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1 Introduction

1.1 Biodiversity and the Acanthocephala

In biology, as in all natural sciences, particular concepts come into and go out of fashion. Biodiversity, including species richness, is currently in fashion. This is in large measure a consequence of concerns about species rarity and threats of global and local extinction of organisms in response to human activities and global warming. Conservation interests in particular stress the importance of biodiversity and the need to preserve or restore it as the case may be. The term is found in a wide range of conservational, ecological and biological literature. In practice it is seldom defined and even though it is clear that it means different things to different people, it is always regarded as 'a good thing'. Definitions aside, biodiversity in practice is often used to justify the conservation of a rare species or of a particular habitat on a local or a regional scale. Emphasis on rare species has always been a feature of research and conservation interests. This has often been at the expense of understanding widespread, common and successful species and the ways in which they can adapt to human influences and their consequent changes in habitat and land use.

Biodiversity concerns are also frequently subjective and anthropocentric. They are all too often centred on particular types of habitat, communities and ecosystems that contain species that are considered particularly attractive. There is more concern about the possible loss of one species of mammal or bird than ten species of insect or crustacean. Moreover, there is also a strong bias in conservation towards free-living organisms and communities and against organisms that may cause disease or be considered harmful in any other context. Concerns about the reductions in biodiversity stemming from loss of tropical rainforest or heathland, for example, are not matched by a comparable concern

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about any loss of communities of bacteria or viruses; and protestors about the possible extinction of the smallpox virus are not thick on the ground, even though this would be a deliberate and wilful human act of extinction. Indeed, it is very seldom appreciated that superimposed on the populations and communities of free-living organisms there are populations and communities of parasitic ones. Since every free-living plant or animal is actually or potentially a host to one or several species of parasitic organism it is likely that there are more species of parasitic organisms than there are of free-living ones (Price, 1980). Parasitic populations and communities are not only superimposed on those of free-living animals but also may interact closely with them. Parasites are an integral and functional part of any ecosystem, and parasite diversity is thus an integral part of biodiversity.

Parasitology, however, is still all too often taught as an independent discipline with minimal or no attempt to integrate it with other biological disciplines such as ecology. Teaching of parasitology often still tends to focus primarily upon parasitic diseases of man and his domestic animals and crops and on the harmful effects of parasites on their hosts. Treatment in textbooks concentrates on malaria, bilharzia and eelworms, for example. Although this is set in the context of parasite species richness and diversity in structure, and especially diversity and complexity of parasitic life cycles, the emphasis is still on medical or veterinary examples. Despite the difficulties in remembering all the hosts and larval stages of parasites, students and the wider public seldom fail to be impressed by the frequently bizarre aspects of parasitic life cycles and by the success and impact of parasites.

Parasitology is nevertheless fundamentally an ecological discipline as it is concerned with the relationships between two species, the parasite and its host—with the relationships between an organism, the parasite, and its environment, which is another living organism, the host. Described thus, parasitology could be considered a specialist branch of ecology. Without attempting to define parasitism (most parasitology textbooks will normally provide one or several, often conflicting, definitions), I should point out that Russian parasitologists in particular, and especially V. A. Dogiel, have always emphasised the ecological nature of parasitism and could be considered to have actually founded the study of ecological parasitology. Dogiel (1964) himself stated clearly that parasitism is an ecological concept, and so parasitology should concern itself with those animals which use living animals of other species as their environment and source of food. Kennedy (1975) also emphasised the value of an ecological approach

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in understanding parasites and their relationships with their hosts. More recently, Combes (2001) has emphasised the prolonged nature of the host–parasite interactions such that the association of parasite–host can be viewed as a system, with novel characteristics of its own that are not just the simple sum of its components. His views are expressed most succinctly in the title of his book *Parasitism: The Ecology and Evolution of Intimate Interactions.* Since parasite–host systems are integral parts of every ecosystem, and since parasites can affect the life of practically every other organism (Price, 1980), one might expect the ecological literature to give as much prominence to parasites as to free-living organisms. However, this is not the case as very few ecology textbooks, with the notable and laudable exception of Townsend *et al.*, (2000), consider parasites at all: they are left to zoological, and specifically parasitological, texts. General zoological texts and parasitological texts tend to concentrate on the parasitic Protozoa, Platyhelminthes and Nematoda as these phyla contain the greatest number of parasitic species, including those pathological to man, his domestic animals and his crops. Other small parasitic groups, and parasitic members of phyla of predominantly free-living species, are ignored or at best given a cursory treatment.

