesnilella*, this lies within the cytoplasm and cannot function directly as an attachment organelle. There is a ribbon-like macronucleus and a row of contractile vacuoles.

(k) *Collinia circulans* parasitizes, the haemocoel and entire circulatory system of *Proasellus meridianus*.

Organisms belonging to the ciliate order Apostomatida are characterized by a high degree of polymorphism in complex life cycles involving phoretic stages. The life cycle (Text Fig. 1) and physiology of *C. circulans* from *P. meridianus* at Slapton has been studied by Aidley (1972). At Slapton up to 30 per cent of *P. meridianus* were infected, when collected from a site of high density.

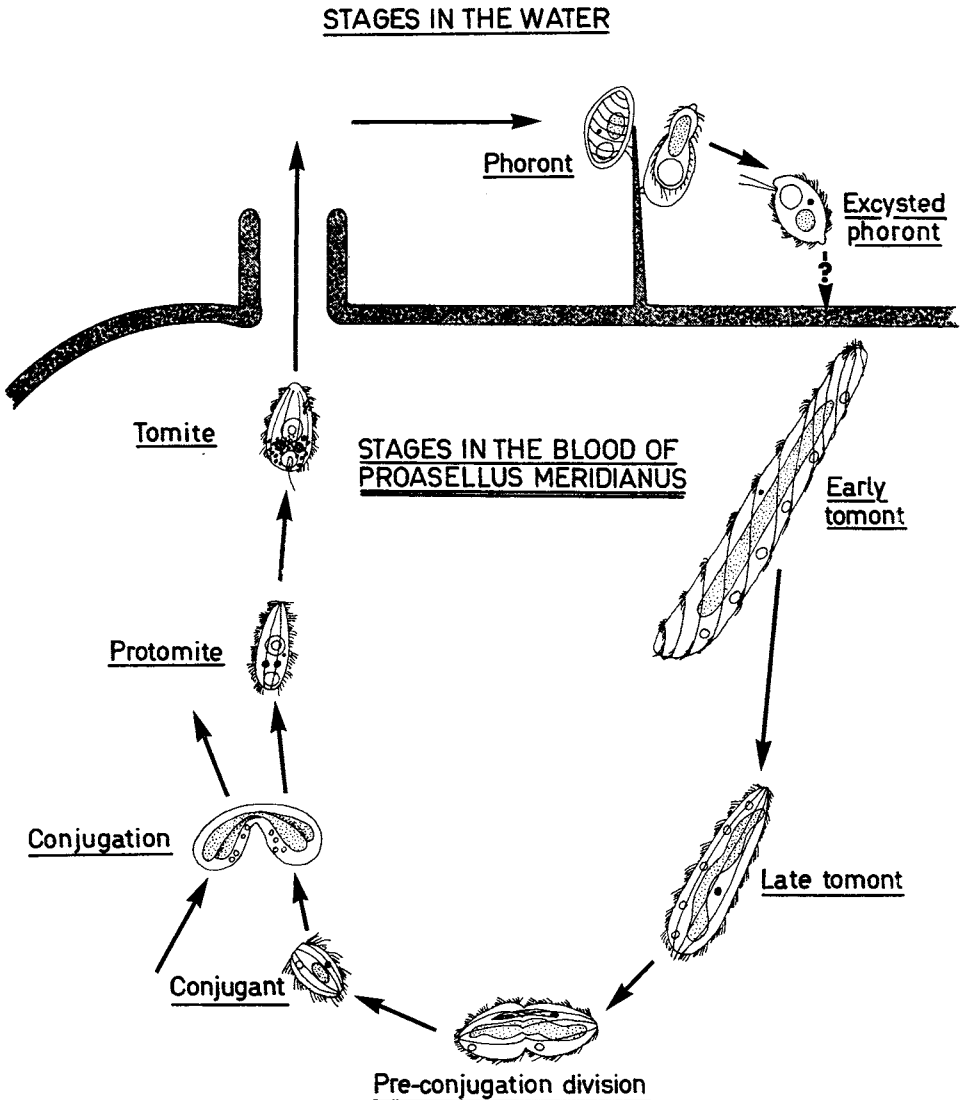


FIG. 1. Life cycle of *Collinia circulans*. (Courtesy of J. S. Aidley.)

Stages which feed, grow and divide in the hosts' blood are tomons (110–120 μm .), characterized by sparse, spiral rows of cilia. Small tomons, in which the ciliary rows are straightened out, are produced by division and become pre-conjugants. Conjugation is obligatory in the life cycle and is unusual in that macronuclei are exchanged as well as micronuclei. The exconjugants become pro-tomites which feed and grow into tomites: these have only eight straight ciliary rows. Tomites do not feed; they are active swimmers, even against the circulatory current and are released, with other stages, on injury of the host. Many are released through damaged antennae which become fragile in infected hosts. Only the tomites survive. Outside the host they encyst, usually on the cuticle of the host, in the fork between the exopodite and endopodite of the uropods, and are known as phoronts. Excystment of phoronts occurs within 3 days. It is not known how these stages gain entry to the host but possibly through an injury to the cuticle.

If the parasites are not released from the host, their numbers increase to a level where they pack the haemocoel and cause stagnation in the circulation and the host dies.

Tomons are completely unable to withstand fresh-water conditions, dying within 2 minutes. The ability to tolerate fresh water is developed progressively from the pre-conjugant stage onwards but only tomites survive long in fresh water. There is a well-developed system of contractile vacuoles: in tomons there are 11–12 vacuoles working in series, emptying every 30–120 seconds. There is a single vacuole in each conjugant, this persisting in tomites where it empties infrequently. Within the cyst, the phoront has a vacuole emptying three times a minute for a few hours. It then disappears and at this stage the cyst wall is presumably used to exert a turgor pressure and stop the inflow of excess water. The vacuole reappears on the second or third day but does not empty: it becomes unusually large as the phoront protrudes through a hole in the cyst and bursts when most of the ciliate has left, thus facilitating the escape of the last part.

