Description of Larval Acanthocephalus parksidei Amin, 1975 (Acanthocephala: Echinorhynchidae) from Its Isopod Intermediate Host

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ABSTRACT: Stages of larval Acanthocephalus parksidei Amin, 1975 were identified and sequentially traced from natural infections in the isopod intermediate host, Caecidotea militaris (Hay, 1878), in the Pike River, southeastern Wisconsin. Acanthor structures and their fate were delineated. Young acanthellae completed their development with the formation of proboscis receptacle, proboscis primordia, and early elements of genital primordia that were not yet assignable to either sex. Further organogenesis in subsequent stages of male and female acanthellae was not, however, correlated with time of giant subcuticular nuclei fragmentation. Acanthellae and/or cystacanths of either sex appear precocious and have actively eversible proboscis and bursa. This is the first account of larval development for any species of genus Acanthocephalus from North America.

The early monographs by European workers (e.g., Linstow, 1872; Leuckart, 1876; Hamann, 1891; Kaiser, 1893) contained detailed descriptions of developmental stages of various acanthocephalans including Acanthocephalus anguillae, A. clavula, A. lucii, and A. ranae. More recent accounts were presented by Rojanapaibul (1976, on A. clavula), Hine (1977, on A. galaxii), Kurbanov (1978, on A. ranae), Andryuk (1979a, b on A. anguillae and A. lucii), and Brattey (1980, on A. lucii). This is the first description of larval stages of any member of the genus Acanthocephalus in North America.

Materials and Methods

The material described in this report includes about 240 specimens obtained from natural infections of the isopod Caecidotea militaris (Hay, 1878) from the Pike River, southeastern Wisconsin, between May 1976 and May 1977 (as reported by Amin et al., 1980), as well as about 140 other specimens obtained during summer 1978. Isopods were refrigerated in stream water until dissected shortly after collection. Obtained A. parksidei larvae were refrigerated overnight in distilled water, then fixed in chilled AFA, stained in Mayer’s acid carmine, cleared in terpineol, and whole-mounted in Canada balsam.

Four major developmental stages were recognized and are herein defined: (1) acanthor: with no primordia; (2) young acanthella: with primordia of organ systems except reproductive; (3) male and female acanthellae: with genital primordia of each sex recognizable, proboscis apparatus not fully developed, body wall soft and delicate; (4) cystacanth: with all adult structures present, proboscis apparatus functional, body wall tough and leathery.

All line drawings were made with the aid of a microprojector. All measurements are in micrometers. Structures labelled proboscis retractor occasionally also include uncinogenous bands that were less distinct and thus not drawn. Some of the structures common to both sexes were more elaborately demonstrated in males or females to avoid duplication. The following abbreviations are used in Figures 1–34:

A, acanthor; AN, apical nucleus; AS, acanthor spine; Br, brain; BrP, brain
primordium; Bu, bursa; BuP, bursa primordium; BWMP, body-wall musculature primordia; C, cortex; CG, cement gland; CGD, cement-gland duct; CGP, cement-gland primordium; E, entoblast; EN, entoblast nuclei; FM, fertilization membrane; FNLR, fragmented nuclei of lemnisci ring; FSN, fragmented subcuticular nucleus; GG, genital ganglion; GP, genital primordium; GPo, genital pore; GSN, giant subcuticular nucleus; HP, hook primordium; IM, inner membrane; IPr, invaginated proboscis; L, lemniscus; LSa, ligament sac; LSt, ligament strand; NLR, nuclei of lemnisci ring; NNR, nuclei of neck retractor; NPrRt, nucleus of proboscis retractor; NR, neck retractor; NRPr, nuclear ring of proboscis; NRcW, nuclei of receptacle wall; NRWM, nuclei of receptacle wall musculature; OB, ovarian ball; OM, outer membrane; Pe, penis; PBC, pockets of bursal cap; Pr, proboscis; PrN, proboscis nuclei; PrP, proboscis primordium; PrRe, proboscis receptacle; PrRt, proboscis retractor; PUC, pouch of urogenital canal; R, retinaculum; SN, subcuticular nuclei; SP, Saefftigen's pouch; SV, seminal vesicle; T, testis; TP, testicular primordium; U, uterus; UB, uterine bell; UBP, uterine bell primordium; UP, uterus primordium; V, vagina; VD, vas deferens; VE, vas efferens; VP, vagina primordium.

