FIRST RECORD OF ACANTHOCEPHALA IN MARINE COPEPODS

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ABSTRACT

Late cystacanth stages were discovered in the haemocoel of the marine benthic harpacticoid *Halectinosoma herdmani* (T. & A. Scott, 1896) (Copepoda: Ectinosomatidae) collected off La Rochelle, France. This represents the first record of Acanthocephala infesting marine copepods. On the basis of the hook formula on the proboscis and the spine pattern on the trunk, the parasites were identified as juveniles of *Acanthogyrus* (*Acanthosentis*) *lizae* Orecchia, Paggi & Radujkovic, 1988 (Eoacanthocephala: Gyracanthocephala: Quadrigyridae) which utilizes the golden grey mullet *Liza aurata* (Risso, 1810) as the definitive host. The literature on acanthocephalans utilizing copepods as intermediate hosts is reviewed and some morphological details of both the cystacanth and host copepod are presented using differential interference contrast and scanning electron microscopy. *Halectinosoma porosum* Wells, 1967 from Inhaca Island (Mozambique) is formally transferred to *Ectinosoma* Boeck, 1865 as *E. porosum* (Wells, 1967) comb. nov.

INTRODUCTION

The Acanthocephala is a small but important phylum of endoparasitic helminths. They live as adults in the alimentary tract of both poikilothermic and homeothermic vertebrates and require an arthropod as first intermediate host. The latter is either a crustacean in aquatic species or an insect or isopod (or rarely a myriapod; e.g. Crites 1964, Fahnestock 1985) in terrestrial species.

Although relatively few life cycles have been elucidated, they seem to take a similar course in all acanthocephalans studied. Eggs discharged through the efferent duct of the adult female worm in the faeces of the definitive host contain a partially developed acanthor. On ingestion by a susceptible host arthropod the acanthor is liberated from its surrounding envelopes, completes its development and actively penetrates the intestinal wall of the intermediate host. Within the haemocoel the acanthor further differentiates to become an

acanthella and eventually an inactive juvenile enclosed within a sheath. This juvenile, commonly referred to as the cystacanth, is infective to the definitive vertebrate host. The life cycle may be prolonged by the inclusion of obligatory or facultative transport or paratenic hosts.

Members of the Palaeacanthocephala and Eoacanthocephala are known to utilize crustaceans as intermediate hosts. Most life cycles known involve either amphipods, ostracods, isopods or decapods, although a few species may develop in mysids and copepods. With the exception of the freshwater harpacticoid *Cletocamptus deitersi* (Richard, 1897), the few copepod species known to serve as intermediate hosts for acanthocephalans are all limnetic zooplankters.

During the course of a survey of the marine benthic harpacticoids from soft sediments near La Rochelle in the Golfe de Gascogne in the late 1960s, one of us (P.B.) discovered three specimens of the harpacticoid *Halectinosoma herdmani* (T. & A. Scott, 1896) (Ectinosomatidae) that were infested by fully developed cystacanth stages. Though juvenile acanthocephalans have been recorded in various marine crustaceans such as shore crabs, hermit crabs and amphipods, the present find of an acanthocephalan stage in a marine harpacticoid is the first for the entire phylum (Ho & Perkins 1985, Buron & Golvan 1986).

MATERIAL AND METHODS

Copepods were examined in lactophenol and illustrations have been prepared using a camera lucida on a Zeiss Axioskop differential interference contrast microscope. The descriptive terminology for body and appendage morphology is adopted from Huys & Boxshall (1991). Infested copepods were examined with a Hitachi S-800 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter-coated with palladium.

IDENTIFICATION OF ACANTHOCEPHALAN

Material examined. Two adult ♀♀ of *Halectinosoma herdmani* collected on intertidal mudflat at Châtelaillon and another ♀ at Aytré, near La Rochelle, France; all specimens infested by a single cystacanth stage each; leg. P. Bodin.