Collinia is unusual in the Apostomatidae: it is an internal parasite except in its phoretic stage; the tomont has no cytostome nor the rosette organelle usually associated with it; it has more than one contractile vacuole in the tomont stage; and conjugation involves crossing over of macronuclei as well as micronuclei.

NOTES ON THE PARASITES OF MOLLUSCS

In most cases the cercariae found from snails in the Ley were not made the object of detailed study and there is therefore scope for improving on the observations made here. A few *Helix aspersa* were collected at the Centre.

Lymnaea pereger

Williams (1966*b*) found no less than eight different digeneans using *L. pereger* as intermediate host in a pond near Glasgow. In the Ley *L. pereger* has been observed to produce at least two kinds of furcocercariae, at least one kind of xiphidiocercaria, the echinostome cercariae of *Echinoparyphium recurvatum* and at least one kind of monostome cercaria. These were found in the digestive glands of snails as were cysts of the strigeid *Cotylurus cornutus* (see p. 693). The furcocercariae were, as mentioned, of two kinds; one with two pigmented eyespots is probably *Cercaria ocellata* of a bird schistosome, perhaps that of *Dendritobilharzia pulverulenta* which was found in the renal vein of coot (see p. 694 and Wesenburg-Lund, 1934). *C. ocellata* has been found

Table 7. *Parasites of molluscs in Slapton Ley*

Parasite	Host
ANNELIDA, OLIGOCHAETA <i>Chaetogaster limnaei</i>	<i>Lymnaea pereger</i> , <i>Planorbis</i> sp. <i>Physa fontinalis</i>
PLATYHELMINTHES, DIGENEA Furcocercariae Echinostome cercariae <i>Echinoparyphium recurvatum</i> cysts <i>Cotylurus cornutus</i> (tetracotyle cysts) Monostome cercariae and cysts Xiphidiocercariae	<i>L. pereger</i> , <i>P. fontinalis</i> , <i>Planorbis</i> sp. <i>L. pereger</i> <i>P. fontinalis</i> , <i>Sphaerium corneum</i> <i>L. pereger</i> <i>L. pereger</i> <i>L. pereger</i> , <i>Planorbis</i> sp.
PROTOZOA, MASTIGOPHORA <i>Cryptobia helicis</i>	<i>Helix aspersa</i> spermathecae

to be the cause of swimmer's itch in large freshwater lakes in Europe and America. Also known as schistosome dermatitis, swimmer's itch is caused by the cercariae of bird schistosomes penetrating human skin and setting up a hypersensitive reaction before being destroyed. Other kinds of furcocercariae in *L. pereger* from the Ley need further examination, since *Cercaria A.* Szidat of *Cotylurus cornutus* and *Cercaria Apatemon gracilis minor*, both strigeid parasites of water birds, should be present in the Ley (see p. 693). *L. pereger* is also the first intermediate host to *Cercaria C.* Szidat (syn. *Cercaria diplostomi spathacei*) the larval stage of *Diplostomulum spathaceum* which is prevalent, particularly as the diplostomulum stage in fish eyes, in the Ley. Descriptions of these and other furcocercariae are given in Wesenburg-Lund (1934) and in Iles (1959).

The monostome cercariae had three pigmented eyespots and may have been the larvae of the monostome *Notocotylus gibbus* found in the caecum of coot. The cercariae of *Echinoparyphium recurvatum*, a gut parasite of birds, were also found in *L. pereger* and were identified by their 43-45 collar spines (see p. 694). Some of the xiphidiocercariae in *L. pereger* may have been those of *Crepidostomum metoecus*, an allocreadid digenean found in the pyloric caeca of *Salmo trutta* (see p. 684), although the xiphidiocercariae were not identified and trout were not commonly found in the Ley and could have become infected elsewhere.

The oligochaete *Chaetogaster limnaei* is a common commensal of snails and shelters within the snail shell from which it emerges to feed, sometimes on snail parasites. There have been reports of *Chaetogaster* consuming both miracidia and cercariae and it has been suggested that this annelid commensal might be useful in the biological control of digeneans such as *Fasciola* and *Schistosoma* (see Boray, 1969).

Planorbids

Few detailed observations were made on the furcocercariae and xiphidiocercariae from planorbids. *Planorbis corneus* has been reported as the first intermediate host of *Typhlocoelum sisowi*, adult in the tracheae of swans, but monostome cercariae have not so far been found in planorbids in the Ley.

Physa fontinalis

Cysts of *Echinoparyphium recurvatum* were found in the digestive gland of this snail but no echinostome cercariae, so presumably cercariae of *E. recurvatum* emerge from

L. pereger and penetrate into both *Physa* and the bivalve *Sphaerium corneum*, where they become infective to water birds. *Chaetogaster* was also found associated with *Physa*.

Sphaerium corneum

These bivalves were often heavily infected with metacercarial cysts of the bird fluke *Echinoparyphium recurvatum*, as already mentioned (p. 694). Around 100 per cent of the hundred or so bivalves examined were infected. These bivalves act as second intermediate hosts for the parasite. *Limnaea pereger* is the first intermediate host. Adult *Echinoparyphium recurvatum* were found in the intestine of the moorhen.

Helix aspersa

Cryptobia helicis was commonly found in the spermathecae of *Helix aspersa*. Unlike the cryptobias of fish and leeches (p. 687), the body form is highly polymorphic, ranging from elongate to almost round. The kinetoplast is elongate and anterior but the position of the nucleus varies according to the shape of the organism. Dividing forms with two nuclei and two kinetoplasts were common.

