ORIGINS AND EVOLUTION OF ACANTHOCEPHALAN WORMS

BY

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INTRODUCTION

The case for considering the Acanthocephala as a separate phylum was clearly presented by Van Cleave (1948), and since then most authorities have accepted and supported his view (Petrotschenko, 1956, 1958 ; Golvan, 1958 ; Yamaguti, 1963 ; Bullock, 1969 ; Schmidt, 1969). All known living species of Acanthocephala are endoparasites which attain sexual maturity in the vertebrate alimentary tract ; most appear to be confined to the small intestine (Crompton, 1975). Throughout this review, we have adopted the simple classification of Bullock (1969) which recognizes 3 orders, Palaeacanthocephala, Archiacanthocephala and Eoacanthocephala, within the phylum. The purpose of our contribution is threefold. First, we intend to augment the view that acanthocephalans have affinities with the aschelminths (see Whitfield, 1971b), and the priapulids in particular (Meyer, 1933 ; Lang, 1953 ; Golvan, 1958), by considering the possibility that a Cambrian fossil worm (Conway Morris, 1977) might be related to the ancestors of the Acanthocephala. An ingenious suggestion by Nicholas (1971) that such ancestors might have been minute animals inhabiting the interstices of marine sediments is supported by other evidence. Secondly, we wish to discuss how parasitism in acanthocephalans might have originated and developed. This topic is based on various observations and ideas in the literature. Thirdly, we hope to highlight some problems of understanding evolution within the Acanthocephala itself. In this context, we have found the approaches of Llewellyn (1965) and Inglis (1971) to parasite evolution most stimulating.

LIVING ACANTHOCEPHALA

The adults of most species of Acanthocephala are relatively small worms measuring a few millimetres in length (see Meyer, 1933 ; Yamaguti, 1963). Nearly all acanthocephalans are easily recognisable. They have a retractable proboscis, which nearly always bears hooks, a muscular proboscis sheath or receptaculum, a pair of lemnisci and a characteristic body wall. There is an extensive body cavity, which is usually assumed to be a pseudocoel (Hyman, 1951), but no alimentary tract has been observed at any stage of the life cycle. The male reproductive system consists in essence of paired testes, cement glands and copulatory apparatus, while the female system comprises an efferent duct

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and ovarian tissue (Parshad & Crompton, 1981). The main parts of the female efferent duct are the vagina, uterus and uterine bell (Whitfield, 1968). The ovarian tissue is composed of a variable number of free ovaries which float in the fluid of the body cavity, either freely or loosely constrained in the ligament sacs. Where known, the life-cycle is indirect and development always involves an arthropod as intermediate host. Ostracodes, amphipods and isopods, all of which are crustaceans, are frequently encountered as intermediate hosts for palaeacanthocephalan and eoacanthocephalan species, and insects for archiacanthocephalans (Yamaguti, 1963 ; Bullock, 1969). After development within the body cavity of the adult female worm, the shelled acanthors are released through the efferent duct and eventually are discharged in the faeces of the definitive host. On ingestion by a susceptible arthropod host, the acanthor is liberated from its surrounding envelopes and bores through the intestinal wall into the haemocoel. The definitive host acquires acanthocephalans by eating arthropods containing infective juvenile or cystacanth stages. The life cycle may be prolonged and made more complicated by the inclusion of transport or paratenic hosts (Van Cleave, 1953).

The degree of host specificity in acanthocephalans was reviewed by Golvan (1957), who emphasized that any generalizations are difficult because relatively few life cycles have been fully elucidated and most of those are for the Eoacanthocephala. Golvan (1957) concluded that host specificity for the intermediate arthropod host is sometimes moderately strong, and in some cases markedly so. Host specificity for the definitive vertebrate host appears generally to be weaker. Host specificity in paratenic hosts appears to be unproven, and is guided mostly by their being intercalations in the food chain between intermediate and definitive hosts with the eating habits of the latter determining the type of paratenic host.

