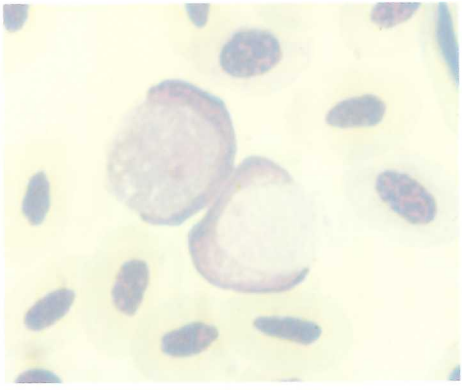
PARASITIC PROTOZOA IN BRITISH WILD ANIMALS



Institute of Terrestrial Ecology
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Cover

At the top: a rookery at Breamore, near Fordingbridge, Hampshire, where research funded by NERC led to the identification of the insect transmitter of a blood parasite (*Leucocytozoon sakharoffi*), shown at bottom left highly magnified, of rooks (*Corvus frugilegus*), shown at bottom right – see page 11. Photographs J. R. Baker.

Acknowledgements

The Institute wishes to thank Sarah Anthony for drawing some of the figures in this booklet. The work formed part of her year's sandwich course at the Monks Wood Experimental Station, Huntingdon. Sarah is a cartography student at the Luton College of Higher Education, Bedfordshire. Michael Woodman drew two of the figures. The remainder were drawn by the author. Our thanks to Peter Ainsworth and Kenneth Clarke for printing photomicrographs; and Mrs. H. V. Clements for the typing.

The **Institute of Terrestrial Ecology (ITE)** was established in 1973, from the former Nature Conservancy's research stations and staff, joined later by the Institute of Tree Biology and the Culture Centre of Algae and Protozoa. ITE contributes to and draws upon the collective knowledge of the fourteen sister institutes which make up the *Natural Environment Research Council*, spanning all the environmental sciences. The Institute studies the factors determing the structure, composition and processes of land and freshwater systems, and of individual plant and animal species. It is developing a sounder scientific basis for predicting and modelling environmental trends arising from natural or man-made change. The results of this research are available to those responsible for the protection, management and wise use of our natural resources.

About one quarter of ITE's work is research commissioned by customers, such as the Nature Conservancy Council who require information for wildlife conservation, the Department of Energy, the Department of the Environment, and the EEC. The remainder is fundamental research supported by NERC.

ITE's expertise is widely used by international organizations in overseas projects and programmes of research.

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A note on the Figures. Except for Figures 3, 15, 26 and 27, all were drawn specially from stained specimens. All except numbers 3, 8, 11, 13 and 26 are printed at a magnification of × 1000 (so that 1 mm on the Figure is equivalent to 1 μm on the specimen).

Introduction

Protozoa* are almost all minute, single-celled animals, too small to be seen without the aid of a microscope. (The unit by which protozoa are measured is the micron or micrometre, abbreviated as μm; 1 μm = 0.001 mm.) They are abundant in soil and water everywhere (both fresh and saline waters). Perhaps the best-known, because it is usually referred to in school biology classes, is *Amoeba*. Each protozoon is structurally equivalent to a single cell, many millions of which constitute the bodies of "higher" (more complex) animals and plants – from apples to zebras (including ourselves). Like our own body cells, each protozoon consists of a nucleus, surrounded by cytoplasm, all contained within a "bag" or limiting membrane of some kind (see Figure 6). Most contain other structures also – mitochondria, Golgi apparatus, endoplasmic reticulum, all of which are essential to the normal functioning of the cell. Many protozoan cells (like those of many-celled animals) also have structures concerned with locomotion: flagella, cilia, or pseudopodia. The first two of these structures are, respectively, longer and shorter hair-like outgrowths from the cell which function more or less like oars in propelling the organism through a liquid environment (see Figures 5 & 26). Pseudopodia are temporary "foot-like" extensions by means of which amoebae creep about. Use of one or other of these organelles as their main means of propulsion has traditionally separated the protozoa into three major groups (see Annex I): the flagellates (using flagella) or Mastigophora, the ciliates (using cilia) or Ciliophora, and the amoebas (moving mainly by means of pseudopodia) or Sarcodina. A fourth large group, usually lacking special structures to aid in locomotion, is the Sporozoa, or, to use its more modern name, Apicomplexa. There are a few other minor groups, two of which (Microspora and Myxosporea) will be mentioned below as parasites of fish. Some protozoa contain green chloroplasts, like the "higher" plants. Such forms are indistinguishable from single-celled algae, which are traditionally regarded as the intellectual property of botanists. In fact, demarcation disputes rage continually between botanists and zoologists over these microscopic organisms. One way to avoid such disputes is to adopt the holistic view that the two groups (protozoa and algae) are fundamentally indivisible, and call them both protists (= Protista).

In spite of its structural resemblance to a single component cell of the body of, say, a whale, elephant, man or woman (an arbitrary selection!), each protozoon is functionally equivalent to the whole whale, elephant, man or woman. Each individual protozoon (or woman, etc) can exist independently and perform all necessary functions for life support. In fact, many protozoa may be more independent than men or women, in that most can reproduce unilaterally by non-sexual processes. John Donne's stricture, that no man is

*This and other technical terms are defined in the Glossary

an island, may be less applicable to protozoa than it is to ourselves. However, many, though by no means all, indulge in sex as well as reproducing asexually.

In addition to the myriad protozoa living in soil and water, many species inhabit the bodies of other plants and animals, obtaining nourishment from their (usually unwilling) hosts and sometimes causing the latter considerable damage. It is, however, exceptional for such organisms to be significantly harmful. Various grades of association exist between two organisms of different species; unfortunately, there is little agreement about the names applied to them. One simple scheme is to refer to all degrees of association as **parasitism**, and subdivide it into three categories. First, **commensalism**, when one organism (the parasite) uses the other (the host) mainly for shelter, though it may also benefit by eating some of the host's food; the host is essentially unharmed. Many amoebae and flagellates live as commensals in the intestines of vertebrates (including human beings). Second, **symbiosis**, in which both parasite and host benefit. This kind of relationship is exemplified by ciliated protozoa living in the rumen of cattle and red deer in Britain. The protozoa assist in digesting the grass eaten by the ruminant, and help to make more of it available as soluble nutrient material which can be absorbed. It has been estimated (perhaps rather wildly!) that the protozoan population of the rumen of a single ox is about 10^{10} – more than double the global human population – and that they supply about one-fifth of the ox's daily protein requirement. Third, **tissue parasitism**; in this association, the parasite feeds on the host's own body tissue. All harmful parasites are tissue parasites, but not all tissue parasites are harmful. Some writers restrict the term "parasitism" to this kind of association, using "symbiosis" as a general name for all three categories; what I have called "symbiosis", they refer to as "mutualism". Parasites benefit from shelter and a ready supply of food from their hosts, but they are also faced with particular problems: notably, how to evade the efforts of the host's immune defensive system to expel or eradicate them, and how to travel from one host to the next. Their solutions to the first problem are fascinating and as yet imperfectly understood, but they are beyond the scope of this account. The second problem (inter-host transport) has usually been solved in one of two ways: transport within a second host (vector) – usually an insect, tick or leech, in the case of protozoa; or the occurrence of a resting stage within a protective cyst, which waits passively after leaving one host (usually in faeces) until it is swallowed by the next. The cyst protects the enclosed protozoon from dessication and other hazards of exposure to the great wide world. Obviously, this means of transport is used mainly by parasites inhabiting the host's gut. Vector transmission is generally adopted by parasites of the blood. A few organisms (eg two flagellates, *Trichomonas vaginalis*, which may cause vaginitis in women, and *Trichomonas foetus*, a cause of abortion in cattle) have solved the transmis-

sion problem in a more sophisticated way: they are transmitted venereally, during sexual intercourse; but no example is known of this or other esoteric modes of transmission amongst the parasites of British wild animals.