SUMMARY OF AQUATIC LIFE CYCLES

(1) *Direct life cycles*

The monogenean gill parasites *Dactylogyrus* and *Neodactylogyrus* spp. from rudd and roach and *Tetraonchus monenteron* from pike all have direct life cycles which involve the egg, a free swimming ciliated oncomiracidium larva and the adult. The eggs of monogeneans tend not to float in water but sediment to the bottom where they lie until they hatch. Hatching is an active process and in many cases the ciliated oncomiracidium which has pigmented eyespots responds to light by an increase of activity which then assists in hatching. The larval eyes of *Dactylogyrus*, *Neodactylogyrus* and *Tetraonchus* are in fact retained into the adult flukes. This larva actively infects the gills of the correct species of host fish. Monogeneans are highly host specific and there is evidence that chemotaxis is involved in some host location.

Aplectana, *Oswaldocruzia* and *Rhabdias* from amphibians all have direct life cycles, the infective larvae of these nematodes enter contaminatively on food or penetrate (*Rhabdias bufonis*) through the host skin.

Most of the protozoan parasites of fish and amphibians have direct life cycles. Those commonly found in the gut of amphibians are normally transmitted directly by cysts, passed in the faeces. Ciliates form cysts during both their asexual and conjugation phases. *Opalina ranarum*, however, forms cysts only in the sexual phase, influenced by the reproductive state of the host. *Trichomonas* does not form cysts. *Trichodina* which skims over the skin and gills of fish, probably transfers from one fish to another while they are in close contact.

(2) *Indirect life cycles with one intermediate host*

The particular kind of invertebrate host utilized tends to be characteristic for particular groups of parasites. Digeneans nearly always have a snail first intermediate host to which they are highly specific and this may reflect the fact that they are primitively parasites of molluscs and only came to parasitize vertebrates much later in their evolution. Digeneans with aquatic life cycles tend to infect snails actively by means of a ciliated, gutless, miracidium larva which hatches from an operculate

egg and homes upon a suitable snail which is usually penetrated by means of enzymes produced by the miracidium. Once inside the snail a remarkable process of asexual reproduction commences; the miracidium transforms into a sporocyst or redia (or both) and germ balls within these larvae differentiate into tailed cercariae which in aquatic life cycles are liberated from the snails as free-swimming dispersal phases. The incredible adjustment between digeneans and their snail hosts is reflected in the fact that enormous amounts of tissue damage to the nutrient-rich digestive glands of snails caused particularly by rediae seems to be tolerated without snails dying or showing obvious ill effects. The dispersive cercariae may infect the final vertebrate host either actively by penetrating into it, or passively by encysting and being consumed as a contaminant. The bird schistosome *Dendritobilharzia* infects its host actively and furcocercariae with penetration glands are stimulated by the higher body temperature of birds and perhaps by skin secretions such as cholesterol to bore in through the epidermis and into the blood vessels of the bird. Once in the blood vessels the schistosomula, as the tailless post-larva is now termed, drifts for a while in the circulation until pairing occurs and males and females take up residence in the renal vein. The eggs of this parasite presumably work their way through the wall of the renal vein into the kidney and out via the ureter. The monostome digeneans *Notocotylus* and *Typhlocoelum* infect their respective coot and swan hosts in a passive manner. Monostome cercariae encyst readily and *Notocotylus* cercariae may encyst on the outside of *Lymanaea pereger* its intermediate host, shortly after being liberated, or on weeds or other snails. *Typhlocoelum* is said to encyst within its planorbid snail intermediate host, the snails then being consumed by swans.

Cestodes and acanthocephalans nearly always infect both their intermediate and final hosts in what may be termed a "passive" manner, although once consumed the larvae are activated to hatch, excyst and locate their site within the host. Pseudophyllidean cestodes have free-swimming coracidium larvae but these tapeworms were not found in the Ley. In general, cestodes and acanthocephalans with aquatic life cycles both use microphagous crustaceans as intermediate hosts and these become infected by eating the eggs of these parasites. The triturating action of the jaws of these arthropods may be important in assisting hatching. *Caryophyllaeides fennica*, however, an unstrobilate cestode, uses a nauid as intermediate host and the operculate eggs hatch in the intestine of the annelid before the 6-hooked larva bores out into the coelom and transforms into a proceroid larva. The unstrobilated adult of this worm which occurs in the gut of roach may be equivalent to the plerocercoid stage of pseudophyllidean tapeworms. Some unidentified bird hymenolepid cysticeroid larvae were found in tubificids in the Ley, but the hymenolepid *Diorchis inflata* from the gut of coots is thought to use ostracods as an intermediate host.

"Aquatic" acanthocephalans use water shrimps as their intermediate hosts and *Acanthocephalus clavula* from perch and roach uses *Proasellus meridianus*. *Filicollis anatis* from the swan uses *Asellus aquaticus* as does *A. lucii* from eels and *Polymorphus minutus* from ducks and swans has a cystacanth stage in *Gammarus pulex*. *Asellus aquaticus* was not found in the Ley so final hosts carrying *Filicollis* and *A. lucii* may have become infected elsewhere. The intermediate host of *A. ranae* from toads and newts is not known.