This summary of the biology of living Acanthocephala is given here because satisfactory hypotheses and explanations about the origins and evolution of these worms should attempt to account for their major morphological and biological features.

ORIGINS

The majority of workers consider the Acanthocephala to be related to one or more of the 6 phyla that are grouped as the Aschelminthes. Two phyla have been particularly linked with the Acanthocephala : the Rotifera (Haffner, 1950 ; Wright & Lumsden, 1969 ; Storch & Welsch, 1969 ; Whitfield, 1971b ; Graeber & Storch, 1978) and the Priapulida (Meyer, 1928, 1933 ; Lang, 1953 ; Golvan, 1958 ; Crompton, 1975 ; Conway Morris, 1977). The most detailed arguments for a relationship between Acanthocephala and Priapulida are given by Golvan (1958). More recently an important source of fossil evidence has emerged that not only supports Golvan's suggestions, but appears to throw further light on the antiquity of the Acanthocephala (Van Cleave, 1924) and their origins.

The fossil evidence comes from a mid-Cambrian unit known as the Burgess Shale (about 530 million years old), which is exposed in the Canadian Rockies of southern British Columbia. The fauna was marine (Conway Morris, 1979 ; Conway Morris & Whittington, 1979 ; Whittington, 1980) and most of it lived in or on muddy sediments at over 100 m depth close to the base of a large reef. The diversity of the fauna exceeds that of any other Cambrian locality. It is dominated by arthropods (37 % of genera, 57 % of individuals), but other groups include priapulids, polychaetes, molluscs, chordates, cnidarians and sponges.

Although it had long been known that there is a diverse collection of fossil worms in the Burgess Shale, the existence of a prominent assemblage of priapulids is a more recent discovery (Conway Morris, 1977). One of these worms, *Ottoia prolifica*, had already been compared to priapulids as well as acanthocephalans (Meyer, 1933 ; Lang, 1953 ; Golvan, 1958). Although Meyer (1933) and Lang (1953) compared *O. prolifica* with Acanthocephala and Priapulida, there is amongst the Burgess Shale assemblage a much rarer species (18 specimens as against about 1495 of *O. prolifica*), known as *Ancalagon minor*, that would appear to have even closer affinities with the Acanthocephala than *O. pro-

lifica (Conway Morris, 1977). The significance of *A. minor* is that it shows some striking similarities with the reconstruction by Golvan (1958) of an ancestral proto-acanthocephalan worm.

Ancalagon minor averaged about 60 mm in length and was divided into a proboscis and annulated trunk. The proboscis bore numerous simple hooks and a series of about 10 circumoral teeth. If Acanthocephala and Priapulida are related, an important comparison lies in the homologies of the proboscides. In priapulids, the proboscis armature or scalids are usually hook-like. They are separated from the oral teeth by a more or less unarmed region known as the collar. It seems credible that the scalid-bearing part of the proboscis is equivalent to the hooked section of the acanthocephalan proboscis (Lang, 1953 ; Conway Morris, 1977). In comparison with *O. prolifica* rather little is known about the internal anatomy of *A. minor*, although there is evidence for a straight gut with terminal openings as in Golvan's hypothetical proto-acanthocephalan.

The Burgess Shale priapulids probably lived for much of their life within the sediment and some appear to have been active burrowers. Nicholas (1971) and Whitfield (1971a) have emphasized that the free-living ancestors of the Acanthocephala may have been burrowers in marine sediments. Nicholas (1971) has further suggested that the ancestors of the Acanthocephala may have been minute animals, living between sediment grains as members of the interstitial meiofauna. Meiofaunal animals have been defined as those animals which can pass through a 500 µm seive, but which are retained by a 50 µm mesh (Eltringham, 1971). Only one of the Burgess Shale priapulids (*Lecythioscopa simplex*, adult length c. 5 mm) approaches the meiofaunal size range.