Probably the best-known human diseases due to protozoan parasites are malaria and African sleeping sickness (trypanosomiasis), caused by species of the genera *Plasmodium* and *Trypanosoma* respectively. The former inhabit red blood cells and liver cells of human beings, and are carried by mosquitoes; the latter parasites, trypanosomes, live free in the blood plasma or tissue fluids and are carried by tsetse flies. In South and Central America, another species of trypanosome causes human disease (Chagas's disease) and is carried by winged "kissing bugs"; this trypanosome lives inside cells in its mammalian host, as well as free in the blood plasma. Close relatives of these parasites occur commonly in many British wild animals; luckily, none of them infects human beings. Other protozoan parasites infect domestic mammals and poultry in this country, and one – *Toxoplasma gondii* – occurs in cats and can cause human disease. Species of *Plasmodium* (none infective to man) occur in wild birds, as do members of the related genera *Haemoproteus* and *Leucocytozoon*. The prevalence varies – but it has been found that about 5% of wild birds (rooks, jackdaws, blackbirds)* in one area of England harboured species of *Plasmodium*, about 40% of woodpigeons had *Haemoproteus*, 27% of adult blackbirds and 15% of adult rooks were infected with *Leucocytozoon*. Trypanosomes are also common in birds, mammals and fishes. Detailed surveys have seldom been done, but – for example – trypanosomes have been found in about 50% of several populations of pipistrelle bats and in over 50% of thornback rays caught at Plymouth by the Marine Biological Association. In rabbits and rodents, they are probably at least equally common. As far as is known, few, if any, of these parasites are harmful.

A species of *Leucocytozoon* was at one time investigated as a possible cause of "grouse disease", but found not to be. An ecological study of a fluctuating population of field voles near Oxford failed to reveal any relationship between population decline and parasite prevalence. However, on the whole, these parasites have been very little studied, and they may affect their host's well-being in rather subtle ways which have so far passed unnoticed. It is known, for example, that many species of trypanosomes can reduce or even abolish their host's ability to produce antibodies, and to respond immunologically in other ways, to infection by other organisms including bacteria and viruses. No such instance is known to occur among the British fauna, but this could be because no-one has looked for such an effect.

Some of these parasitic protozoa of our native fauna will now be discussed in a little more detail, grouped under the animals which they infect.

*Scientific names of wild animals are given in Annex 2.

Nothing will be said about the parasites of domestic animals, though some of these are of economic importance – eg coccidia (*Eimeria* species) of chickens and rabbits, some species of *Babesia* which cause red-water fever in cattle, and the flagellate *Trichomonas foetus*, referred to above, which may induce abortion in cattle. Further information about these parasites can be obtained from the ARC Institute for Research on Animal Diseases, Compton, Newbury, Berkshire, RG16 0NN; Houghton Poultry Research Station, Houghton, Huntingdon, PE17 2DA; and the MAFF Central Veterinary Research Laboratory, New Haw, Weybridge, Surrey, KT15 3NB. Many British wild animals also harbour parasitic worms (tapeworms, roundworms and flukes), but these too will be omitted from the ensuing discussion; information about them is given in a short book by Lyons (1978).

Fish

The parasites of British fish have not been much studied, particularly in recent years. The growing importance of fish-farming may lead to a resurgence of interest, as the "unnatural" conditions of "domestication" (crowding, stress, etc) amongst other groups of animals (including mankind) have often upset the delicate balance between host and parasite which has evolved over millions of years, leading to disease where previously the two

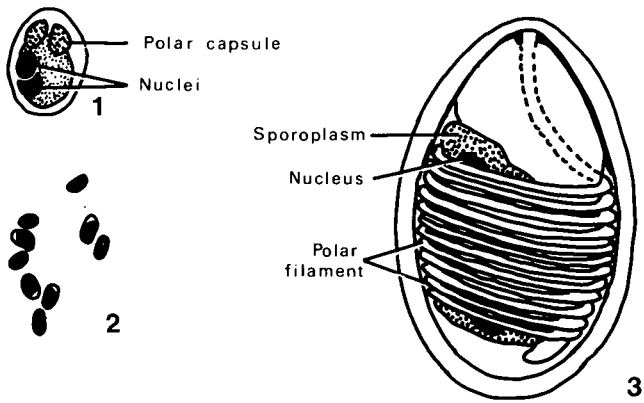

Fig. 1. Myxosporidan spore from fish (*Myxosoma heterospora* from the African fish *Tilapia*): when the spore is swallowed by an appropriate fish, two "anchoring" filaments are ejected from the polar capsules and the sporoplasm, with two nuclei, emerges from the spore wall.

Fig. 2. Spores of the microsporidan *Glugea anomala*, from stickleback. Although so small that almost no detail can be discerned by light microscopy, the electron microscope has revealed a complicated internal structure (see Fig. 3).

Fig. 3. Diagram of the structure of a microsporidan spore (redrawn from Fig. 127 of Baker, 1973; greatly magnified). After being swallowed by a susceptible host, the polar filament is ejected, and the sporoplasm migrates down it – a "built-in" hypodermic syringe.

lived together in mutual harmony. Two groups of parasitic protozoa are known to be harmful to fish: the Myxosporea and the Microspora. Members of both infect various tissues, including skin and the underlying muscles of the body wall, often producing large, easily visible lumps. Both groups are transmitted from fish to fish by means of resistant spores, which are quite complicated structures – though, of course, microscopic in size (Figures 1–3). Sufficiently heavy infections with these organisms can kill the fish; no means of prevention or treatment is known. Fish are also sometimes affected by sessile ciliates (*Trichodina* is one example), which attach themselves to the outer surface of the gills. The water current passing through the gill chamber brings with it a ready source of food for the ciliates. If present in large numbers, the latter may interfere mechanically with the function of the gills, and the effect may be worsened by secretion of mucus as a result of the irritation produced by the protozoa.

Trypanosomes occur in British fish, but none is known to be harmful. In 1911, Muriel Robertson discovered trypanosomes infecting goldfish in a pond at Elstree and demonstrated that they were carried from fish to fish by leeches; this is true of all other piscine trypanosomes, as far as is known. *Trypanosoma rajae* (Figure 4), a large and elegant species found in about half of the rays (cartilaginous fish) in the English channel, has already been mentioned. Two out of four dace and one gudgeon caught in the river Cam in Cambridge in the summer of 1972 had trypanosomes in their blood (Figure 5). What was presumably the same species, *T. cobitis*, from the river Lea north of London, was studied in some detail by Carol Letch and her colleagues in 1979 (in work supported by the Natural Environment Research Council). They found that 50–70% of the "bottom-living" fish (bullheads, stone loach and gudgeon) but only 6–18% of the pelagic species (sticklebacks and minnows) were infected. The trypanosomes were transmitted by a leech, *Hemiclepsis marginata*, which presumably fed more readily on fish lying on the river bed.

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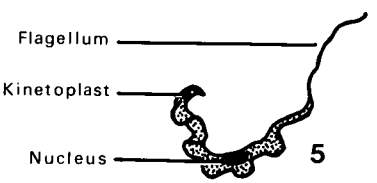

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Fig. 4. *Trypanosoma rajae* from the blood of a ray caught off Plymouth.

Fig. 5. *T. leucisci* from the blood of a dace caught in the river Cam.

The red blood cells of fish (and other vertebrates) may be infected with sporozoan parasites (Apicomplexa) called haemogregarines, a rather dull and poorly studied group about which I propose to say little.

Amphibia and Reptilia

I am unaware of any British records of parasitic protozoa from these animals. However, haemogregarines (Figure 6) and trypanosomes are widely distributed parasites of frogs, so it is quite likely that they would be found in British species, if looked for carefully.