Trypanosomes and cryptobias of aquatic vertebrates are transmitted by leeches. *Hemiclepsis marginata* attaches temporarily to a host, takes a blood meal and drops off. The flagellates taken in the blood meal, develop to infective metacyclic stages in the

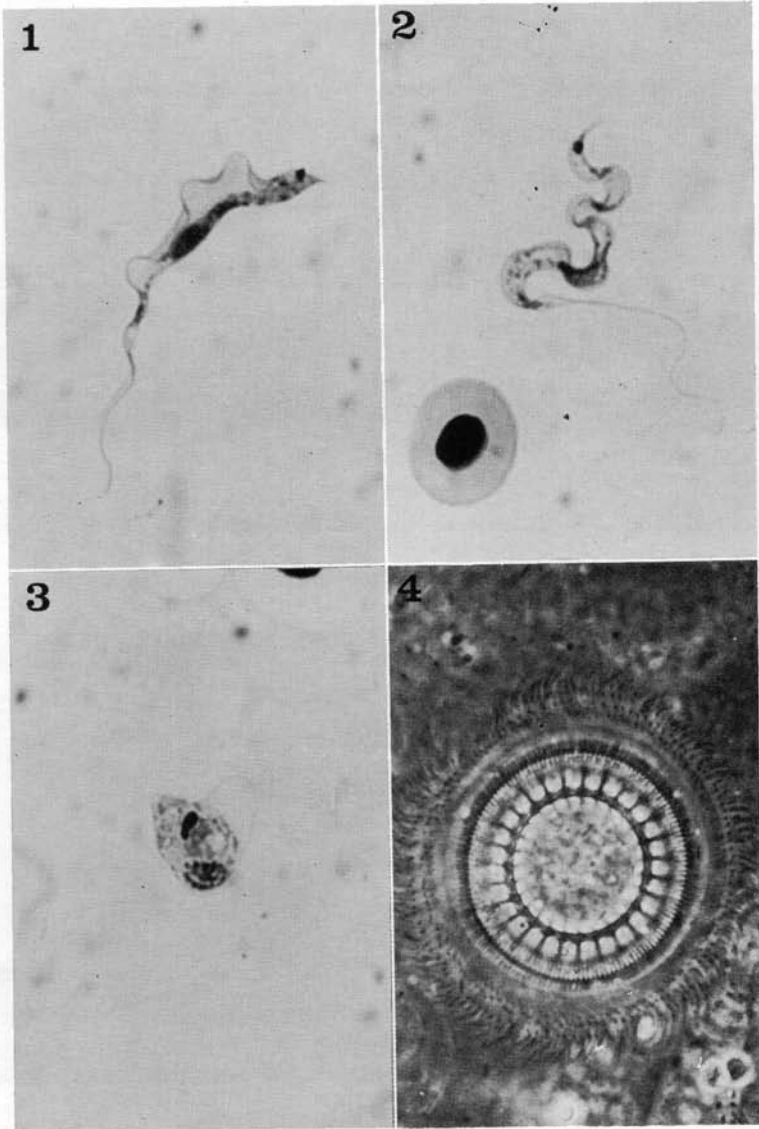
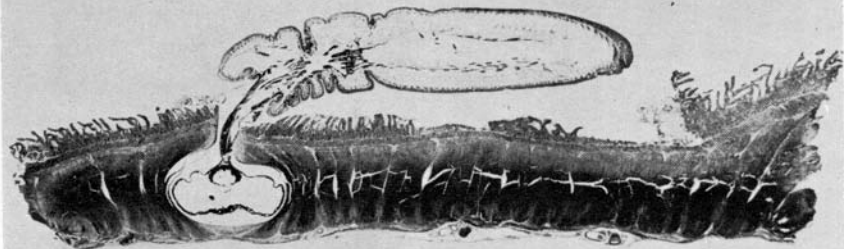


PLATE I.

Protozoan parasites of fish (scale see text): (1) Blood stream form of *Trypanosoma percae* (Giemsa stained); (2) Blood stream form of *T. granulorum* (Giemsa stained); (3) Blood stream form of *Cryptobia borelli* (Giemsa stained); (4) *Trichodina* sp., on skin of fish (size range of genus 50–100 μm .). (Nos. 1–3, courtesy Dr. E. A. Needham; No. 4, courtesy Dr. J. Shillcock.)

1



2



PLATE II.

(1) *Filicollis anatis*, an acanthocephalan with its proboscis embedded in the intestinal wall of the swan (L.S. fixed material); (2) "Tetracotyle" cysts of *Apatemon* or *Cotylurus* (see text) in T. S. Leech, *Erpobdella octoculata*. Cysts in botryoidal tissue, gut caeca, genital system. (Cysts 0.3–0.4 mm. across, courtesy Mr. T. McCaul.)

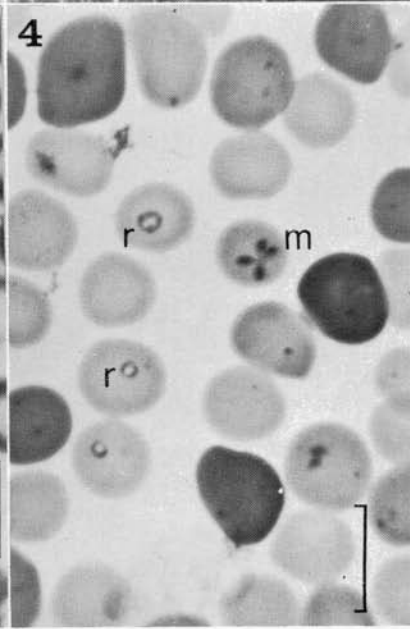
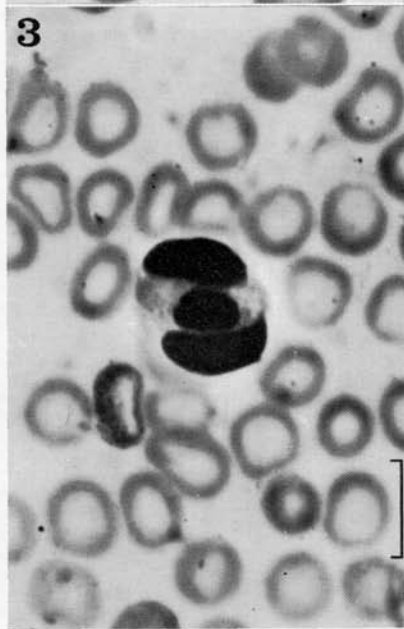
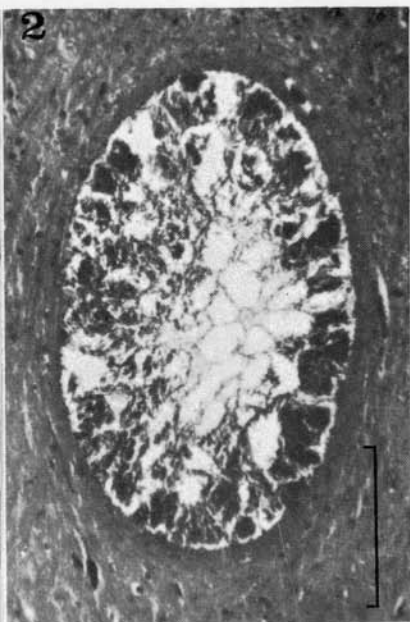
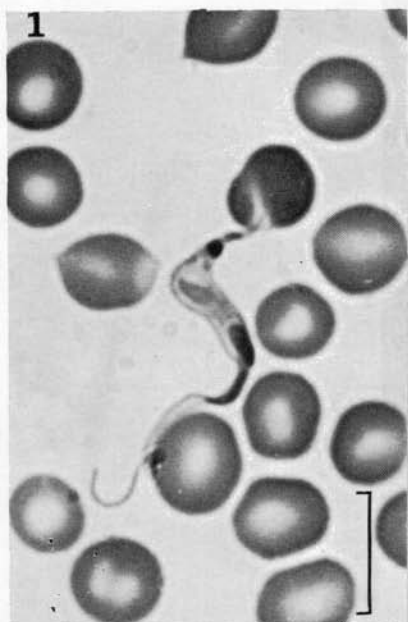