In all three host specimens the cystacanth had its proboscis everted showing the full complement of hooks (Figs 1B, 2). It is however likely that at the time of collection the cystacanths had already entered a quiescent state during which the proboscis is entirely retracted. Once fully developed the cystacanth serves as a resting stage, seldom dying within the host but surviving as long as its host. It can be stated with reasonable assurance that evagination of the proboscis and subsequent rupturing of the host's integument have been induced
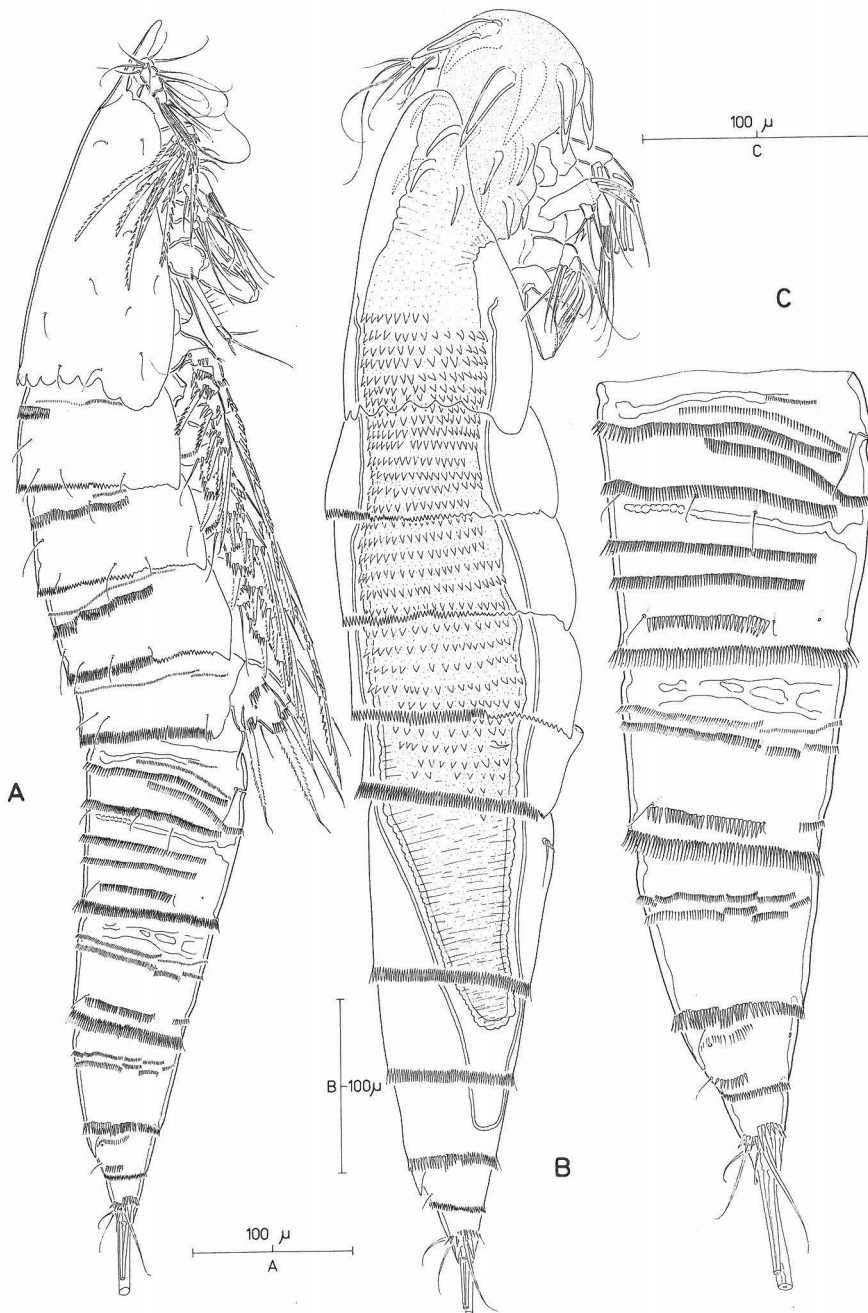
Fig. 1. *Halectinosoma herdmani* (T. & A. Scott, 1896). (A) Adult female, lateral view. (B) Adult female infested by cystacanth of *Acanthogyrus* (*Acanthosentis*) *lizae*. (C) Female urosome (excluding P5-bearing somite), lateral view.