Amongst these groups are the Acanthocephala, a small monophyletic phylum of which all species are obligatory endoparasites: it is in fact one of only two phyla to be exclusively parasitic and with no free-living members (the other is the Nematomorpha). Earlier zoological texts, such as Barnes (1963), devote only a few paragraphs to them, stressing the large numbers that may be found in a host and the damage this may do to the host intestine; and even in some later texts, for example Barnes *et al.* (1988), they are given a very cursory treatment. Many current general biology texts, however, for example Campbell (1996), do not even mention the phylum. Even parasitology texts give them little prominence in comparison with cestodes or digeneans. Cox (1993), for example, does not discuss them at all in the systematic section of the book, although he devotes seven pages to cestodes, and only mentions a few specific examples as appropriate. Smyth (1994), however, does devote a short chapter exclusively to the Acanthocephala, but stresses their lack of diversity in structure, life cycles and habits. Roberts & Janovy (1996) also devote a chapter to them, but claim (incorrectly) that they are seldom encountered and are rare in comparison with cestodes and nematodes, and that they are also capable of traumatic damage to their hosts, on occasion attaining epizootic levels leading to host mortalities. Only Bush *et al.* (2001)

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give them extensive coverage and treat them on a par with cestodes. Most authors consider the Acanthocephala as a minor phylum, equating this with their being relatively unimportant. Even a book on parasite ecology (Kennedy, 1975) does not single them out for any special emphasis.

Until recently, the few books devoted exclusively to the Acanthocephala tended to be primarily or even exclusively systematic in treatment. Included within this category are Meyer (1938), Petrochenko (1956, 1958) and Yamaguti (1963). The most recent books are those of Crompton (1970), which adopted an ecological approach to acanthocephalan physiology, and Crompton & Nickol (1985), in which contributors covered many aspects of acanthocephalan biology and in which were chapters on epizootiology, life history models and population dynamics. Until now, however, there has been no single book that has been devoted exclusively to the ecology of the Acanthocephala.

This disproportionate treatment of the Acanthocephala and their ecology probably reflects three things: the relatively small number of species, their relative lack of pathogenicity to their vertebrate hosts and the perceived lack of diversity in acanthocephalan structure and life cycles. The Acanthocephala are undeniably only a small phylum with current estimates of around 1000+ species (based on Amin, 1985a). They may cause local damage to the intestine of their vertebrate hosts, but they are very seldom the cause of any serious damage or death to man himself or to his domestic animals. It is also undeniable that they are characterised by great uniformity of structure, larval stages and life cycles. They are in many ways a systematist's nightmare as they have few organs upon which to base their taxonomy (Brown, 1987). The only hard structures they possess are the hooks on their probosces (Fig. 1.1), and we do not even begin to understand the adaptive significance of the differences in hook numbers, size and arrangement between species. Moreover, there is considerable intraspecific variation in the arrangement of the hooks (Brown, 1987). The internal structures are few and remarkably similar (Fig. 1.2), differing between species only in such details as the number and arrangement of cement glands in the males or the position of the neural ganglion. Furthermore, all species have the same fundamental life cycle and developmental stages: all have a free-living egg (acanthor), all require an arthropod intermediate host for the larval acanthella and cystacanth stages and all utilise a vertebrate definitive host as adults (Fig. 1.3).

This lack of anatomical diversity may, however, be deceptive, as will become evident, and the rigidity of the life cycle may be more