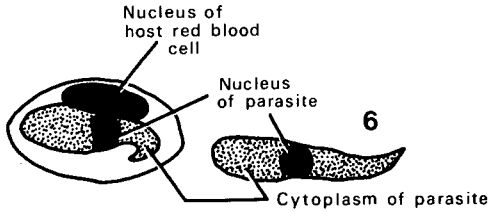


Fig. 6. Haemogregarine (*Haemogregarina* species) from the blood of a Mexican frog (*Rana montezumae*): the individual on the left is within a red blood cell; that on the right has emerged from its host cell.

Birds

Some of the pioneering research on trypanosomes was done about 100 years ago in studies on birds by a famous Russian parasitologist – Basil Danilewsky. The best-known British example is *T. corvi*, which infects about 30% of corvids (rooks and jackdaws). It is a large trypanosome by protozoan standards (about 50 μm long), and very graceful in appearance (Figures 7, 8 and Plate 1). Its transmitting host (vector) is a louse fly (*Ornithomyia avicularia*), an insect which belongs to a curious group of ectoparasitic Diptera known as Pupipara because the females retain eggs and larvae within their body until the larva is mature; after parturition the latter rapidly pupates. (This feature is also possessed by the tsetse flies, vectors of trypanosomes in Africa which can cause serious disease in man and domestic stock.) Trypanosomes have also been reported from woodpigeons, blackbirds, song thrushes, little owls, swallows, chaffinches and yellow-hammers in Britain. Many of these records date from the early part of this

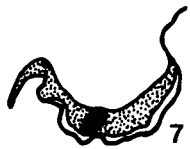


Fig. 7. *Trypanosoma corvi* from the blood of an experimentally infected canary (*Serinus canaria*): see Plate I.

century, having been published in 1905 by G. F. Petrie. There is no evidence that any of these trypanosomes is harmful.

Various parasites classified in the Apicomplexa ("sporozoa") occur in birds in Britain; they are more common in birds than in other groups. Species of the genus *Plasmodium*, which also contains the true malaria parasites of man, have been recorded from rooks, jackdaws and blackbirds, but seem rather uncommon. More common, and more studied, in British birds are members of the related genera *Leucocytozoon* and *Haemoproteus*. The

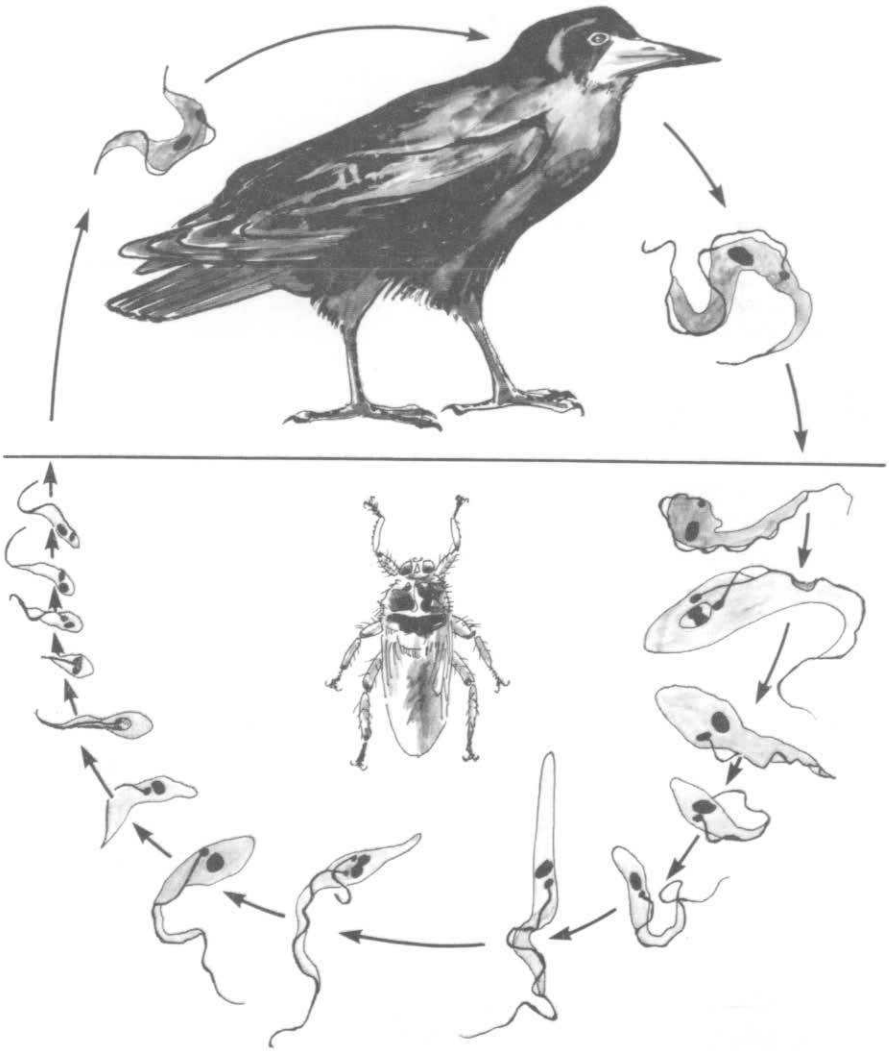


Fig. 8. Diagram illustrating the life cycle of *T. corvi* in rook (or other bird) and louse fly. (Modified from Fig. 4 of Baker, 1956: *Parasitology 46*, 335–352.)

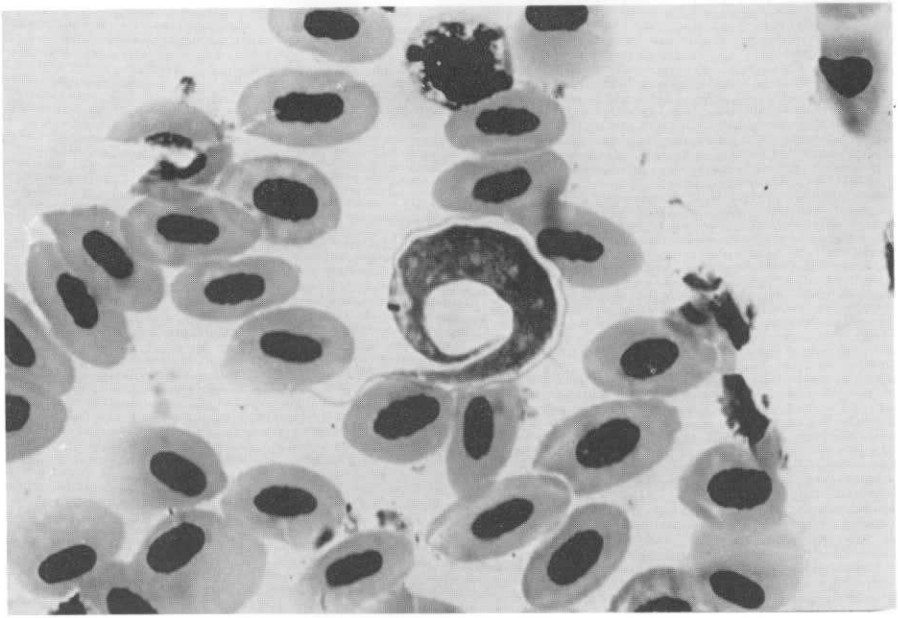


Plate 1. *Trypanosoma corvi* in blood of a canary (cf. Fig. 7), magnified about 1500 times.

