Cambridge University Press
978-0-521-10470-8 - An Ecological Approach to Acanthocephalan Physiology
D. W. T. Crompton
Excerpt
More information

CHAPTER I

General Introduction

ALTHOUGH most groups of helminths were known to the ancients, the Acanthocephala remained unrecognized until the late 17th century when individuals parasitic in eels were described independently by Redi (1684) and Leeuwenhoek (1692). Redi stated that in all types of eels he often found tiny white worms which were tightly fixed by their extremities to the intestinal wall. He also reported, 'the worms possess a proboscis which is equipped with hooks and which the worms are accustomed to send out and draw in'. Leeuwenhoek wrote in a letter on reproduction in eels, sent to The Royal Society on 16 September 1692, that he had noticed two types of Acanthocephala in the eel's intestine. His first impression was that the worms were young eels of the next generation, but after dissecting one he changed his mind. One type of worm was reported to be small and red and to contain a great number of little worms. He was probably describing mature female acanthocephalan worms, which may have been specimens of *Pomphorhynchus laevis*. The other type was described as white with tiny joints, which is at first suggestive of a cestode; but many acanthocephalans will contract in an irregular manner on interference and Leeuwenhoek not only described but also figured an unmistakable acanthocephalan proboscis belonging to this parasite. He wrote that the heads of these worms were sticking to the intestine and, when he examined them under the microscope, it was with amazement that he saw numerous 'hooky' parts. He also commented that he saw, when he could manage to wrench them away unharmed from the intestines, that they retracted this 'hooky' part inside their bodies. It is not unlikely that these worms, and those found by Redi, were specimens of *Acanthocephalus anguillae*.

Since these early descriptions, approximately 650 species of acanthocephalans have been identified from all over the world, and, as Redi and Leeuwenhoek observed, the retractile proboscis is the most obvious and characteristic feature of adult worms (fig. 1). In addition, acanthocephalans are diœcious, pseudocoelomate worms without an alimentary tract at any stage of their development. They are endoparasitic throughout their indirect life cycles and the structure of the body wall and the anatomy of the reproductive systems are peculiar to the group. Acanthocephalans appear to be related to the aschelminths, but it is probably most satisfactory to consider them as a separate phylum. In this book, the classifications of Hyman (1951) and Rothschild (1961) have been adopted for the acanthocephalans and their hosts; the letter A denotes order Archiacanthocephala, P denotes Palaeacanthocephala and E denotes Eocanthocephala on the figures and tables.

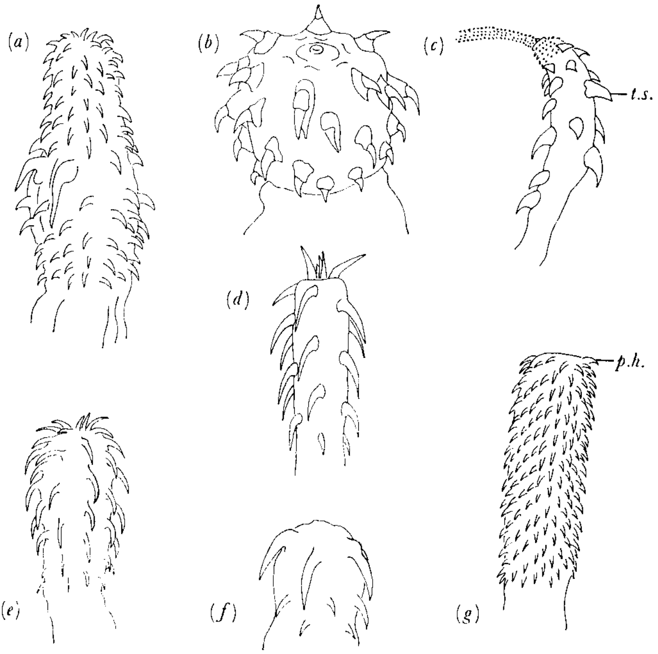

Fig. 1. The proboscides of seven species of Acanthocephala. (*a*) *Corynosoma turbidum*; (*b*) *Macracanthorhynchus hirudinaceus*; (*c*) *Rhadinorhynchus horridum*; (*d*) *Acanthocephalus tenuirostris*; (*e*) *Acanthocephalus anguillae*; (*f*) *Neoechinorhynchus rutili*; (*g*) *Echinorhynchus gadi*. (After Yamaguti, 1963; figs. 6, 134, 150, 194, 328, 416 and 630) *p.h.*, proboscis hook; *t.s.*, trunk spine.