PLATE III.

Protozoan parasites of mammals. (1) Blood stream form of *Trypanosoma evotomys* (Giemsa stained); (2) Section through a cyst of *Frenkelia glareoli*, from brain of bank vole (Heidenhain's haematoxylin); (3) Gametocyte of *Hepatozoon erhardovae* in leucocyte of blood of bank vole (Giemsa stained); (4) *Babesia microti*, heavy infection from laboratory mouse (Giemsa stained) (r, ring form; m, Maltese cross form). Scale 1, 2, 3 = 10 μ m; 2 = 10 μ m.

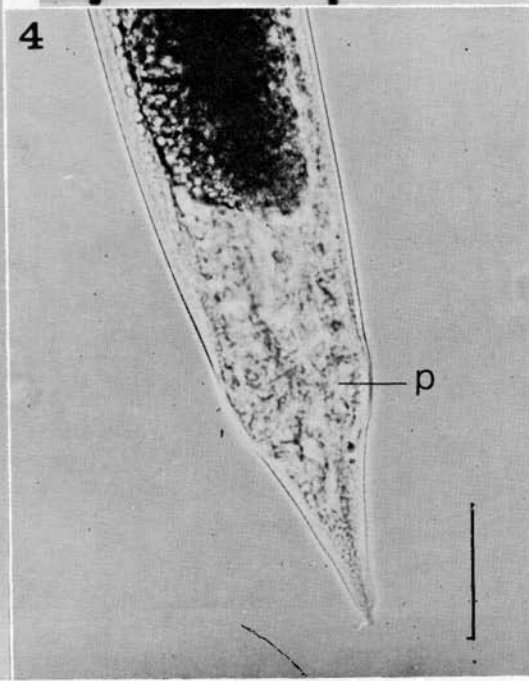
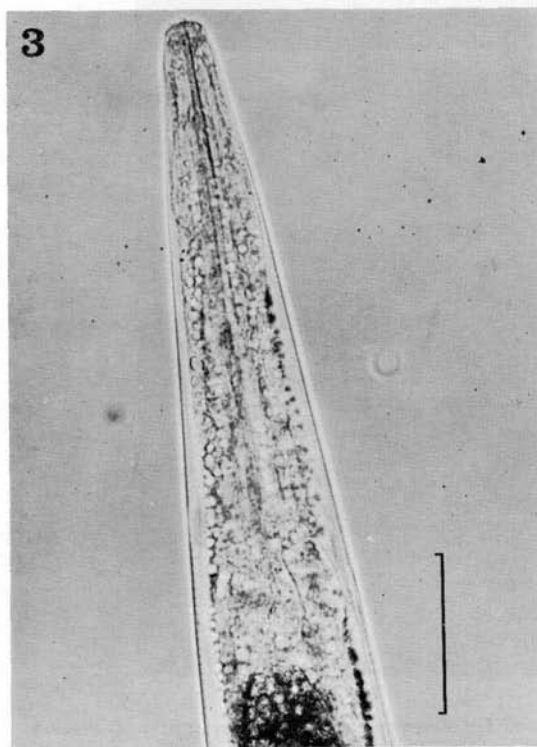
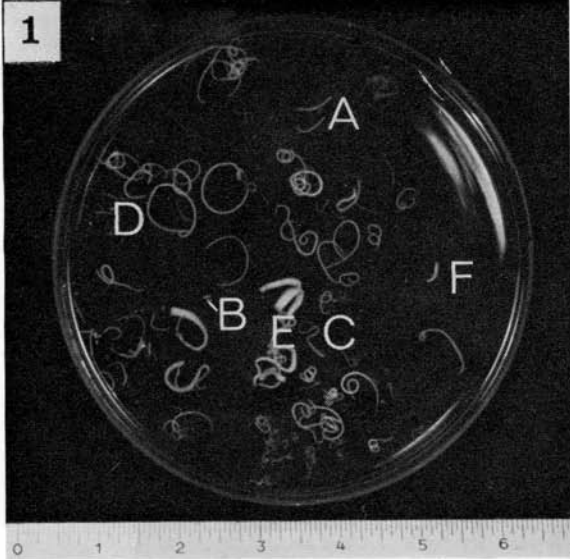


PLATE IV.