former are transmitted by blackflies (Simuliidae) and the latter by louse flies (Hippoboscidae), like some at least of the avian trypanosomes. Species of *Leucocytozoon* have been reported from a range of birds in Britain, including blue tits, thrushes, blackbirds, crows, rooks, jackdaws, jays, tawny owls, red grouse, chaffinches, redpolls, woodpigeons and moorhens (Figures 9, 10). There is no evidence of any disease in British birds resulting from *Leucocytozoon* infection, though in the USA and Canada considerable mortality among ducks and turkeys is caused by species of this genus fortunately not recorded from this country. *Leucocytozoon* species have a complicated life cycle (Figure 11), involving first a phase of asexual multiplication (schizogony) in cells of the liver or other internal organs, followed by the appearance of sexual individuals (gametocytes) in red blood cells. These stages enter very young blood cells and considerably deform them – leading to an increase in size and, with some species, marked elongation of the host cells also. Infected cells are somehow prevented from producing the red respiratory pigment haemoglobin, which led to the naming of the genus on the mistaken supposition that it inhabited white blood cells – leucocytes. The sexual stages are destined to complete their development only in the stomach of an appropriate vector insect – a female, blood-sucking blackfly (*Simulium*). After fertilization in this insect, another multiplicative phase (sporogony) occurs, the progeny of which (sporozoites) enter the blackfly's salivary glands. When the insect next sucks blood from a bird, sporozoites are injected together

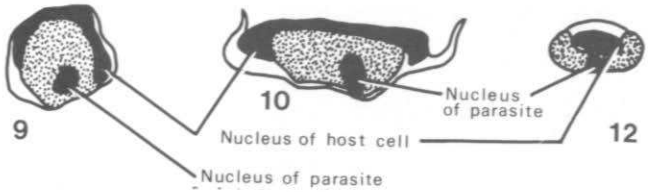
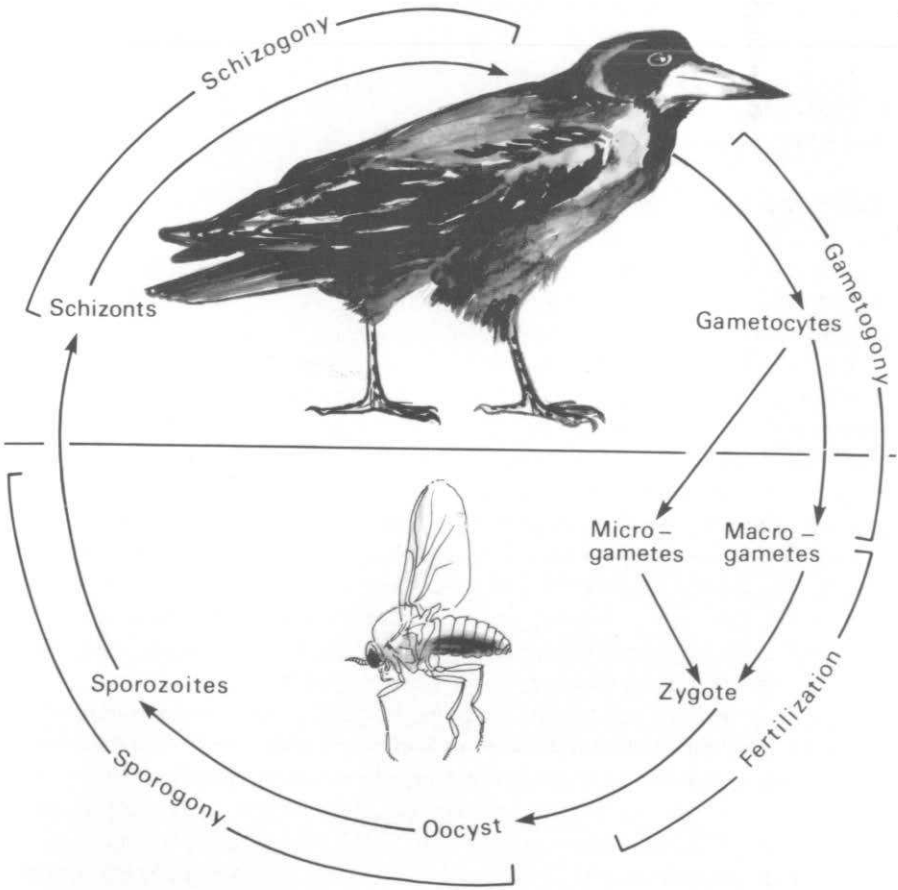


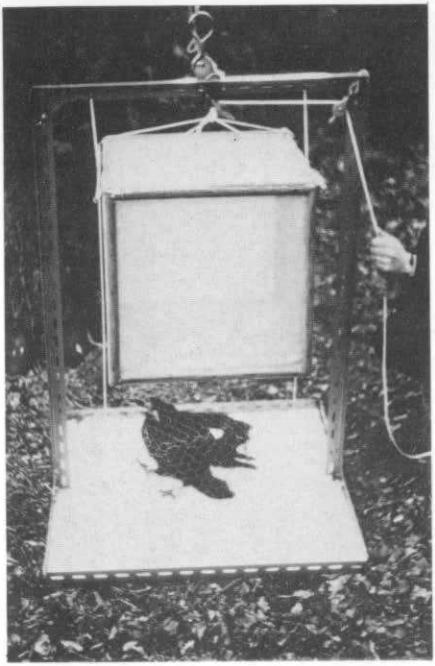
Fig. 9. *Leucocytozoon sakharoffi*: female gametocyte within blood cell of crow.

Fig. 10 *L. danilewskyi*: female gametocyte within blood cell of tawny owl. Note how the parasite has deformed the host cell, causing it to develop two lateral projections like horns.

Fig. 12. *Haemoproteus palumbis*: female gametocyte in red blood cell of woodpigeon.

Fig. 11. Diagram summarizing the life cycle of *Leucocytozoon*, exemplified by *L. sakharoffi* in rook and blackfly. (Modified from Fig. 86 of Baker, 1973.)





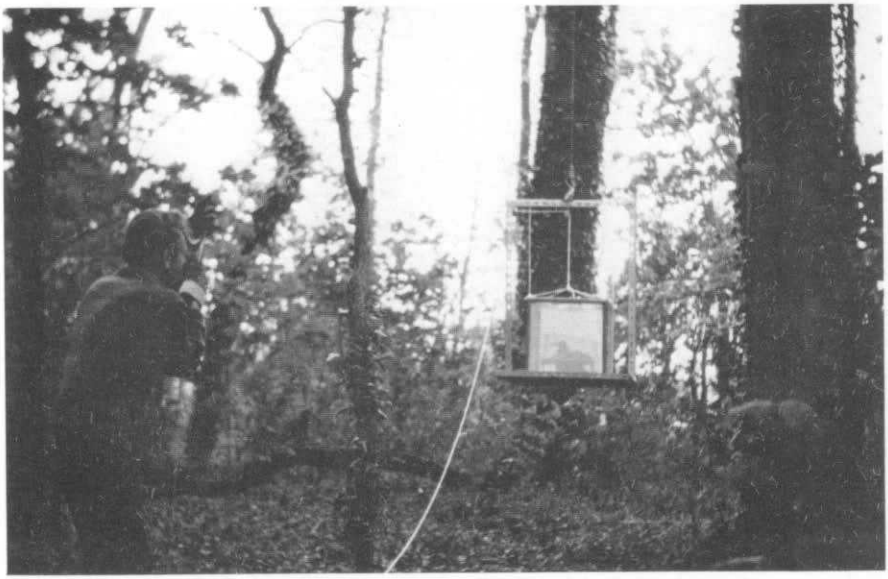


Plate 2. Placing a rook, infected with *Leucocytozoon sakharoffi*, inside an insect trap.

Plate 3. The "baited" trap hanging from a tree branch.