CAMBRIDGE
Cambridge University Press
978-0-521-10470-8 - An Ecological Approach to Acanthocephalan Physiology
D. W. T. Crompton
Excerpt
More information

ANATOMY OF ADULT WORMS

Mature male acanthocephalans are usually smaller than mature females of the same species. The majority of species are about 1 to 2 cm long, but some are much longer, notably female *Macracanthorhynchus hirudinaceus* from pigs (Kates, 1944) and female *Nephridiacanthus longissimus* from aardvarks (Golvan, 1962) measuring 45 cm and 93 cm respectively. The worms are unsegmented, but superficial annulations are often present and may give the impression of segmentation.

Various aspects of the anatomy of adult acanthocephalans are shown diagrammatically in figs. 2 and 3. The term praesoma was coined by Rauther (1930) for the proboscis sheath, the lemnisci and all the structures involved in the function of the proboscis as an organ of attachment. The remaining structures form the metasoma, which includes all the body wall situated posterior to the partition. This partition ensures the flow of fluid between the lemnisci and the wall of the neck (figs. 2*a*; 3*a*) and prevents the movement of fluid between the metasomal body wall and the lemnisci. The division of the acanthocephalan body into the praesoma and metasoma is a matter of descriptive convenience only; the regions are interdependent and integrated and cannot function alone.

The proboscis is equipped with a variety of hard, sharp hooks and the anterior portion of the body wall often bears trunk spines which also assist in the attachment of the parasite to its host's intestinal wall. The proboscis is withdrawn into its sheath by contraction of the proboscis retractor muscles and is everted within a few seconds by a hydrostatic system (Hammond, 1966*a*, *b*). After withdrawal of the proboscis, the neck may also be withdrawn when the neck retractor muscles contract. The compact folding of the worm, resulting from contractions of this type, may be observed *in vitro*. It is unlikely to occur in the intestine where the worms must maintain contact with their hosts by means of either their proboscides or trunk spines to avoid being expelled by peristalsis. Contraction of the retractor muscles by an attached worm will pull the metasoma or trunk against the intestinal wall and away from abrasive or solid material in the lumen. One layer of circular muscles and one of longitudinal muscles are found beneath the body wall. All