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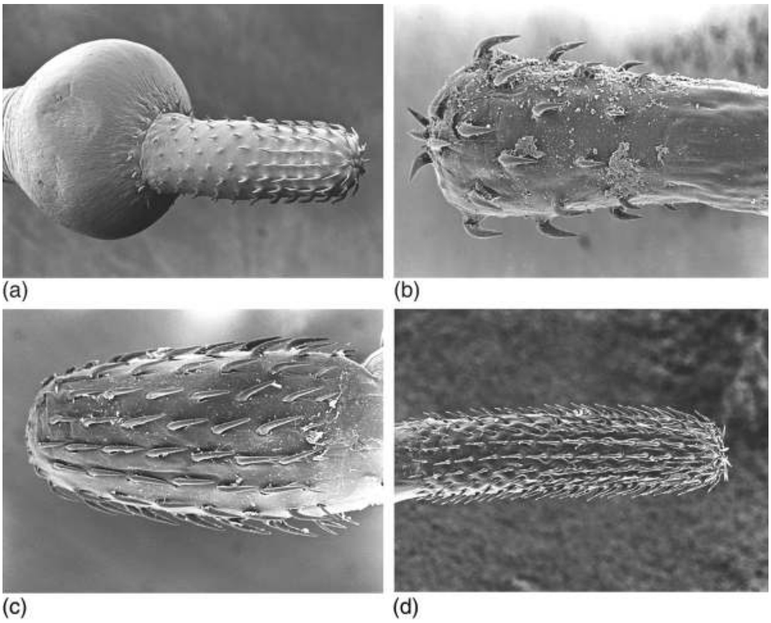

Fig. 1.1 Scanning electron micrographs of acanthocephalan probosces. (a) *Pomphorhynchus laevis* from chub *Leuciscus cephalus*; (b) *Acanthocephalus anguillae* from chub; (c) *Acanthocephalus lucii* from perch *Perca fluviatilis*; (d) *Acanthocephalus clavula* from eels *Anguilla anguilla*.

apparent than real. Concentration on such uniformity is certainly misleading as it deflects attention from the accomplishments of the acanthocephalans as parasites and from their ecological achievements. However success may be defined, they can be considered a highly successful group of parasites in that they infect all classes of vertebrates: they are to be found in the sea, in fresh water, on land and, in birds, in the air, and they occur on all continents and in all biomes. In comparison, it has taken the parasitic platyhelminths some 25 000 species and an enormous diversity of larval stages and life cycles to achieve a similar distribution across hosts and in space (Kennedy, 1993a). Throughout the phylum as a whole, the platyhelminths exhibit wide diversity in larval stages, especially within the cestodes, and in the number and identity of intermediate hosts utilised. They may be said to exhibit high diversity and high achievement, whereas the acanthocephalans have attained a similar high level of achievement with, apparently, minimal diversity. Even the parasitic Crustacea, with almost 3000 more species and which exhibit a more diverse use of hosts in their life cycles, have failed to make the transition to infecting

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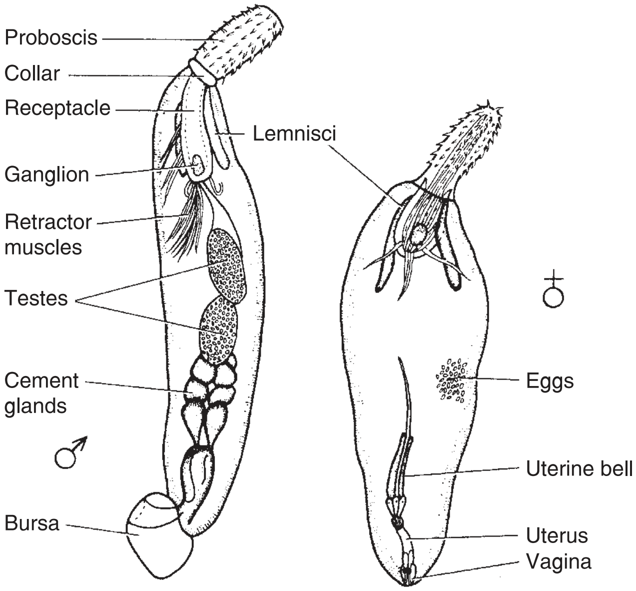

Fig. 1.2 Morphology of an adult male and female *Acanthocephalus* sp. (From Smyth, 1994.)

terrestrial vertebrates. The nematodes, which are similar to acanthocephalans in some respects in that they exhibit a high degree of uniformity of adult and larval structure and life cycle stages, show very wide flexibility and diversity in numbers and identity of intermediate hosts in their life cycles, in the stage at which they are parasitic and also in the degree of pathogenicity towards their definitive hosts. The acanthocephala are thus one of the smallest and least diverse groups of metazoan parasites, yet are as widely distributed amongst vertebrate hosts and biomes as are the larger and more diverse parasitic groups.