(1) The helminth parasites of a single starling (scale inches): (A) *Syngamus trachea*, (B) digenean, (C) *Capillaria* sp., (D) ascarids, (E) tapeworms, (F) *Prosthynchus cylindraceus*; (2) *Pelodera strongyloides* from the lachrymal fluid of the bank vole (scale = 100 μ m); (3) Anterior end of *P. strongyloides* (scale = 50 μ m); (4) Posterior end of *P. strongyloides* (scale = 50 μ m) (p is a phasmid).

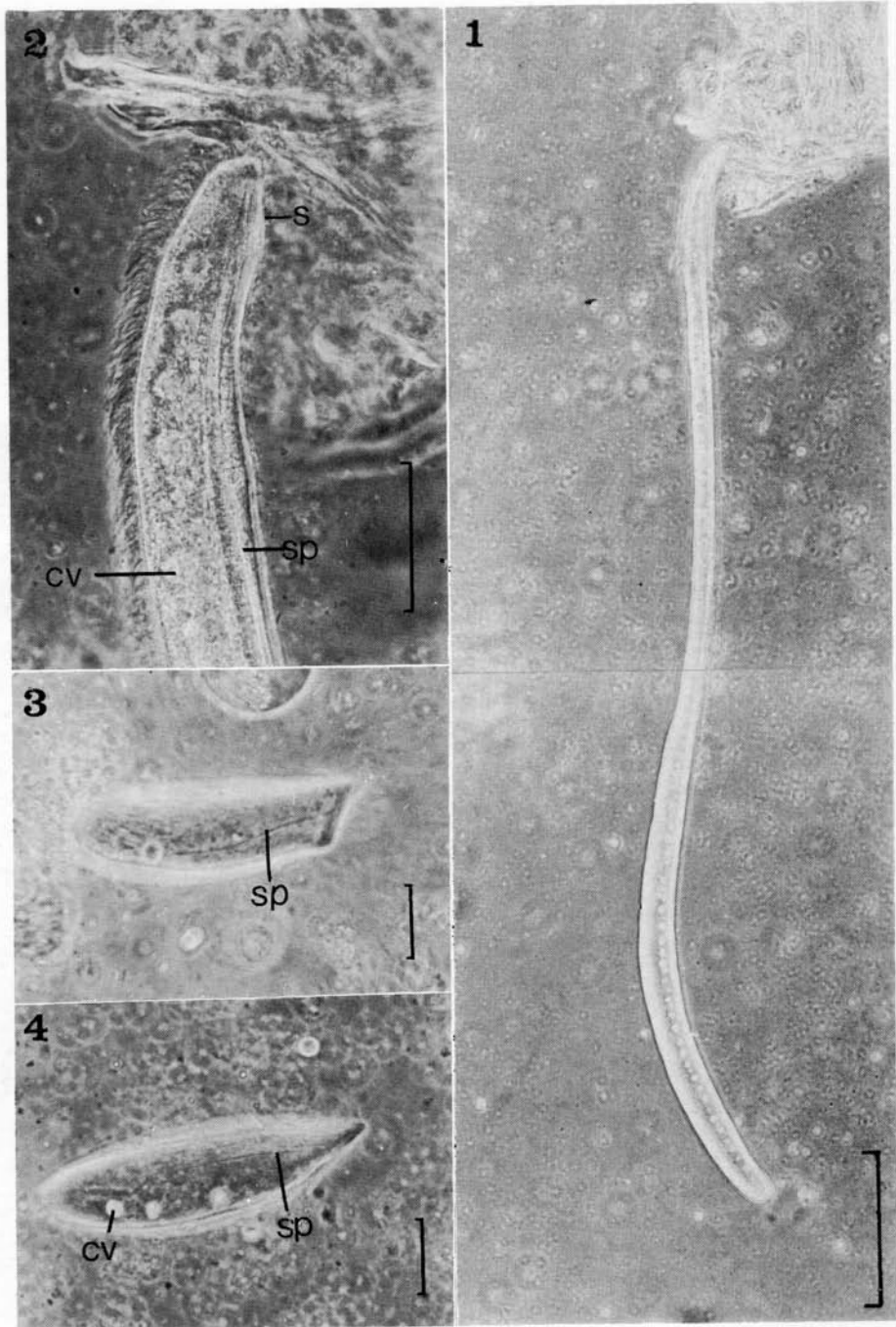


PLATE V.

Protozoan parasites from the gut of the tubificid annelid *Peloscoclex benedeni* (living, phase): (1) *Mesnilella rostrata*, large form (scale = 200 μm); (2) Anterior end of *M. rostrata*: large form (scale = 50 μm); (3) *M. rostrata* small form, note blade-shaped anterior end in "lateral" view (scale = 50 μm); (4) *M. rostrata*, small form "dorsal" view (scale = 50 μm). (cv, contractile vacuole; s, suckers; sp, spicules.)

gut and some invade the proboscis sheath. Infection of another fish occurs by inoculation of the flagellates. *Piscicola geometra* remains attached to the same host between blood meals. Thus *Cryptobia* is repeatedly inoculated into the same host fish, which may result in very high infections. *Trypanosoma* spp. are not transmitted by *Piscicola*.