Plate 4. Examining the "catch".

with saliva and, via the bird's bloodstream, reach its liver (or other organ appropriate to the next stage of development – schizogony). Another piece of research supported by the Natural Environment Research Council some years ago investigated whether *Simulium* transmitted *Leucocytozoon sakharoffi* in rooks and other corvids in England. Previously, this insect had been shown to transmit *Leucocytozoon* in North America only. Some aspects of this investigation are illustrated in Plates 2–4 and on the cover. Naturally infected rooks from a rookery near Fordingbridge in Hampshire were used as "bait" in insect traps suspended from a tree in the rookery, and the insects caught were subsequently examined for developing stages of the protozoon. As expected, a species of *Simulium* was the vector. *Haemoproteus* is a related parasite with a similar life cycle, though schizogony occurs in the infected bird's lung cells. The sexual gametocytes do not significantly deform their host's red blood cells. Amongst British species, transmission has been studied only in *H. palumbis* of woodpigeons (Figure 12); its vector is the louse fly already mentioned, *Ornithomyia avicularia*. Other recorded avian hosts in Britain include blackbirds, thrushes, starlings, finches (unspecified) and jays; it is possible that some of the earlier reports may have been confused with *Plasmodium*. Both *Leucocytozoon* and *Haemoproteus* persist in the tissue cells of infected birds for many years. Infections may be reactivated annually, in the spring, with a "flush" of gametocytes appearing in the blood (Figure 13). This is presumably related to the seasonal occurrence of the transmitting insects; there is evidence to suggest that the reactivation is controlled by hormones concerned with the bird's reproductive

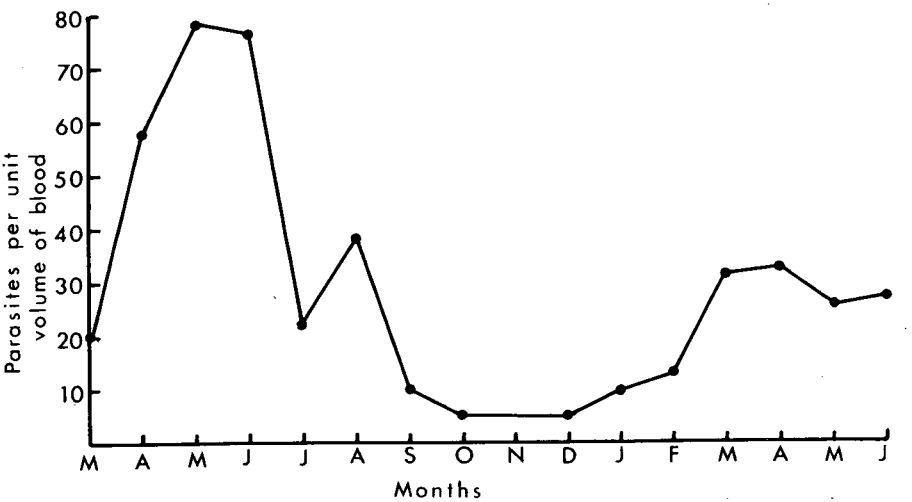


Fig. 13. Graph showing average monthly counts of *Leucocytozoon dubreuili* in the peripheral blood of a blackbird; the first peak probably represents initial infection and the second, relapse (the "hiccough" in August is probably experimental error).

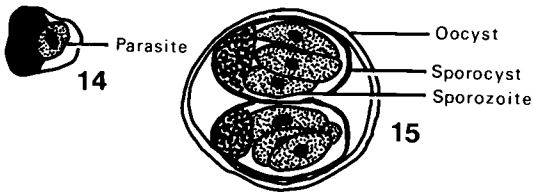


Fig. 14. *Lankesterella garnhami*, a haemogregarine, in spleen cell of sparrow (*Passer domesticus*).

Fig. 15. Oocyst of *Isospora lacazei* (redrawn from a photomicrograph in Fig. 351 of Wenyon, 1926).

cycle. The life cycle of *Plasmodium* is similar to that described above for *Leucocytozoon* and *Haemoproteus*, but there is an extra phase of asexual multiplication (schizogony) in red blood cells, as well as in the tissue cells – usually fixed tissue macrophages of various organs. Sexual development occurs in, and the parasites are transmitted by, female mosquitoes (Culicidae).

Haemogregarines inhabit the blood cells of some British birds, but are not very common (Figure 14). There is another group of Apicomplexa (the "coccidia"), members of which commonly inhabit the intestines of British wild birds. They pass directly from bird to bird by means of resistant cysts (oocysts) in the faeces (Figure 15). Some related species occurring in domestic fowl can cause serious disease, but it is not known whether this is so in wild birds.

Mammals

Probably the commonest parasites of British wild mammals are trypanosomes. These have been seen in the blood of rodents, rabbits, insectivores, bats and badgers. Those parasitizing the first three groups all belong to the subgenus *Herpetosoma* of the genus *Trypanosoma*, and are transmitted by fleas; those in bats belong to the subgenera *Schizotrypanum* and *Megatrypanum*; the species from the badger belongs to the last-named subgenus. Vectors of species of the two latter subgenera in Britain have not been identified, and little is known about these parasites generally. *Herpetosoma* species have been studied more fully, as two species (*T. lewisi* of black and brown rats and *T. musculi* of mice; Figure 16) are commonly used in laboratories. (*T. musculi* was apparently first recorded in Britain from a mouse captured in the bathroom of a house in Shenley, Hertfordshire.) Other members of the subgenus have been recorded in Britain from field mice (Figure 17), bank voles, harvest mice, water shrews and moles. *T. lewisi* and *T. musculi* cannot normally infect any mammal other than rats or mice respectively, and it is generally assumed (without too much evidence) that the trypanosomes found in the other rodents and insectivores listed above

are equally restricted in their range of hosts. The parasites of each host genus are therefore usually treated as separate species: some have been named and some have not. As far as is known, they are all transmitted by fleas, and there is no evidence that any of them harms its host. The relatively recent (1974) discovery of a trypanosome (*T. pestanai*; Figure 18) in badgers in this country was a by-product of the campaign to control bovine tuberculosis by killing badgers. Blood samples from some of the dead badgers were found by a Ministry of Agriculture scientist to contain the trypanosomes (previously recorded from France and elsewhere).

Schizotrypanum, the subgenus recorded from bats (pipistrelles and noctules), contains a species (*T. cruzi*) which is a serious public health hazard in South America, where it infects a large number of people (perhaps 7 million, or more) and may cause serious ill-health or death; no adequate treatment is yet available. It is thought by some historically-minded protozoologists that Charles Darwin may have acquired the infection (Chagas's disease) during the voyage of the Beagle: if so, his so-called hypochondria during later life may have had a basis in reality. Fortunately, the related species infecting bats are unable to infect any other mammal (as far as is known), and certainly not human beings. They can, however, easily be grown in test-tubes and in cell cultures (at one stage of their development they live inside cells; Plate 5) and this has made them useful laboratory models for studies on some aspects of the biology of *T. cruzi*, without the risks involved in handling this dangerous pathogen. Pipistrelles and noctules in Britain are known to be infected with two species of trypanosomes belonging to this subgenus – *T. dionisii* and *T. vespertilionis* (Figures 19, 20) – and with a third species, in the subgenus *Megatrypanum*, known as *T. incertum* (Figure 21). *T. dionisii* (which was named after an Italian parasitologist, Dionisi, and not – regrettably – in honour of the god Dionysius) has been found in about 50% of the populations of pipistrelles which have been examined in Britain (mostly from East Anglia). Very little is

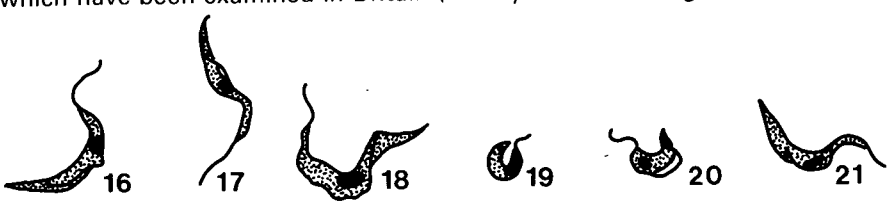


Fig. 16. *Trypanosoma lewisi* from rat blood.