If it be accepted that the ancestor was meiofaunal, meaning that *A. minor* and other Burgess Shale priapulids would have been more distantly related to the ancestor than has been implied so far, we may imagine that the evolution of meiofaunal species transitional from priapulids to acanthocephalans could have arisen through the process of progenesis. In progenesis, sexual development is accelerated relative to somatic development to produce an animal broadly equivalent to a sexually mature larva. Gould (1977) has emphasized the probable importance of progenesis in the evolution of both meiofaunal and parasitic animals. Gould links progenesis with a life history showing r-selection. An organism showing pure r-selection will have features such as high fecundity, rapid maturation and short life, rapid development, small egg size and limited parental care (see Jennings & Calow, 1975). These features are regarded as an emphasis on production in unstable and patchy environments with unpredictable resources.

If progenesis was involved in the early evolutionary history of Acanthocephala as parasites, as against their origins in the meiofauna, it would appear that the advantage lay in the development of a reproductive system that ensured high fecundity. The unique reproductive system of Acanthocephala (Parshad & Crompton, 1981) may owe its arrangement to two major evolutionary steps during their early evolution. Firstly, the development of internal fertilization and associated modification of the reproductive system in meiofaunal forms. Secondly, the continued specialization of the reproductive organs to maximize egg production in parasites.

ACANTHOCEPHALA AND ENDOPARASITISM

It is now appropriate to consider how and when the first Acanthocephala, or their ancestors, became endoparasites. Barring some extraordinary fossil discovery, the original course of events will remain speculative. The best approach involves extrapolation back in time from present knowledge of host-parasite relationships and the unsettled question of the evolutionary significance of host-specificity. As Llewellyn (1965) has pointed out, parasites which include two or more hosts in their life cycle could have acquired the different hosts either simultaneously or in succession, with the latter alternative appearing to be the more plausible. In the case of the Acanthocephala it might be argued that arthropods represent the original host with the vertebrates, now the definitive hosts, being an interpolation in the life cycle. Perhaps the eggs or larvae (or even adults) of the ancestral acantho-

cephalans in the mid-Cambrian period were raked up from the sediments and eaten by deposit-feeding arthropods. The early acanthocephalans may then have become encysted in the tissues of their arthropod hosts. Perhaps their reproduction could not be completed, or their eggs released, until they were liberated from the arthropod after its death. The aquatic arthropods that act as intermediate hosts for modern Acanthocephala are usually representatives of the ostracodes, amphipods or isopods, all of which belong to the Crustacea. The presence of predatory vertebrates which fed on arthropods, including those harbouring acanthocephalans, may have marked the first steps towards the complete life cycle seen today. The entire acanthocephalan life cycle with transmission between hosts is dependent on host feeding habits. Many definitive hosts of modern acanthocephalan appear to be predators either near or at the top of the trophic pyramid. By encysting in an arthropod host, which operate at a lower level of the trophic pyramid, the parasite joins a " ladder " that can move it up the pyramid through predator-prey relationships (see Van Cleave, 1953). Golvan (1957) has emphasized the importance of paratenic hosts as links in the " ladder " through the trophic pyramid.

EVOLUTION WITHIN THE ACANTHOCEPHALA

Sufficient time has probably elapsed since the appearance of the first acanthocephalans for many new species to have arisen and for their morphology and physiology to have changed under selection pressures imposed by endoparasitism and the evolution of their hosts. No group of Acanthocephala can be identified as being more primitive than the others solely on the basis of characters that are shared either with the fossilized remains or living examples of free-living relatives.