(3) *Indirect life cycles with two intermediate hosts (helminths only)*

These are summarized below:

	Ist intermediate host	2nd intermediate host	Final host
<i>Cotylurus</i> and <i>Apatemon</i> spp.	<i>Lymnaea pereger</i>	Tetracotyle stage in leeches	Water birds
<i>Diplostomum</i> <i>spathaceum</i>	„ „	Fish eyes; lens and humour in diplostomulum stage	Gulls
<i>Echinoparyphium</i> <i>recurvatum</i>	„ „	Metacercarial cysts in <i>Sphaerium</i> , a bivalve	Water birds
<i>Crepidostomum</i> <i>metoecus</i>	„ „	Metacercarial cysts in <i>Gammarus</i> sp.	Trout
<i>Cryptocotyle</i> <i>lingua</i> (marine)	<i>Littorina littorea</i>	Metacercarial cysts in marine fish, e.g. herring	Herring gull

Helminths with two intermediate hosts in their life cycles seem to be more conspicuous in the Ley and the various larval stages were encountered more frequently than those of parasites with one intermediate host in the life cycle. This may be partly because more larval stages are produced by parasites with three hosts as they stand less chance of infecting the final host as the number of hosts, and conditions to be satisfied by the various stages of the life history, increases. It may also be partly because resistant and dormant infective stages accumulate in the second intermediate hosts and therefore become conspicuous in the host population. *Sphaerium* infected with *Echinoparyphium* metacercariae is an example of this kind of build-up. Nearly 100 per cent of the *Sphaerium* examined were infected with cysts of this echinostome fluke and some of the bivalves contained several hundred cysts. It might be expected therefore that a mass infection with *Echinoparyphium* could be obtained by the final host merely consuming a single infected bivalve. The same is true of *Cotylurus* tetracotyle stages in leeches and *Diplostomum* larvae in fish eyes, both of which occur in fairly large numbers in these intermediate hosts. The fact that a parasite may alter the behaviour of an intermediate host and lead to it being more easily predated by the final host is interesting. This is said to occur in the case of *Diplostomum* in fish eyes, the larvae blinding the fish, changing its feeding

behaviour and making it more easily available to piscivorous birds which are the final hosts of this parasite. The most famous example of this kind of effect is that of the cercaria of *Dicrocoelium lanceolatum* the lancet liver fluke, which encysts in the brain of an ant (the second intermediate host) with the specific result that infected ants then bite on to a grass blade when the temperature is low during the night and early morning, from which site they are consumed by sheep, which form the definitive host for this fluke. The plerocercoid stage of *Schistocephalus solidus* which occurs in the body cavity of sticklebacks (not found in the Ley but recovered from Gara stream) may make the stickleback more conspicuous to a gull (the final host) by altering the body shape so that reflected light from the scales under the body becomes visible from above, thus destroying the natural camouflage of the fish.

There is a tendency when thinking of parasites to place more importance upon the adult parasite than on the larvae. It is perhaps worth remembering that, in terms of time, some of the aquatic parasites mentioned here are more conspicuous as larvae and have a longer life as larvae than as adults. Often the greater part of the life history may be spent in the intermediate host or hosts. *Caryophyllaeus laticeps* for instance, may spend two years or so in its tubificid host, but may persist in the gut of the final fish for only three months.

Finally, there is some evidence that some of these "aquatic" life cycles have a seasonal incidence as do terrestrial life cycles. This did not emerge from the present findings as parasites were nearly always sampled in September and not at other times of year, but it is known that *Cotylurus tetracotyle* stages, for instance, are more common in leeches during the warmer months of the year and that *Caryophyllaeus laticeps* from dace (not found in the Ley) is most common in its fish host during the coldest months of the year.

SUMMARY OF TERRESTRIAL LIFE CYCLES

(1) *Direct life cycles*

Transmission usually relies on food chains, the parasites in a relatively resistant form (an egg or cyst) entering the host passively. Even the apparent exceptions, such as the motile infective larva of *Nematospiroides dubius*, is ensheathed and enters rodents as a contaminant of food.

The eggs of *Capillaria hepatica* which are laid in the liver of small rodents, depend on a predator in the food chain for their release from the liver. Earthworms and snails also serve as transport hosts for the eggs of *Syngamus trachea* in birds. In the context of resistant phases developing among parasites in the terrestrial habit, it is interesting to note that *Pelodera strongyloides* was commoner in the orbits of rodents in and following periods of drought. This may be a nematode which is flirting with parasitism, and it is noteworthy that the selective pressure may be one of avoiding desiccation.

Most of the protozoans of mammals have direct life cycles. The parasites are ingested and eventually reach the large intestine or caecum where they divide asexually and may reach considerable numbers. In *Entamoeba muris* cysts are formed and these pass out with the faeces and are ingested to initiate new infections. This pattern is characteristic of the Protozoa in the guts of mammals, for example, *Hexamita* and *Giardia*, but for some unknown reason *Trichomonas* does not form cysts but must, nevertheless, be able to survive in the world outside the mammal host. The fact that these parasites are the most common protozoans in small mammals

indicates that whatever method of survival has been adopted it is extremely successful. The life cycle of *Eimeria* is more complex in that there is a stage of multiplication within the cells of the gut walls and this is followed by a sexual stage, as a result of which resistant oocysts are formed and pass out with the faeces.

In general therefore the terrestrial life cycles of parasites tend to lead to a substitution of the free-living dispersive larval stages, for stages that are protected by eggs, cysts, sheaths or are in carrier hosts. The result of this tendency is an increasing "insulation" of the life cycle, the parasites being transmitted along food chains.

(2) Indirect life cycles

The so-called "terrestrial" life cycles of parasites of terrestrial definitive and (sometimes also) intermediate hosts, are characterized by passive transfer between these hosts, usually along a food chain. Correlated with this passive transfer is a reduction in the free-living stages in digeneans and cestodes. Where a terrestrial snail is used in a digenean life history the miracidium larva tends not to hatch but be retained inside the egg which is eaten by the snail (e.g. for *Brachylaimus* and presumably *Corrigia*). Similarly the cercarial stage is reduced and encystation may occur in the same snail in which the cercariae developed (see p. 696). The acanthocephalan parasite of owls, *Centrorhynchus aluconis*, provides a good example of a parasite that passes along a food chain into its predatory host. The first intermediate host of *Centrorhynchus* is not known but it is presumably an arthropod of some kind; these arthropods must form part of the diet of shrews since the latter act as paratenic hosts for the cystacanths, i.e. shrews become infected but the larvae that excyst in the gut of these insectivores do not remain in the gut and develop to maturity, but bore out into the body cavity where they became more or less dormant once more. The shrews then distribute the parasites to the "correct" final host since owls prey on shrews but not on invertebrates which form the normal intermediate hosts of acanthocephalans. *Hydatigera taeniaeformis* also reaches its final carnivore hosts (foxes, owls, etc.) via a small mammal, this time *Clethrionomys*, which become infected directly by eating the eggs of *Hydatigera*.