by fixation and/or osmotic shock of the host harpacticoids. Keppner (1974) reported sensitivity to osmotic pressure in *Paulisentis missouriensis* Keppner, 1974 and demonstrated how in cystacanth stages evagination of the proboscis can be artificially induced by exposing them to tapwater.

Many acanthocephalan larvae can affect intermediate host growth and development as they grow and develop (see Kennedy (1985) for review) and some of them can render their hosts completely sterile. Careful examination of the three infested harpacticoid specimens revealed no trace of ovarian tissue whereas uninfected females from the same site (and probably same cohort) showed a fully developed reproductive system. Acanthocephalans of many species are surrounded by a thin, transparent envelope as they develop in the haemocoel of the arthropod intermediate host. Such a membranous coat was clearly present in all infested individuals of *H. herdmani* (Fig. 1B). Since copepod haemocoel space is obviously a limiting factor in the growth of the parasite it can be assumed from the size of the cystacanth (Fig. 1B) that it had almost completed its development.

The cystacanth which is essentially a juvenile differing from the adult only in size and sexual development could be identified to species on the basis of the number and arrangement of the hooks and spines on the proboscis and trunk. Following Golvan's (1959) classification of the Eoacanthocephala and Amin's (1987) key to the families of the Acanthocephala the species keys out to the Quadrigyridae, the only family in the order Gyracanthocephala which are parasites of freshwater and marine fishes characterized by a trunk that is entirely or only anteriorly spined. The presence of numerous complete circles of spines on the trunk clearly identifies the parasite as a representative of the subfamily Pallisentinae. The hook formula of the proboscis comprising six spiral rows of three hooks (Figs 1B, 2) unequivocally places the species in the genus *Acanthogyrus* [subgenus *Acanthosentis*].