Fig. 17. *T. grosi* from blood of field mouse (drawn from a preparation made in 1914 by A. C. Coles).

Fig. 18. *T. pestanai* from blood of a badger.

Fig. 19. *T. dionisii* from blood of a pipistrelle.

Fig. 20. *T. vespertilionis* from blood of a noctule.

Fig. 21. *T. incertum* from blood of a pipistrelle.

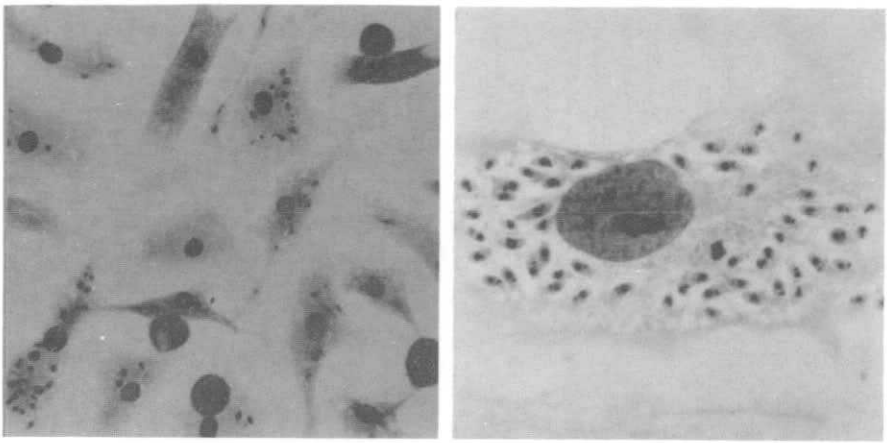


Plate 5. Photomicrographs of *Trypanosoma dionisii*, a parasite of British pipistrelles and noctules, growing inside cells in culture (stained with Giemsa's stain). Left, low-power view: the large 'blob' in each cell is its nucleus, the smaller objects in some cells are the parasites (these cells are mouse peritoneal macrophages); right, high-powered view of one infected cell (a bison lung cell), magnified 1000 times.

known about the life history of the trypanosomes of bats, or about their transmission from bat to bat (presumably by means of a blood-sucking insect), or whether they can in any circumstances be harmful to their hosts.

Apicomplexan parasites of the genus *Babesia*, rather distantly related to malaria parasites, have been seen in red blood cells of common and pygmy shrews, pipistrelles (Figure 22), field and harvest mice, and field and bank voles (Figure 23). In parts of the USA, a species of *Babesia* from voles has caused rare infections in human beings, and, although in Britain too a very few human babesial infections have been reported (always in persons whose spleens had earlier been surgically removed, and always with a fatal result), the guilty species in this country seems to be not the vole parasite, but one normally parasitizing cattle. The ubiquitous haemogregarines, already mentioned, have also been seen in pipistrelles, in all the rodents listed above except water voles, harvest and house mice, and in red and grey squirrels (Figure 24). Over half of the the wild grey squirrels being studied by Dr R. E. Kenward at Monks Wood Experimental Station have haemogregarines (*Hepatozoon sciuri*) in their blood. As with birds, various "coccidia" inhabit the intestines of mammals: one species (*Eimeria stiedai*) infects the liver of wild rabbits and – at least in captive rabbits – may cause serious disease. Another related parasite, *Toxoplasma gondii* (Figure 25), has been found in wild rabbits, rodents and insectivores. This is the only protozoan parasite of the British fauna which can also infect human beings; it rather rarely causes serious illness (toxoplasmosis), and is one of the few infections which can cross the placenta and affect the foetus of an infected pregnant woman. The

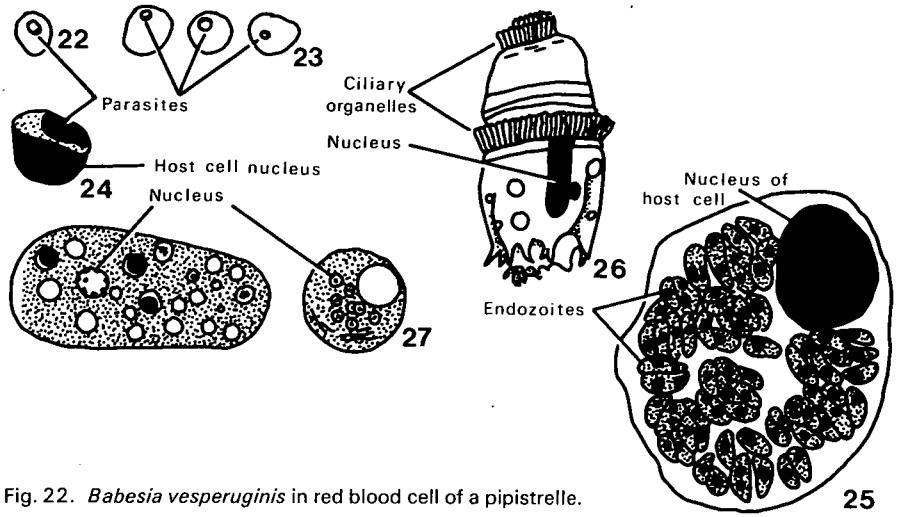


Fig. 22. *Babesia vesperuginis* in red blood cell of a pipistrelle.

Fig. 23. *Babesia microti* in red blood cells of a bank vole.

Fig. 24. Haemogregarine (*Hepatozoon* species) in white blood cell of a field vole (drawn from a preparation made in 1914 by A. C. Coles).

Fig. 25. *Toxoplasma gondii*: about 65 individuals (endozoites) in a macrophage cell from liver of an experimentally infected mouse; some are dividing (indicated by presence of two nuclei). *T. gondii* also encysts in the brain and other organs of infected mice (and other animals), and cats can become infected by eating infected prey. The parasite develops further in cells of the wall of the cat's intestine and finally produces oocysts, similar to those of *Isospora* (see Fig. 15), which may infect human beings, other cats, rats, mice, etc.

Fig. 26. *Ophryoscolex caudatus*, a ciliate found in the rumen of oxen; similar or identical species occur in wild ruminants (redrawn from Fig. 132 of Baker, 1973; magnified × 200 only). In these very specialized ciliates, the cilia are united in groups to form compound organelles, instead of covering most or all of the cell surface.

Fig. 27. *Entamoeba muris*; on left, active form (trophozoite), as seen in intestinal contents of a mouse; on right, cyst (in faeces). (Redrawn, by permission, from Figs 1 and 1A of Cox, 1970.)

most important host of *T. gondii*, however, from the point of view of human infection, is the domestic cat. Parasites called *Sarcocystis* and *Frenkelia*, related to *Toxoplasma* but not infective to human beings, have rarely been reported from various wild mammals.

Amoebae and flagellates (*Trichomonas* and other genera) occur in the intestines of many wild mammals, in this country and elsewhere; ciliates are less common, except in ruminants such as red deer (Figure 26). Not much is known about these (in my opinion) rather uninteresting organisms. The amoeba *Entamoeba muris* (Figure 27), a relative of the species causing human amoebic dysentery (*E. histolytica*), has been reported from up to 50% of field mice, field and bank voles, house mice and rats in England.