The indirect life cycles exhibited by the Protozoa of mammals all involve arthropod vectors. *Hepatozoon* has a life cycle similar to that of *Eimeria*, but in deep tissues and not the gut. The sexual stages are released into the blood and enter white blood cells. They are taken up by arthropods, probably fleas, in which the cycle continues and a new cycle begins when the flea is eaten by another host. Fleas are also vectors of the trypanosomes of some mammals. The trypanosomes are taken up from blood when the flea feeds and develop in the posterior part of the flea's intestine. When the flea feeds, it defaecates and the infective stages may enter the wound. Alternatively, the flea may be eaten and the infective trypanosomes reach the blood through damaged tissues in the mouth or gut. This kind of life cycle contrasts with that of the African trypanosomes that cause sleeping sickness in man and his domesticated animals. In such cases the vector is a biting fly and the trypanosomes develop in the anterior part of the gut and reach the salivary glands from which they are injected directly into the blood stream of a new host. The vectors of *Babesia* are ticks. Blood is taken up when the tick feeds and a series of developmental cycles occur in the tick with the result that it is the ticks of the next stage of the life cycle that are infective. In other words, if the larva becomes infected it is the nymph which is infective and similarly with the nymph and adult. There is no transovarian transmission as occurs

in *Babesia* in cattle. Eventually infective stages reach the salivary glands of the tick and are injected into the clean host. In the case of *B. microti* the vector has been shown to be *Ixodes trianguliceps* in the laboratory, but this requires confirmation.

GENERAL DISCUSSION OF THE PARASITES OF SLAPTON LEY

This survey has presented a few features of particular interest, which merit further investigation. The Ley experiences algal blooms resulting from the extensive use of fertilizers on the surrounding fields. This may be related to an apparent reduction in the levels of acanthocephalans in the fish over the years of our sampling, through the direct or indirect reduction in the crustacean hosts.

The total absence of digenean flukes from all the amphibians over all the years is most striking, particularly with an abundance of freshwater snails. The fish also have only low levels of adult digeneans, but most carry diplostomulum larvae in the lens and humour of their eyes. The infestations of snails, leeches and tubificid annelids with larval parasites seem to be very largely those of the birds in the Ley.

Bufo bufo, was commonly infected with *Acanthocephalus ranae*. The number of parasites tending to increase in the larger hosts. A number of student projects showed the actively boring mechanism of the proboscis in *A. ranae*, and its highly localized distribution in the host gut. When individuals were removed and stained in aqueous methylene blue and fed to another host, upon dissection a few hours later, the stained parasite was found amongst the existing parasites of the recipient host. The life cycle is not verified but we found the cystacanth of *A. ranae* in *Proasellus meridianus*. This is a strictly aquatic isopod, not found in the areas where we collected the toads. Either the parasites live for considerable periods (years!) or there is another intermediate host in a more "terrestrial" situation, possibly a woodlouse or insect.

Collections of leeches were made and the number of tetracotyle cysts counted in each. By far the most commonly infected leech was *Erpobdella*, some with over 50 cysts in a single leech. *Glossiphonia* and *Helobdella* were also commonly infected, but *Theromyzon* and *Hemiclepsis* were less frequently infected. The highest infections were found in areas E₁ and E₂. The frequency distribution of tetracotyle cysts followed a negative binomial, as is common among many helminth parasites (Crofton, 1971).

Any future survey work on small mammals at Slapton (or elsewhere) could develop our findings on the orbit nematode *Pelodera strongyloides*. We found highest numbers during or following drought, this is a consequence of the nematode's biology.

The finding of *Frenkelia glareoli*, a report subsequently published by two students on the course (Toye and Tappin, 1972), was noteworthy. The very impressive ciliate, *Mesnillella* one type of which was 1.0 mm. long, was common in the tubificid *Pelosclex benedeni* and would provide excellent research material.

The complex life cycle of the apostome ciliate *Collinia circulans*, in the haemocoel and entirely circulatory system of *Proasellus meridianus* in the Ley, was elucidated by another former student of our course, Aidley (1972).

It has been suggested that the lung nematode *Rhabdias bufonis* of the toad, *Bufo bufo* has a preference for one lung. Over the years of our records, 192 individuals came from left lungs and 208 from right lungs—strongly suggesting the absence of any preference.

Our observations have been made concurrently with extensive surveys on the population biology of the fish in the Ley and many other incidental recordings.

We believe our data will provide insight to teachers and students studying the biology of the Ley and similar habitats, not only about the parasites but also about their hosts.

We have described how the feeding habits of leeches is related to the transmission of fish trypanosomes and cryptobias. Similarly how the distribution of tetracotyle cysts must relate to the infection of the aquatic bird hosts which feed on the leeches. The widespread infections of diplostomula in the eyes of fish also relates to the piscivorous habits of the birds. Numerous ecological links, through feeding, contact and topography are suggested by our findings, and we hope they will be used as biological indicators of the relationships between the animals in the Ley.

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ADDENDUM

Since the submission of this manuscript Dr. C. R. Kennedy has kindly brought to our attention that an adult of *Caryophyllacus laticeps* and one plerocercoid of *Ligula* sp. have been found in roach from Slapton Ley.