Clearly there is something distinctive about the acanthocephalans: they appear to have evolved as a group and co-evolved with their hosts in a different way from other parasitic groups. The aim of this book is to challenge many of the assumptions about them that may make them initially appear dull, uniform and uninteresting, even to many parasitologists, by showing that such appearances may be deceptive. It is the intention of this book to show that an ecological approach can open up a whole new perspective on the acanthocephalans. In this light, the phylum appears very different. Such an approach to the group is novel and differs from previous treatments of the

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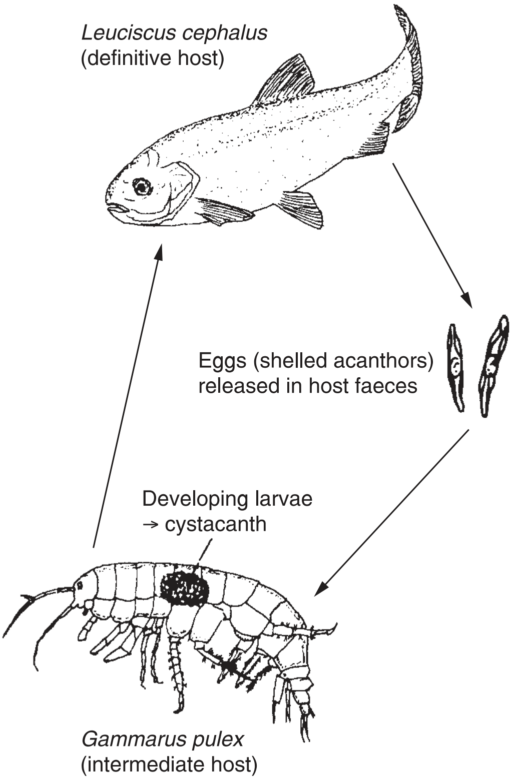

Fig. 1.3 The basic life cycle of an acanthocephalan. *Pomphorhynchus laevis* eggs released into fresh water in the fish's faeces are eventually eaten by a *Gammarus*. They hatch in the intestine and the released acanthors move into the haemocoel, where they develop into the orange-coloured cystacanth. This infective stage remains in the *Gammarus* until the amphipod is eaten by the fish, when the larva develops into an adult in the intestine and the cycle is completed. (From Brown & Thompson, 1986, with permission, Institute of Biology.)

phylum. It involves a change in emphasis and a concentration on many aspects of acanthocephalan biology other than morphology. For example, it will be shown that the acanthocephalans can exhibit diversity at the molecular level and that they can escape the restriction of requiring only a single intermediate host in their life cycle. They can have a major impact on their intermediate hosts at individual and population levels by altering the behaviour of infected individuals which results in the host's death by predation. This in turn means that they can have important effects on the communities and food webs of

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free-living organisms. This has been demonstrated to be the case for virtually all freshwater species, yet even some of the very best freshwater textbooks such as that of Moss (1988) make no mention of their effects on individuals, populations and communities of freshwater organisms, any more than books on freshwater pollution such as that by Mason (1991) discuss their role as bioindicators of heavy metal pollution.

It is the contention of this book that the key to understanding the success of the Acanthocephala and their different pattern of evolution lies in an understanding of their ecology. One can then begin to appreciate that their relationships with their intermediate hosts may be more important in ecological and evolutionary contexts than their relationships with their vertebrate hosts. It may also help one to appreciate that the term minor phylum should not carry any implications of importance, as the impact of members on free-living organisms may be out of all proportion to the numbers of species. Above all, it may cause us to think harder about the importance of diversity: it is not the beginning and end of everything and it should be instructive to all biologists to realise that a phylum with apparently little biodiversity may be as successful as many far more diverse phyla.

1.2 An ecological approach to the Acanthocephala

Ecology can be defined in many ways. At its simplest it can be defined as the study of the relationships between an organism and its environment, and this of course is effectively a truism as far as parasites are concerned since their host is their environment. Russian parasitologists (Pavlovski, 1934, and Dogiel, 1964, in particular) further distinguish two types of environment in the case of parasites: the micro-environment, or the immediate environment within the host, and the macro-environment, or the external environment of the host. However, in the context of the present book it is the definition of Andrewartha & Birch (1954) that has been adopted: ecology, in their view, is the study of the factors affecting the distribution and abundance of an organism (or, strictly, the abundance, since absence of a species is the same as zero abundance). They considered these factors under headings such as food, a place to live and impact of other species; but this is not the easiest approach for parasites as we know very little indeed about their food requirements and may also know very little about where they live.