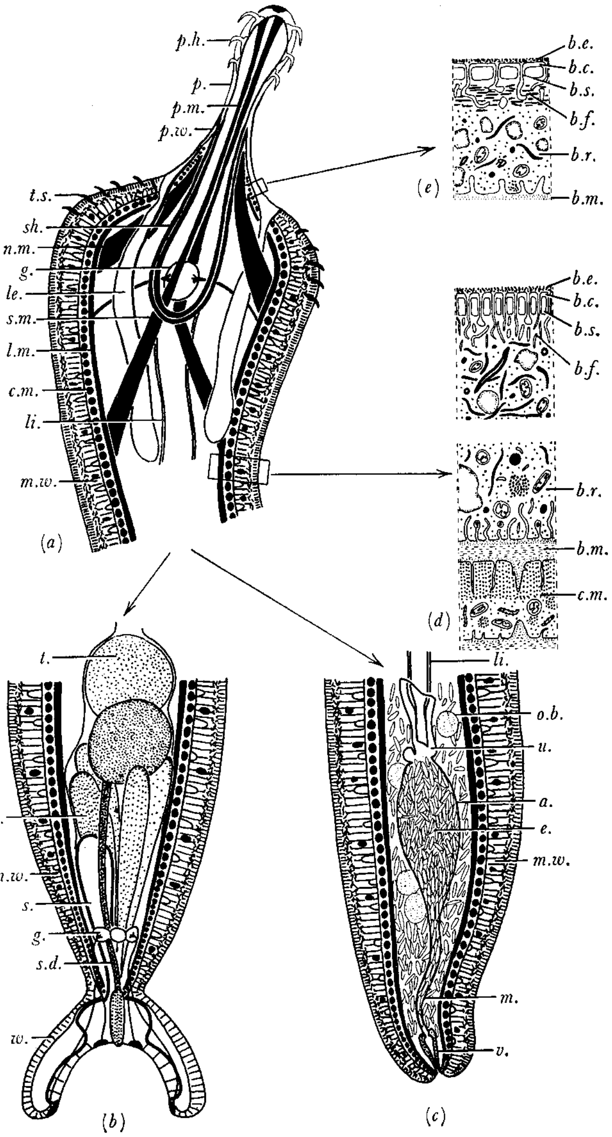

Fig. 2. Diagrammatic representations of the anatomy of an adult acanthocephalan worm. (*a*) Structures common to both sexes; (*b*) male reproductive organs; (*c*) female reproductive organs; (*d*) metasomal body wall; (*e*) praesomal body wall. *a.*, anterior uterus; *b.c.*, cuticle; *b.e.*, epicuticle; *b.f.*, felt layer; *b.m.*, basement membrane; *b.r.*, radial layer; *b.s.*, striped layer; *c.g.*, cement gland; *c.m.*, circular muscle; *e.*, eggs; *g.*, ganglion; *le.*, lemniscus; *li.*, ligament; *l.m.*, longitudinal muscle; *m.*, muscular lower uterus; *m.w.*, metasomal wall; *n.m.*, neck retractor muscle; *o.b.*, ovarian ball; *p.*, proboscis; *p.h.*, proboscis hook; *p.m.*, proboscis retractor muscle; *p.w.*, praesomal wall; *s.*, Saefftigen's pouch; *sh.*, proboscis sheath; *s.d.*, sperm duct; *s.m.*, proboscis sheath retractor muscle; *t.*, testis; *t.s.*, trunk spine; *u.*, uterine bell; *v.*, vagina; *w.*, bursa.

acanthocephalan muscle so far examined in detail has been found to consist of a contractile and a non-contractile portion (fig. 2*d*).

Simplified representations of the reproductive systems of male and female worms are shown in fig. 2*b* and *c*. The male system, which is completely enclosed in the ligament, consists of a copulatory bursa, several cement glands, a pair of testes and a sperm duct. The female system, with which the ligament is only partly associated, is composed of the uterine bell where mature and immature eggs are sorted, and the uterus from which mature eggs are released. The eggs develop in the body cavity of the female and are nourished from the pseudocoelomic fluid, which surrounds the reproductive organs of both male and female worms. The male system includes a complex of ganglia connected to sense organs located on the copulatory bursa (fig. 2*b*). The greater part of the nervous system in both male and female worms is the ganglion situated in the proboscis sheath through which the lateral nerves emerge (fig. 2*a*).

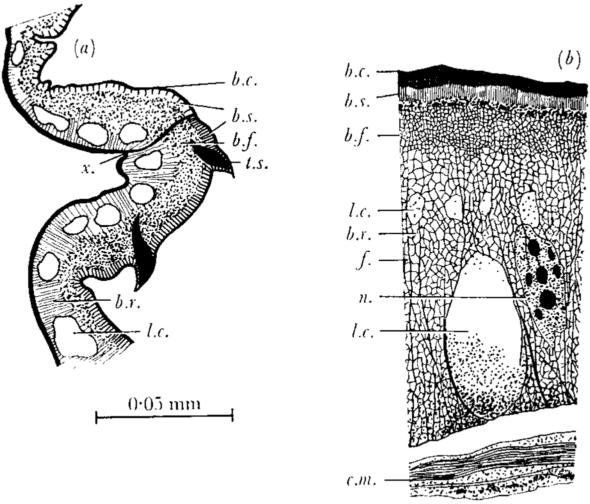

Fig. 3. (*a*) The junction of the praesomal and metasomal body wall of *Polymorphus minutus*; (*b*) the metasomal body wall of *P. minutus* (after Crompton, 1963; fig. 12) *b.c.*, cuticle; *b.f.*, felt layer; *b.r.*, radial layer; *b.s.*, striped layer; *c.m.*, circular muscle; *f.*, fibre; *l.c.*, lacunar channel; *n.*, nucleus; *t.s.*, trunk spine; *x.*, partition between praesoma and metasoma.