Amin (1985) lists 26 valid species of *Acanthogyrus* (*Acanthosentis*) and another 9 species have been described since (Agrawal & Singh 1982, Gupta & Fatma 1986, Chowman et al. 1987, 1988, Farooqi & Sirikanchana 1987, Mashego 1988, Orecchia et al. 1988, Khan & Bilqees 1990). The majority of these species complete their life cycle in freshwater habitats and usually utilize members of the Cichlidae (*Tilapia* spp.) or Cyprinidae as the definitive host. Exceptions include *A.* (*A.*) *acanthuri* (Cable & Quick, 1954) found in acanthurid hosts off the Puerto Rico coast (Cable & Quick 1954), *A.* (*A.*) *lizae* Orecchia, Paggi & Radujkovic, 1988 found in a mullet in the Adriatic (Orecchia et al. 1988) and *Quadrigyrus polyspinosus* Li Minmin, 1984 which was also recorded from a mugilid in Bohai Gulf (China) and according to Orecchia et al. (1984) should be placed in *Acanthogyrus* (*Acanthosentis*). Our material is clearly referable to the Mediterranean species *A.* (*A.*) *lizae* which was discovered in the intestine of the mugilid *Liza aurata* (Risso, 1810). Complete agreement exists in the relative dimensions of the various hooks on the proboscis. According to Orecchia
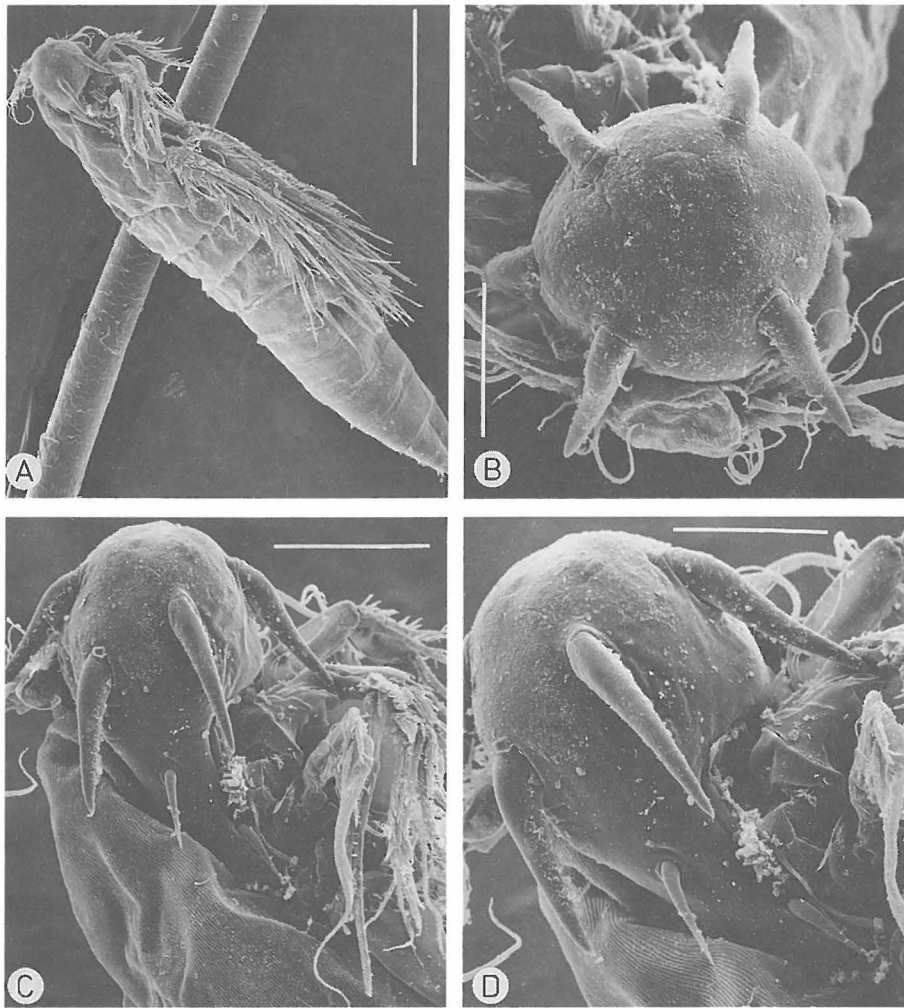
Fig. 2. SEM micrographs. (A) *Halectinosoma herdmani* ♀ infested by acanthor. Scale bar: 150 µm. (B) Proboscis of cystacanth, frontal view. Scale bar: 30 µm. (C) Lateral view of cystacanth protruding from host's cephalothorax. Scale bar: 45 µm. (D) Same, close-up showing full complement of hooks. Scale bar: 30 µm.