Conclusions

This rather sketchy review has emphasized two things: (1) how common are parasitic protozoa in the British wild fauna, and (2) how little is known about them. In particular, very little is known about the possible damaging effects on their hosts. Generally not causing obvious harm, they may insidiously affect the host's well-being in times of stress due to overcrowding, food shortage, other infections or even reproductive behaviour. The uneasy balance between parasite and host may be tilted in favour of the former, by a variety of circumstances. The immunosuppressive effect of some exotic species of trypanosomes has already been mentioned. Further study of indigenous parasites might reveal a greater involvement in the population dynamics of wild animals in Britain than has been suspected hitherto. Such studies, however, depend on the acquisition of basic knowledge of the parasite's life cycles, including the identification of vectors where these exist; these fundamental biological facts are known for remarkably few of the parasites of our native fauna. Another aspect of the study of these organisms is their possible use as safe laboratory models for related species causing disease in man or domestic animals. Examples have already been mentioned: *Trypanosoma lewisi* and *T. musculi* have provided information about the immunological defence mechanisms of mammals; *T. dionisii*, grown in artificial cultures, can be used in the preliminary "screening" of drugs to cure Chagas's disease without using laboratory animals or risking accidental infection of laboratory workers with *T. cruzi* itself.

The indigenous parasitic protozoa are as much a part of our natural environment as the roach, rabbit or rook, which may act as their hosts. Therefore, their study is a part of that wider acquisition of ecological knowledge and eventual understanding of the complex web of life itself, which is such an intellectually satisfying and, surely, morally worthwhile human activity.

Further Reading

INTRODUCTORY ACCOUNTS OF PARASITIC PROTOZOA:

Baker, J. R. 1973. *Parasitic protozoa*. 2nd ed. London: Hutchinson. [Out of print.]

Baker, J. R. 1982. *The biology of parasitic protozoa*. (Institute of Biology's studies in biology, no. 138.) London: Edward Arnold.

GENERAL ACCOUNTS OF PROTOZOA:

Farmer, J. N. 1980. *The protozoa*. St. Louis: Mosby.

Kudo, R. R. 1966. *Protozoology*. 5th ed. Springfield, Illinois: Charles C. Thomas. [Out of print and somewhat out of date, but valuable systematic account for reference rather than general reading.]

Sleigh, M. A. 1973. *The biology of protozoa*. London: Edward Arnold.

GENERAL TEXTS, WITH THE EMPHASIS ON PARASITES:

Manwell, R. D. 1968. *Introduction to protozoology.* 2nd ed. New York: Dover. [Out of print.]

Wenyon, C. M. 1926. *Protozoology*. London: Baillière, Tindall & Cox. [The "bible" of protozoologists: like the original Bible, inspired, outdated, but invaluable. Reprinted in 1965, but regrettably again out of print.]

REVIEW ARTICLES:

Baker, J. R. 1974. Protozoan parasites of the blood of British wild birds and mammals. *J. Zool.*, **172**, 169–190.

Cox, F. E. G. 1970. Parasitic protozoa of British wild mammals. *Mammal Rev.*, **1**, 1–28.

INTRODUCTION TO HELMINTHS:

Lyons, K. M. 1978. *The biology of helminth parasites.* (Institute of Biology's studies in biology, no. 102.) London: Edward Arnold.

ANNEX 1. OUTLINE CLASSIFICATION OF PROTOZOA MENTIONED IN THE TEXT

Phylum SARCOMASTIGOPHORA
- Subphylum MASTIGOPHORA
  - Class ZOOMASTIGOPHOREA
    - Order KINETOPLASTIDA – *Trypanosoma*
    - Order TRICHOMONADIDA – *Trichomonas*
- Subphylum SARCODINA
  - Order AMOEBIDA – *Amoeba, Entamoeba*

Phylum APICOMPLEXA
- Class SPOROZOEA
  - Subclass COCCIDIA
    - Order EUCOCIDIIDA – *Haemogregarina, Eimeria, Sarcocystis, Toxoplasma, Haemoproteus, Leucocytozoon, Plasmodium*
  - Subclass PIROPLASMIA
    - Order PIROPLASMIDA – *Babesia*

Phylum MICROSPORA

Phylum MYXOZOA
- Class MYXOSPOREA

Phylum CILIOPHORA
- Class OLIGOHYMENOPHOREA
  - Subclass PERITRICHIA
    - Order PERITRICHIDA – *Trichodina*

ANNEX 2. SCIENTIFIC NAMES OF WILD VERTEBRATES MENTIONED IN THE TEXT

PISCES	
Ray	*Raja clavata*
Goldfish	*Carassius auratus*
Dace	*Leuciscus leuciscus*
Gudgeon	*Gobio fluviatilis*
Bullhead	*Cottus gobio*
Stone loach	*Nemacheilus barbatulus*
Stickleback	*Gasterosteus aculeatus*
Minnow	*Phoxinus phoxinus*
AMPHIBIA	
Edible frog	*Rana esculenta*
AVES	
Crow	*Corvus corone*
Rook	*C. frugilegus*
Jackdaw	*C. monedula*
Jay	*Garrulus glandarius*
Woodpigeon	*Columba palumbus*
Blackbird	*Turdus merula*
Song thrush	*T. ericetorum*
Starling	*Sturnus vulgaris*
Little owl	*Athene noctua*
Tawny owl	*Strix aluco*
Swallow	*Hirundo rustica*
Chaffinch	*Fringilla coelebs*
Yellowhammer	*Emberiza citrinella*
Bluetit	*Parus caeruleus*
Redpoll	*Carduelis flammea*
Red grouse	*Lagopus lagopus*
Moorhen	*Gallinula chloropus*
MAMMALIA	
INSECTIVORA	
Mole	*Talpa europaea*
Common shrew	*Sorex araneus*
Pigmy shrew	*S. minutus*
Water shrew	*Neomys fodiens*
CHIROPTERA	
Pipistrelle	*Pipistrellus pipistrellus*
Noctule	*Nyctalus noctula*
RODENTIA	
Black rat	*Rattus rattus*
Brown rat	*R. norvegicus*
House mouse	*Mus musculus*

Field mouse	*Apodemus silvaticus*
Harvest mouse	*Micromys minutus*
Bank vole	*Clethrionomys glareolus*
Field vole	*Microtus agrestis*
Red squirrel	*Sciurus vulgaris*
Grey squirrel	*S. carolinensis*
LAGOMORPHA	
Rabbit	*Oryctolagus cuniculus*
CARNIVORA	
Badger	*Meles meles*
ARTIODACTYLA	
Red deer	*Cervus elaphus*

Glossary

This glossary is not restricted to technical terms mentioned in the text, though it is intended to define simply most of those. Taxonomic names (of phyla, orders, etc) are not, in general, included.

Algae	primitive plants, containing chloroplasts, either uni- or multicellular; unicellular forms often united with protozoa (q.v.) as protista.
Antibody	protein produced by certain white blood cells (lymphocytes) of vertebrate animals, and secreted into blood and tissue fluids, which combines with invading organisms (bacteria or protozoa) and may assist in killing them. Antibodies are produced in response to the presence of a particular invading organism or foreign substance, the antigen, and will combine only with that antigen – ie they are specific for it. (See immunological.)
Antigen	a protein (or other substance) eliciting the production of an antibody (q.v.).
Asexual reproduction	production of more organisms of the same kind, *not* involving fusion of two differentiated sexual cells or organisms; see "sexual reproduction". [Greek prefix "a" = "not".]
Bacteriophage	see "virus".
Basal body	intracellular origin of flagellum or cilium; also called kinetosome.
Cell	smallest individually viable unit of living organism; unicellular organisms (eg bacteria, protista) consist of only one cell; multicellular organisms (including "higher" plants and animals) consist of many.
Chlorophyll	green pigment in chloroplasts (q.v.) of algae and "higher" plants; absorbs energy from incident light, of the longer wave lengths, and makes it available for use in the cell's photosynthetic processes (production of complex molecules – usually polysaccharides – from simpler substances – eg water and carbon dioxide: the basic process essential for maintenance of all terrestrial life).