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A different approach has therefore been adopted here. The overall aim is to explain the distribution and abundance of Acanthocephala in both space and time by searching for repeated patterns. It is essential, however, to appreciate that parasites form a nested hierarchy and, as with free-living animals, they can be studied at the individual, population and community levels. They can also be studied at different spatial scales, from local through regional to global, and over different temporal scales, from seasonal through annual to long term. It is therefore possible to pose a series of questions at each level and scale, and the answer to each question will form the subject of a separate chapter of this book. It is necessary to emphasise, however, that this book does not attempt to be comprehensive, but rather interpretative. Considerations of physiology and phylogeny, for example, are largely ignored in favour of a focus and emphasis on ecological issues and examples are selected to make particular points. This inevitably means that many other excellent examples have had to be omitted, but considerations of space require choices to be made.

The first stage in any ecological appraisal of a group of organisms is to learn as much as possible about their life cycles, and this is particularly important in respect of parasites. In the case of the Acanthocephala it is essential to question whether the number of hosts in the life cycle is really fixed at two, or whether any flexibility and variation in the number of hosts, by addition or deletion, is possible to assist transmission (Chapter 2). It is logical then to place the Acanthocephala in a biogeographical context and to question whether the species are equally distributed between all habitats and host groups and whether patterns in global and regional distribution can be detected (Chapter 3). A major influence on the ecology of all parasites is their host specificity and so it is essential to question how specific to each of their hosts are acanthocephalans and how much variation in specificity exists between species (Chapter 4). It then becomes apparent that there may be much more diversity at the molecular level than is apparent at the morphological one and this will raise yet more questions. A further question at the individual level is whether acanthocephalans are ever pathogenic to their hosts, or alter their host behaviour in any way, and if so under what circumstances and with what consequences and benefit (Chapter 5).

Moving to the population level, the key question is whether acanthocephalan populations are stable and regulated over time and space, or whether they are unstable and liable to local epizootics and, if so, under what circumstances (Chapter 6). Acanthocephalan species

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almost invariably co-occur with other species of parasite in host individuals and/or populations and so form a part of a community. At these levels it is pertinent to question whether species interact with other species of acanthocephalan or of other parasitic groups and compete for occupancy of niches and if so whether this inter-specific competition has wider ecological significance (Chapter 7). Acanthocephalans do not occur in isolation but are components of ecosystems. It is therefore important to query how they transfer from one ecosystem to another and/or colonise new localities (Chapter 8). As members of an ecosystem, they are also responsive to changes in that ecosystem and it is valid to question the extent to which they can act as indicators of such changes: it is equally important to appreciate the impact that they may have on an ecosystem and the extent to which they may affect it (Chapter 9). The answers to many of these questions may be unexpected and surprising and taken together not only aid our understanding of the ecology of the acanthocephalans but also go a long way to explaining their success as a group (Chapter 10). They also take us to the heart of understanding parasitism as a way of life as the Acanthocephala do seem to present a distinctive and successful pathway of host–parasite co-evolution *sensu* Anderson & May (1982) and they are indeed in the words of MacArthur (1972) ‘worth studying’.

All these questions are basically ecological ones and all are answerable to a greater or lesser extent. Many of the answers will come from studies on aquatic species. This is not a bias on my part or a reflection of my particular interests: rather, it reflects the facts that the majority of acanthocephalan species have an aquatic life cycle and that since it is easier to obtain good samples from aquatic populations of fish and invertebrates, most ecological studies have focused on aquatic, especially freshwater, species. It is far easier to collect large and representative samples of fish and aquatic amphipods, for example, than of terrestrial cockroaches and avian raptors (or rhinoceroses!). Schmidt (1985) tabulated summary information on the life cycles of 125 acanthocephalan species, but listed intermediate hosts for only 80. Only 14 of these were terrestrial species. Any apparent bias towards particular species similarly reflects the ecological constraints and information available. Some species have been studied in many localities over wide geographical areas, for example *Pomphorhynchus laevis*, *Echinorhynchus salmonis* and *Macracanthorhynchus hirudinaceus*, and others such as *Mediorhynchus centurorum* have been studied intensively in particular localities. A great deal of information is available on the biology of *Moniliformis moniliformis*, for example, but this reflects the

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