Results and Discussion

The acanthor

The spindle-shaped, blunt-ended, shelled acanthors (may also be referred to as eggs) were 64–70 long (N = 7). Each was surrounded by four membranes and included the acanthor spines, the entoblast, and a number of subcuticular nuclei that appeared to be more numerous anteriorly than posteriorly (Fig. 1). The latter eventually become the giant subcuticular nuclei, giving rise to adult cortical structures. The number and origin of the cortical nuclei appear to be species specific. The pattern described for Polymorphus minutus (14 anterior and 10 posterior cortical nuclei originating from nuclei that always remain outside the entoblast) by Nicholas and Hynes (1963a) appears to be comparable to that of A. parksiei. The entoblast nuclei, destined to give rise to most adult organs and the body-wall musculature, were compacted in two distinct masses.

The young acanthella

Early acanthellae associated with the host gut were not observed. The least developed acanthella obtained (Fig. 2) was a 350 long teardrop-shaped specimen. It included a number of developing giant subcuticular nuclei, entoblast nuclei, and protoplasmic strands and was surrounded, like all subsequent stages, with a thin capsule membrane. The origin of the latter could not be determined. Wansoan and Nickol (1973) reviewed the literature on the envelope surrounding larval acanthocephalans.

The subsequent stage is formed by the growth and elongation of the entoblast nuclei nearly filling the cortical area and pushing the now-enlarged giant subcuticular nuclei to the periphery. The outermost layer of the entoblast nuclei has now formed two layers of myoblast nuclei, which make up the primordia of body-wall musculature (Fig. 3). The anterior part of the entoblast has begun to differentiate, with the giant subcuticular nuclei assuming near-cortical position and the apical nuclei more clearly recognizable.
Figures 1–10. Shelled acanthor, young, and male acanthellae of *Acanthocephalus parksidei*. 1. Acanthor, from within isopod gut (68 μm long). 2–6. Young acanthellae showing progressive organogenesis (350, 476, 392, 588, and 784, respectively). 7–10. Male acanthellae showing successive stages of development of reproductive system and of proboscis apparatus (630, 490, 700, and 728). Value of scale: 50 (Fig. 1), 200 (Figs. 2–10).
As the giant subcuticular nuclei continue to grow, the first differentiated entoblastic structure, the proboscis receptacle, takes shape (Fig. 4), with the enclosed brain primordium and proboscis retractor becoming evident. With the continued growth and elongation of entoblastic material, the giant subcuticular nuclei become less rounded and the proboscis primordium becomes more evident. The latter takes the form of anterior proboscis nuclei, posterior nuclear ring connected by uncinogenous bands overlapping the proboscis retractor (Figs. 5, 6). In the largest young acanthella observed (784 long, Fig. 6), the giant subcuticular nuclei assumed near-symmetrical bilateral organization.

The male acanthella

The smallest male acanthella observed was 490 long (Fig. 8). The posterior group of entoblast cells proliferates into two testicular fields (primordia), the first structure of the male reproductive system to become apparent (Fig. 7). Up to 22 giant subcuticular nuclei were observed (Fig. 7). Hine (1977) observed only 12 giant nuclei, in pairs, in A. galaxii. In A. anguillae, A. ranae, and A. lucii, at least 30, 31, and 18 were evident (Leuckart, 1876, fig. 387b; Kurbanov, 1978, fig. 2; Andryuk, 1979b, fig. 2a, respectively). Leptorhynchoides thecatus, Echinorhynchus lageniformis, and Polymorphus minutus had 14, 18, and 24 (DeGiusti, 1949; Olson and Pratt, 1971; Nicholas and Hynes, 1963b, respectively). As the testicular fields become more distinct and their early side-by-side arrangement evident, the bursa primordium followed by elements of cement-gland primordia starts appearing (Fig. 8). Subsequently, elements of the reproductive system become more independently discernible, e.g., cement-gland primordia, as well as components of the proboscis and the brain (Fig. 9).

The subsequent stage (Fig. 10), observed in acanthella of about the same size as in the previous stage (Fig. 9), is characterized by fragmenting giant subcuticular nuclei, more oblong body form, and more developed reproductive system and proboscis apparatus (Fig. 10). The proboscis develops in an inverted position, as is typical in Palaeacanthocephala, and later everts, then reinverts in the cystacanth stage. In Echinorhynchus truttae, however, the proboscis appears to develop in the everted position (Awachie, 1966). Further elongation of body, differentiation of reproductive system, and fragmentation of the giant subcuticular nuclei correspond with the formation of an anterior constriction girdled by the nuclei of the lemnisci ring at a level dividing the body into presoma and soma (Fig. 11). The giant subcuticular nuclei that eventually become the nuclei of the lemnisci ring mark that same location in earlier developmental stages, though somewhat less conspicuously. All the structures evident in the previous stage (Fig. 11) are differentiated further in these longer acanthella (Fig. 12), particularly the cement-gland primordia and the pockets of the bursal cap.