Chloroplast	many-layered membranous intracellular structure containing the chlorophyll (q.v.) of green algae and "higher" plants.
Cilium	hair-like undulating extension from cell surface, concerned either with locomotion of unicellular (or small multicellular) organisms or the production of currents in surrounding liquid (in multicellular organisms): basic structure as for flagellum (q.v.), but usually smaller, more numerous and beating in phase with its neighbours (with which it is often connected by intracellular fibrils) in characteristic "metachronal rhythm" (resembling a field of wind-swept wheat). [Latin "eyelid", hence "eyelash".]
Commensal, commensalism	see text (p. 2).
Cyst	resistant stage of a protist, surrounded by a tough membrane (cyst wall) outside the plasmalemma (q.v.).
Cytoplasm	the "ground substance" of a cell, containing most of the organelles and surrounded by a cell membrane or plasmalemma (and often additional structures).
DNA	deoxyribonucleic acid, usually attached to a protein to form deoxyribonucleoprotein. The "hereditary material" of a cell, comprising its genes which are themselves spatially arranged along chromosomes.
Endoplasmic reticulum	secretory membranes in cytoplasm of eukaryotic cell; either "rough" (with attached ribosomes) or "smooth"; latter may be organized into a secretory organelle – Golgi apparatus or dictyosome.
Eukaryotic	level of cellular organization indicated by, amongst other things, separation of the deoxyribonucleoprotein from the cytoplasm by its inclusion in a distinct, membrane-bound nucleus; as in protista and all "higher" plants and animals. (See prokaryotic.)
Flagellum	whip-like undulating extension from cell surface usually concerned with locomotion; basic structure as for cilium (q.v.), a tubular membrane surrounding a cylindrical axoneme of nine paired, peripheral and two single, central microtubules, containing two major proteins – tubulin and dynein – somewhat analogous to actin and myosin of muscle cells. Flagella are generally larger and less numerous than cilia, and usually operate independently of one another; an additional paraxial rod, not seen in cilia, accompanies the flagellar axoneme of some protists. [Greek "whip".]
Gamete	sexually differentiated cell (or unicellular organism); male often called microgamete, and female, macrogamete.
Gametocyte	cell (or unicellular organism) which divides to produce gametes (q.v.); micro- and macrogametocytes produce micro- and macrogametes, respectively.
Gene	discrete group of nucleotide bases of DNA (q.v.) molecule, bearing instructions for synthesis of one type of protein molecule by ribosomes (q.v.); arranged spatially along chromosomes within nucleus of eukaryotic cells.
Golgi apparatus (dictyosome)	see endoplasmic reticulum.
Immunological	related to the immune defence system of vertebrate animals, directed against invading foreign organisms (parasitic

	protozoa, bacteria, or viruses); immunity is mediated by certain cells and by soluble products (antibodies – q.v.) produced by some of these cells (lymphocytes). (See also macrophage.)
Invertebrate	animal without a backbone. [Latin "in" = negative prefix.]
Kinetoplast	large mass of DNA within single large, tubular mitochondrion of certain Zoomastigophorea (order Kinetoplastida), including the trypanosomes.
Kinetosome	basal body (q.v.).
Lipoprotein	molecule composed of protein at one end and lipid ("fatty", water-repellent component) at the other.
Macrophage	a phagocytic (q.v.) cell in the body of a multicellular animal, part of the immunological (q.v.) defence mechanism against invading parasites, bacteria, etc; may be either "fixed" – part of one of the viscera such as spleen or liver, or "wandering" – moving through the body, usually in circulating blood.
Merozoite	product of schizogony (q.v.).
Micron	unit of microscopical measurement; properly micrometre; 10^{-6} metre; abbreviated as μm (or, improperly, in older texts, μ). [Greek letter μ, pronounced "mew".]
Mitochondrion	membrane-bound organelle in cytoplasm of many eukaryotic cells, with infoldings of the inner membrane forming cristae; contains enzymes of the Kreb's cycle and cytochrome chain, used in intracellular respiration, and some DNA (q.v.).
Mutualism	see text (p. 2).
Nucleus	membrane-bound organelle in eukaryotic (q.v.) cell containing deoxyribonucleoprotein arranged on chromosomes.
Oocyst	zygote surrounded by a cyst (q.v.) (pronounced "oh-oh-sist").
Ookinete	motile zygote (q.v.) produced during life cycle of some Apicomplexa (pronounced "oh-oh-kīneet").
Parasite, parasitic	see text (p. 2).
Pathogen	parasitic organism (protozoon, bacterium, virus, etc) capable of producing disease in its host.
Phagocytosis	ingestion of relatively large object by cell – either in feeding (phagotrophy) or as part of defensive mechanism of multicellular animals against invasion by bacteria, protozoa, etc.
Photosynthesis	see chlorophyll.
Plasmalemma	single unit membrane bounding cytoplasm of a cell (or protist); two-layered lipoprotein (q.v.) structure.
Prokaryotic	level of cellular organization at which the deoxyribonucleoprotein is not sharply separated from the cytoplasm; as in bacteria. (See eukaryotic.)
Protein	basic component of cellular structures, etc; complex chemical comprised of serially arranged amino-acids, essentially containing nitrogen, carbon, hydrogen, oxygen, and often other elements.
Protista	kingdom of unicellular eukaryotic (q.v.) organisms comprising unicellular algae (with chloroplasts containing chlorophyll) and protozoa (not containing chlorophyll).
Protoplasm	nucleus (q.v.) plus cytoplasm (q.v.).
Protozoon (plural, protozoa)	small, usually microscopic, unicellular animal; protozoa cannot be sharply distinguished from unicellular algae (q.v.),

	with which they are often united as protista.
Pseudopodium	temporary extension of cytoplasm functioning either in locomotion (eg of amoebae) or in phagocytosis (q.v.). [Greek "false foot".]
Ribosome	small unit of ribonucleoprotein within cytoplasm of eukaryotic cell; may be attached to endoplasmic reticulum (q.v.); part of the cell's synthetic apparatus.
RNA	ribonucleic acid, usually attached to a protein to form ribonucleoprotein. Functions as "messenger", carrying information from DNA (q.v.), and also as "manufacturer", producing a protein as instructed by the "messenger".
Schizogony	process of asexual multiple division, undergone by many Apicomplexa, producing merozoites. [Usually pronounced "shy-zog-o-nee".]
Schizont	an individual protozoon which initiates schizogony (q.v.). [Usually pronounced "shy-zont".]
Sessile	attached, not motile. [Latin "sitting down".]
Sexual reproduction	production of more organisms of the same kind following fusion of two different (male and female) cells (or, in protista, organisms) called gametes (q.v.).
Sporocyst	secondary cyst (q.v.), within oocyst (q.v.), surrounding sporozoites (q.v.) of some Apicomplexa.
Sporogony	process of multiple division undergone by zygote (q.v.) of many Apicomplexa, producing sporozoites.
Sporont	individual protozoon which initiates sporogony (q.v.).
Sporozoite	stage in life cycle of Apicomplexa, produced by division (sporogony) of zygote (q.v.) in oocyst (q.v.), which is infective to new host.
Symbiont, symbiosis	see text (p. 2).
Unit membrane	very common membranous structure in cells, forming plasmalemma, nuclear membrane, and often other structures; consists essentially of two layers of lipoprotein molecules (q.v.), with their lipid ends directed outwards on both sides.
Vector	one of the hosts of a parasite with two (or more) hosts in its life cycle; usually the smaller host, which transmits the parasite from one larger host to another; almost always an invertebrate (q.v.), commonly an arthropod or annelid.
Vertebrate	animal with a backbone.
Virus	infectious entity, composed mainly of either RNA or DNA (not both), incapable of independent existence unless incorporated into a cell (either prokaryotic or eukaryotic); minute – visible only by electron microscopy. Viruses infecting bacteria are called bacteriophages.
Zygote	product of fusion of two gametes (q.v.).

Index

Italic numerals indicate illustrations. Vertebrates are indexed under common names only; scientific names are given in Annex 2 (which, with Annex 1 and the glossary, is not indexed).

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