Close attention must be paid to the morphology of the adult

Cambridge University Press
978-0-521-10470-8 - An Ecological Approach to Acanthocephalan Physiology
D. W. T. Crompton
Excerpt
More information

body wall; it has become specialized for feeding, metabolism excretion and protection. Furthermore, the body wall is a component of the hydrostatic skeleton and the tissue in which the hooks and spines develop. In fact, a study of the physiology of the acanthocephalan body wall would involve most aspects of acanthocephalan physiology.

The body wall consists of at least five layers. The outermost layer is a thin epicuticle which appears to contain mucopolysaccharide (Crompton, 1963; Wright and Lumsden, 1968). The next layer is the tough cuticle which is penetrated by many pores. Their existence was postulated from studies with the light microscope, but they were not demonstrated until the body wall was examined with the electron microscope. The pores lead into the canals and ducts of the striped layer which blends into the underlying fibrous felt layer. The fibres, the cuticle, the matrix of the striped layer and all skeletal elements are probably composed of protein, or lipoprotein, stabilized by disulphide linkages (Mueller, 1929; Monné, 1959; Crompton, 1963). The innermost and thickest layer is the radial layer containing nuclei, ribosomes, mitochondria, folded plasma membranes, glycogen and lipids, but showing no evidence of cell walls. This layer is clearly the location of much synthetic and metabolic activity. Finally, the radial layer is separated from the circular and longitudinal muscles of the worm by a relatively thick basement membrane of connective tissue. These aspects of the body wall are illustrated and supplemented by fig. 3*b* and plates 1 and 2.

So far, the ultrastructure of the body wall has been examined in detail for only three palaeacanthocephalans, *Polymorphus minutus* (Crompton and Lee, 1965), *Pomphorhynchus laevis* (Stranack, Woodhouse and Griffin, 1966) and *Acanthocephalus ranae* (Hammond, 1967*a*), and one archiacanthocephalan, *Moniliformis dubius* (Nicholas and Mercer, 1965). In spite of the differences in nomenclature and interpretation of electron micrographs discussed by these authors, it emerges that the adult body wall is a uniform, syncytial tissue. More comprehensive accounts of acanthocephalan morphology are to be found in the works of Meyer (1933), Hyman (1951) and Petroschenko (1956; 1958).

THE LIFE CYCLE

All the known life cycles of acanthocephalans involve an arthropod as an intermediate host in which development occurs, and a vertebrate as a final host in which sexual reproduction takes place (table 1). Mature eggs are released from the body cavities of female worms into the intestine of the final host, from which they are discharged with faeces on to soil or into water. It may be inferred from table 1 that the eggs of many archiacanthocephalans will be deposited on soil and eaten by terrestrial insects, while those of many palae- and eoacanthocephalans will fall into water and be eaten by crustaceans. After ingestion by the correct intermediate host, the egg hatches to liberate the acanthor larva, which moves out of the intestinal lumen into the host's haemocoele and there develops into the acanthella. In some parasites the acanthor is retarded in the intestinal tissues during its migration into the haemocoele and, consequently, the change to the acanthella is delayed. When development of the acanthella is finished, it encysts and becomes a resting stage called the cystacanth which remains dormant until its host is eaten by the correct final host or by a transport host. When a suitable final host ingests a cystacanth, the parasite is activated and an immature worm becomes established in the appropriate place in the intestine. Alternatively, if a suitable transport host swallows a cystacanth, the parasite everts its proboscis, migrates through the intestinal wall and becomes encapsulated in the abdominal tissues where it remains until the transport host is eaten by the final host. The literature contains many references to transport hosts, but these have been omitted from table 1 because direct evidence of the necessity for these hosts in most acanthocephalan life cycles is not available. One exception is provided by the gasteropod, *Campeloma rufum*, which could have been cited as a transport host for the eoacanthocephalan, *Neoechinorhynchus emydis*, but now appears to be as essential a host as the ostracod, *Cypria maculata* (Hopp, 1954). The evidence indicates that the parasite actually grows in *C. rufum*, which is better defined, therefore, as a second intermediate host. Transport hosts are usually assumed to harbour and support an acanthocephalan without any growth occurring. Of course, some final hosts, such as seals, are unlikely to eat