Significant transformations marking the next stage (Fig. 13) include the almost complete fragmentation of the giant subcuticular nuclei, eversion of the proboscis, enlargement and near-complete formation of the bursa and associated structures, formation of the genital ganglion, and the delineation of cement-gland ducts. A closer look at the anterior end of an acanthella at the same stage of development (Fig. 14) shows that hook bulges (primordia) have not yet formed on the uncinogenous bands. Detail of the reproductive system of one of the largest acanthella recovered (1,820; Fig. 15) shows that all the reproductive structures of adult males are now present, complete with vas efferens and vas deferens.

The female acanthella

The sequence of development of proboscis receptacle and proboscis was comparable to that of male acanthellae. The smallest female acanthella recovered (714 long) is illustrated in Figure 20. This figure shows that fragmentation of the giant
subcuticular nuclei might proceed quite early, even before the genital primordia begin differentiating. Detail of the anterior end of a female acanthella (896 long) at a comparable stage of development is shown in Figure 21; note neck retractor and nucleus of proboscis retractor and detail of proboscis receptacle.

The next three stages (Figs. 22–24) are of three progressively more mature acanthellae, as judged by the differentiating proboscis and genital primordia, respectively. In these three acanthellae, the giant subcuticular nuclei have barely begun to fragment, if at all. It thus appears that much of the organ-system primordia, e.g., reproductive and proboscis apparatus, may begin and proceed with differentiation (all the way to the breaking of the ovary into ovarian balls, Fig. 24) before the giant subcuticular nuclei begin to fragment. The opposite is also true (Fig. 20). It is thus suggested that the rate of differentiation and/or growth of the above structures is not parallel and is not essentially correlated with events affecting giant-nuclei fragmentation. The same was observed in developing male acanthellae, though less dramatically.

A developmental stage with a conspicuous ovary, which would have preceded the stage in Figure 24, was not observed. The specimen in Figure 25, although significantly larger than that in Figure 24, demonstrates either delayed formation of ovarian balls and development of proboscis primordium or somatic acceleration. The acanthella in Figure 26 (1,932 long) is twice as large as that in Figure 24 (980 long), but its proboscis primordium is less well developed.

In many acanthocephalans, the ovary does not develop sufficiently to break into ovarian balls while still in the intermediate host (Schmidt and Olsen, 1964). In A. parksidei, this advanced stage of development is attained as early as in an intermediate acanthella stage. This precocious state was previously observed in other acanthocephalans, e.g., Prosthorhynchus formosus and Echinorhynchus truttae, by Schmidt and Olsen (1964) and Awachie (1966), respectively. Such conditions, particularly when associated with related developments, e.g., in bursa and proboscis (see following section on cystacanths), might be conducive to rapid growth and early fertilization once in the final host.

The anterior parts of two 3,150 and 2,240 long acanthellae (Figs. 27, 28, respectively) show two stages of hook-primordia development in the evertible proboscis that occur after the giant subcuticular nuclei are fragmented. Note the neck retractor and the fragmented nuclei of lemnisci ring at the presoma–soma level (Fig. 28). The subsequent stage is characterized by marked elongation of body (Fig. 29) and complete differentiation of the reproductive system (Fig. 30). The last structures to form in the female acanthella are the lemnisci. These start out as two small inpocketings of the body wall directly behind the region of the lemnisci ring (Fig. 31).

The male cystacanth

In early male cystacanths (Fig. 16), the development of the proboscis apparatus, brain, and reproductive system (Fig. 17) is completed. Reproductive structures, however, remain tightly confined within the ligament sac. The proboscis has now reinverted, the bursa is eversible, and the body wall becomes more tough and opaque. The fully grown cystacanth (Fig. 18) is indistinguishable from adult males; the proboscis is eversible and the reproductive system appears to be functional. This precocious state appears to be analogous to the early development
Figures 31–34. Female acanthella and cystacanth of Acanthocephalus parksidei. 31. Anterior part of acanthella (2,800 μm long). 32. Fully developed cystacanth (9,058). 33, 34. Anterior part and reproductive system of cystacanth in Figure 32. Value of scale: 300 (Figs. 31–34).

of ovarian balls in females. Acanthocephalans typically complete their sexual development in the final host, and larval proboscis and bursa do not usually evert in the intermediate host. These events might be correlated. Cystacanths and acanthellae with actively eversible proboscis and bursa appear to be found mostly in precocious species, e.g., A. parksidei and E. truttae, as described by Amin (this paper) and Awachie (1966), respectively.