In our attempt to assess the interrelationships of the 3 orders (Bullock, 1969), we have assumed that 2 of them did not arise simultaneously from the third order to give a trichotomous relationship. It seems plausible that evolutionary branching would have been dichotomous. Such branching means that 2 of the orders would be more closely related to each other than either one to the third. The possible relationships between the 3 orders under a scheme of dichotomous branching may be shown in with cladograms. This simple use of cladistics (see Ashlock, 1974 ; Patterson, 1980) might provide the entry to a more detailed cladistic analysis of acanthocephalan anatomical features that could provide useful pointers to relationships within the Acanthocephala. At present, we feel that the Palaeacanthocephala is more primitive than the other 2 orders. In our view, further evidence of acanthocephalan interrelationships may be obtained from examining host lists, particularly those pertaining to the Palaeacanthocephala. Most species of this order depend upon aquatic crustaceans for intermediate hosts, and not surprisingly the definitive host is usually a teleost fish (Yamaguti, 1963). A number of acanthocephalan genera, however, have been recorded from more primitive fish. Several interesting observations arise from this compilation provided that the parasites attain sexual maturity in these hosts and the identifications are valid. The record of *Acanthocephaloides* in an elasmobranch (*Raja*) is highly unusual for acanthocephalans and may represent an accidental infection. The presence, however, of this genus and *Echinorhynchus* in the lamprey (*Petromyzon*) is especially interesting. Lampreys belong to the Agnatha which were the first fish to appear in the Upper Cambrian (Repetski, 1978). The exact relationship of lampreys (and hagfish) to the extinct agnathans of the Lower Palaeozoic is not clear, but lampreys themselves are known as fossils from the Upper Carboniferous (Bardack & Zangerl, 1971). Equally interesting is the infection by several palaeacanthocephalans of the primitive sturgeon (*Acipenser*, chondrostean) and bowfin (*Amia*, holostean). Although both groups of fish first appear in the Palaeozoic, the families Acipenseridae and Amiidae appear in the Cretaceous and Jurassic respectively. Of special note is the genus *Leptorhynchoides* (Kostileff, 1924 ; Meyer, 1933 ; Yamaguti, 1963) which occurs in both *Acipenser* and *Amia*. Furthermore, one species (*L. plagicephalus*) occurs mainly in *Acipenser*, whereas the other palaeacanthocephalan species are also found in teleosts. The host distribution of *Leptorhynchoides* suggests that it may represent a primitive genus and should be singled out for intensive study. The association of Palaeacantho-

cephala with these ancient types of fish may also indicate that this order is the most primitive of the Acanthocephala.

CONCLUSIONS

We have not come across any convincing evidence to indicate that the Acanthocephala should not be recognized as a separate phylum within the loosely defined superphylum of Aschelminthes. The Acanthocephala may have arisen from a small meiofaunal marine priapulid which arose by progenesis. Alternatively, this meiofaunal worm may have been ancestral to both Acanthocephala and Priapulida. Fossil evidence from a mid-Cambrian locality strongly suggests priapulids flourished at that time and that one species, *Ancalagon minor*, had certain anatomical features comparable with those of both hypothetical proto-acanthocephalans and living forms.

The earliest Acanthocephala or their ancestors probably existed at the same time as an extensive marine arthropod fauna. Aquatic crustaceans and terrestrial insects are major intermediate hosts of living acanthocephalans, and at generic level teleosts provide most of the definitive hosts. Both types of host, and paratenic hosts where present, acquire their acanthocephalans through feeding. It is suggested tentatively that the first Acanthocephala arose as parasites of arthropods only, but the development of vertebrate predator — arthropod prey associations led to the formation of the existing life cycle. The Palaeacanthocephala may be the most primitive order, but in general acanthocephalan phylogeny remains extremely speculative. A cladistic approach may provide new insights.

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DISCUSSION

COMBES. — With Digenea and Cestoda some of us support the hypothesis that the invertebrates are the first "historical" hosts because specificity is narrower at their level than that of the vertebrate host. Could you comment on the Acanthocephala ?

CROMPTON. — We know too few species well enough to even speculate on this.

CHABAUD. — Pour les Nématodes, le phénomène est inverse de celui constaté chez les Digènes. Les travaux de M. Sprent sur les Ascarides de Serpents sont particulièrement démonstratifs. Il s'agit d'une pyramide alimentaire, sans aucune spécificité pour les premiers stades larvaires. A chaque stade du développement, le spectre des hôtes permettant la croissance se rétrécit et la femelle de l'Ascaride ne forme ses œufs que chez une seule espèce de Serpent.