TABLE 1. *Some Acanthocephala of which the life cycles have been determined*

Species	Intermediate hosts	Final hosts	References
Archiacanthocephala			
Macracanthorhynchus hirudinaceus	*Cotinus nitida* *Diloboderus abderus* *Melolontha vulgaris* *Phyllophaga rugosa* (coleopteran larvae)	Wild and domestic pigs	Wolffhügel (1908) Kates (1944)
M. ingens	*Phyllophaga crinita* *P. hirtiventris* *Ligyrus* spp. (coleopteran larvae)	*Procyon lotor* (raccoons)	Moore (1946*b*)
Mediorhynchus grandis	*Arphia luetola* *Chortophaga viridifasciatus australior* *Orphuella pelidna* *Schistocerca americana* (adult orthopteroids)	*Turdus migratorius* *Quiscalus quiscala* and other birds	Moore (1962)
Moniliformis clarki	*Ceuthophilus utahenis* (camel cricket)	*Peromyscus maniculatus sonoriensis* (deer mouse)	Crook and Grundmann (1964)
M. dubius	*Periplaneta americana* (cockroach)	Wild and domestic rats	Moore (1946*a*)
Prosthenorchis elegans	*Blatella germanica* (cockroach) *Lasioderma serricorne* *Stegobium paniceum* (beetles)	*Saimiri sciurea* (squirrel monkey) and other primates	Stunkard (1965)
P. spirula	*Blatella germanica*	*Saimiri sciurea*	Yamaguti (1963)

Palaeacanthocephala			
Acanthocephalus nanus	*Asellus aquaticus* (fresh-water isopod)	*Rana rugosa* *Diemyctylus pyrrhogaster* (amphibians)	Yamaguti (1935)
Echinorhynchus truttae	*Gammarus pulex* (fresh-water amphipod)	*Salmo trutta* (trout)	Awachie (1966)
Filicollis anatis	*Asellus aquaticus*	Anatidae (ducks, geese and swans)	Styczyńska (1958)
Leptorhynchoides thecatus	*Hyalella azteca* (fresh-water amphipod)	*Ambloplites rupestris* *Huro salmoides* (fresh-water fish)	DeGiusti (1949*a*)
Polymorphus marilis	*Gammarus lacustris* (fresh-water amphipod)	*Aythya affinis* (Lesser Scaup; duck)	Denny (1968)
P. minutus	*Gammarus* spp.	*Anas platyrhynchos* (Mallard) and other anatid birds	Hynes and Nicholas (1957); Crompton and Harrison (1965)
Pomphorhynchus bulbocolli	*Hyalella azteca*	*Catostomus commersoni* (sucker; fresh-water fish)	Jensen (1952)
P. laevis	*G. pulex*	*Squalius cephalus* (chub)	Ginetsinskaya (1961); Chubb (1965)
Profilicollis botulus	*Carcinus maenas* (crab)	*Somateria mollissima* (Eider duck)	Garden, Rayski and Thom (1964)
Prosthorhynchus formosus	*Armadillidium vulgare* *Porcellio laevis* *P. scaber* (terrestrial isopods)	*Turdus migratorius* (N. American robin and other birds)	Schmidt and Olsen (1964)

TABLE I. (*cont.*)

Species	Intermediate hosts	Final hosts	References
Eoacanthocephala			
Neoechinorhynchus cylindratus	*Cypria globula* (fresh-water ostracod)	*Huro salmoides* (bass—final host) *Lepomis pallidus* (bluegill—transport host)	Ward (1940*a*)
N. emydis	*Cypria maculata* (1st int. host) *Campeloma rufum* (fresh-water gasteropod; 2nd int. host)	*Graptemys geographica* (Map turtle)	Hopp (1954)
N. rutili	*Cypria turneri*	*Cyprinidae* (and other families of fresh-water fish)	Merritt and Pratt (1964)
Octospinifer macilentis	*Cyclocypris serena* (fresh-water ostracod)	*Catostomus commersoni*	Harms (1965)
Paulisentis fractus	*Tropocyclops prasinus* (fresh-water copepod)	*Semotilus atromaculatus* (Creek chub)	Cable and Dill (1967)