Of 47 male cystacanths studied (like other specimens, all were refrigerated in distilled water overnight before fixing), 13% and 38% had fully and partially evaginated proboscises, respectively. Seventy percent had six cement glands each and 30% had four, five, seven, or eight. Lobed, branched, or multiple lemnisci (three or four) were noted in 22% and subequal lemnisci in 8% of the specimens. Only one spindle-shaped, monorchid male was observed. Another specimen was short and robust with the testes filling practically all the body-cavity space. Another slender cystacanth had two large body-wall bulges extending around its "enormous testes." The contorted and abnormal proboscis hooks observed in the monorchid cystacanth (Fig. 19) might have resulted from improper inversion of hooks as the proboscis reinveted. A similar observation was made in P. formosus by Schmidt and Olsen (1964). The body wall of three specimens had blisterlike swellings, as described in adult A. parksidei by Amin (1975) and Echinorhynchus salmonis by Amin and Redlin (1980), resulting from glycogen-phospholipid metabolic dysfunction (Lester and Wright, 1978).

The female cystacanth

Like the male cystacanth, the fully grown female cystacanth (Fig. 32) is indistinguishable from young adults. It has a functional proboscis apparatus, fully
differentiated tegument (Fig. 33), and a fully developed reproductive system (Fig. 34) that lacks many of the nucleated elements characterizing the earlier stages.

Of 78 female cystacanths studied, 19% and 49% had fully and partially evaginated proboscises, respectively. Twenty percent had lobed, branched, or multiple (3, 4, or 5) lemnisci. Subequal lemnisci were less common, and no specimens with body-wall blisters were observed.

Specimens


Conclusions

The larval development of A. parksdei in Caecidotea militaris is rather similar to that reported for other species of the genus Acanthocephalus, with minor variations. The cortex is considerably thicker, particularly at the terminal regions in the earlier stages of A. anguillae (Leuckart, 1876, fig. 387a, b) compared to those of A. parksdei. The very brief description (with no illustrations) of the developmental stages of A. clavula in Asellus meridianus observed weekly by Rojanapaibul (1976) varies in some minor details from that for A. parksdei (e.g., the lemnisci differentiated earlier in A. clavula). Most notably, however, ovarian-ball formation and bursa eversion in A. clavula occurred only at the end of the first week post-infection of the definitive fish host. Only a few disjunct stages in the development of A. galaxii larvae in Paracalliope fluviatilis have been very briefly described; no early development or proboscis/bursa eversions were noted, and the number of giant nuclei was 12. The development of A. anguillae and A. lucii in A. aquaticus is more similar to that of A. parksdei. However, precocious development was not evident in the two European species, and early eversion of proboscis and bursa was not demonstrated (Andryuk, 1979a, b). Sexual maturity of A. anguillae and A. lucii was attained in fish intestine 15 and 21 days after infection, respectively (Andryuk, 1979a, b). Brattey's (1980) abstract, however, refers to sexually fully developed A. lucii in A. aquaticus, with copulation occurring less than 24 hr at 20°C in the definitive host.

The described pattern of development in A. parksdei is also comparable to patterns described for other palaeacanthocephalans, e.g., L. thecatus by DeGuisti (1949) and Uznanski and Nickol (1980), E. lageniformis by Olson and Pratt (1971), and P. minutus by Nicholas and Hynes (1963b); specific differences are noted in previous sections.

Two significant features appear to distinguish the developmental pattern of A. parksdei. First, the differentiations of the proboscis apparatus and the reproductive system do not appear to proceed in a parallel fashion and are not correlated with the pattern of giant subcuticular nuclei fragmentation, which may begin before the genital primordia start to differentiate or much later in development (after ovarian balls break). It is thus concluded that factors affecting differentiation and growth of various structures might act independently from each other as well as from those regulating fragmentation of the giant subcuticular
nuclei. This observation has not been previously reported. Second, the precious condition observed in the development of *A. parksidei* appears to be correlated with the early eversibility of the proboscis of both sexes and male bursa while still in the intermediate host. Under these conditions, rapid growth and early fertilization in the definitive host might be expected.

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**Literature Cited**


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