En règle générale, il semble donc que l'hôte primordial (Mollusque pour le Digène, Vertébré pour le Nématode) est plus spécifique que l'hôte acquis secondairement.

EUZET. — Pour les Cestodes, la pyramide est la même que pour les Nématodes : le dernier hôte est le plus spécifique. Par exemple, chez les Tétrarhynques, les larves se trouvent dans plusieurs Téléostéens, les adultes dans un seul Sélacien.

COMBES. — Il s'agit de la spécificité au niveau du procercoïde.

EUZET. — La spécificité du procercoïde n'est en général pas connue. Chez certains *Triaenophorus*, le procercoïde peut parasiter différents Copépodes suivant la saison.

LLEWELLYN. — La spécificité varie avec l'époque de l'année. D'autre part, certains Cestodes sont spécifiques pour les hôtes intermédiaires, d'autres pas.

BURT. — Les Cestodes les plus primitifs s'opposent aux plus évolués. Chez les primitifs, la spécificité du 1er hôte est la plus forte ; chez les plus récents, il y a inversion du phénomène ; pour les Taenias, la spécificité est la même pour larves et adultes.

ADAMSON. — I was struck by the superficial similarity between the fossil Priapulids and the Acanthocephalids. What are the major differences between the groups that lead you to place them in separate orders ?

CROMPTON. — The structure of the reproductive tract in Acanthocephalids is quite different from that of any other group.

SPRENT. — Why did you choose crustaceans as the first hosts ? What percentage of known life histories of Acanthocephala involve Crustacea ? Do you consider that Crustacea ever acted as definitive hosts ?

CROMPTON. — Most Acanthocephala use Crustacea but I said arthropods and *not* Crustacea.

LAVOCAT. — Comment les Acanthocéphales seraient-ils devenus adultes chez des Vertébrés au Cambrien ?

CROMPTON. — Ils auraient été d'abord parasites de Crustacés au Dévonien, puis des premiers Poissons. L'hôte Vertébré est venu après l'hôte Invertébré.

SCHAD. — Is anything known about the chemistry of the hooks of the Acanthocephala and the priapulids that would indicate a relationship ?

CROMPTON. — No.

INGLIS. — I will comment on two things, the first is specific to Dr. Crompton's thesis, and the second is general to the Colloque.

Firstly, and very briefly, if Acanthocephala arose from Priapulids, they are both either Coelomate or Pseudocoelomate. The general view, at present, is in disagreement and is that Priapulids are Coelomate and Acanthocephala are not. It is not easy to establish the condition with rigour but I would not be surprised if the Acanthocephala were Coelomate.

Secondly, I suggest that this meeting would do a service to Parasitology if we established what we mean when we say that a species or group of species is very (= highly) host specific, slightly host specific, not specific, etc... and if we also agreed to always give some indication of the evidence on which the claim is based. For example, is it from taxonomic studies of a genus, family, order, etc... or one experimental life cycle, or three life cycles in a superfamily of three hundred species. We seem to be giving equal weight to all these evidences to-day and are, consequently, concealing the fragility of much of the argument.

Finally, I believe that we must also recognize that much of the argument depends on thinking that a genus of Nematodes (for example) is somehow the same as a genus of Mammals or Birds or Crustacea. This is not, I think, true since I suspect that a genus of Nematodes is probably equivalent to a family of Birds or Mammals while an order, such as the Primates equates to a superfamily, or less, of most Invertebrates. The question is not simply academic since it seems to be the basis for some, possibly most (?), of the arguments that parasites are, or may be, more narrowly specific to an Invertebrate intermediate host than to their Vertebrate final host.

ANDERSON. — Do fossil priapulids differ greatly from modern species ?

CROMPTON. — Apparently little.