et al. (1988) the hooks range in size between 50-60 µm for the distal circle, 35-40 µm for the middle circle and 20-30 µm for the proximal one; in our specimens the average hook length is 53 µm, 34 µm and 24 µm, respectively. Apart from two records in checklists (Radujkovic 1989, Radujkovic & Raibaut 1989) *A. (A.) lizae* has not been reported again and its intermediate host has thus far remained unidentified.
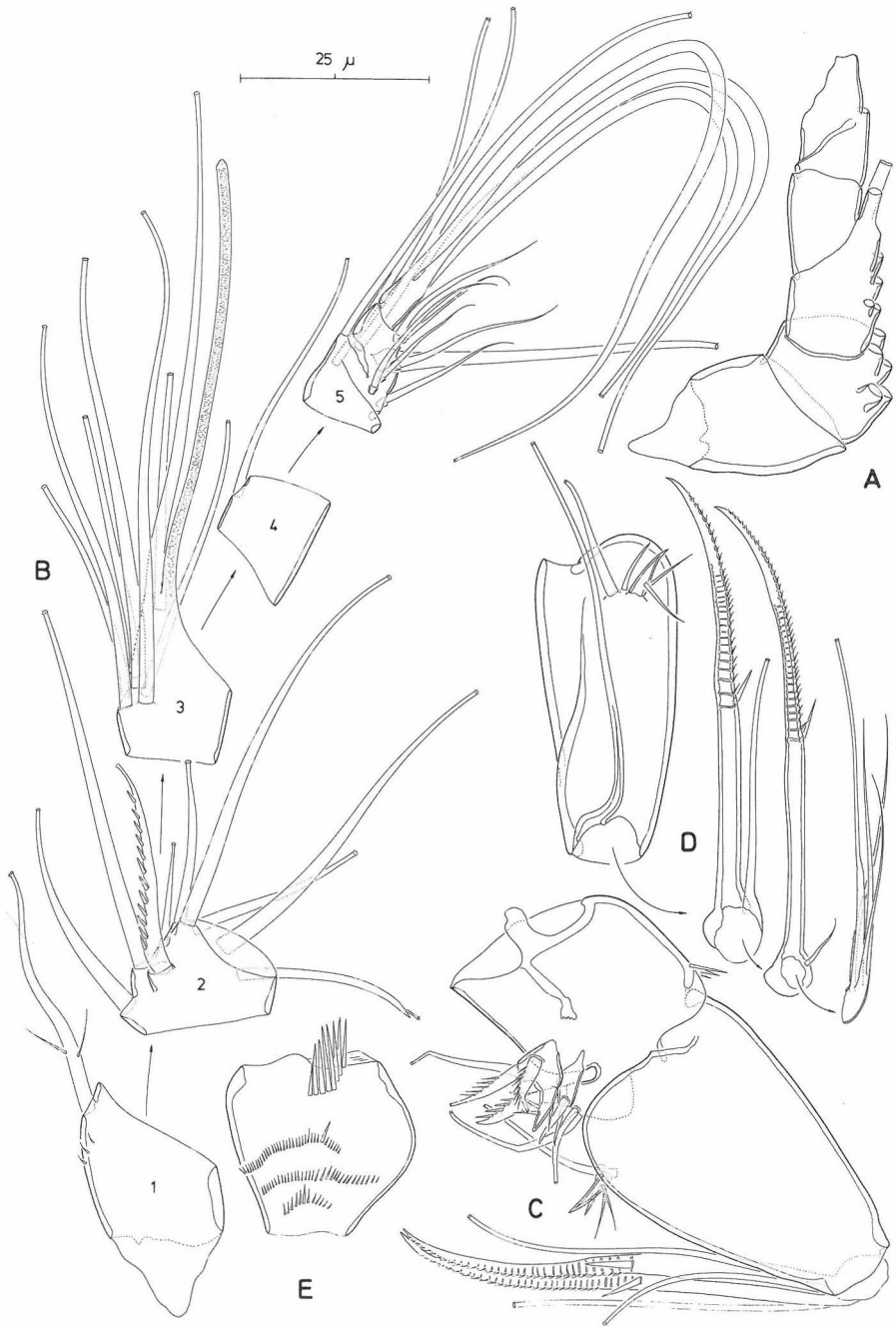
Fig. 3. *Halectinosoma herdmani.* (A) Antennule ♀ [armature omitted]. (B) Antennule ♀, showing setation elements on disarticulated segments. (C) Maxilla, lateral view. (D) Maxillary allobasis and endopod, disarticulated, anterior view. (E) Maxillary syncoxa, posterior view.

THE INTERMEDIATE HOST

Halectinosoma herdmani is the first marine copepod known to serve as interme-diate host for acanthocephalan helminths. Bodin (1970: 393), misled by the high numbers of kinorhynchs in virtually all samples taken at Châtelaillon, initially thought that the harpacticoids had "... avalé chacune un Kinorhynque (*Echinoderes*?): l'une l'avait ingurgité en commençant par la trompe, l'autre dans le sens inverse". In the specimen collected at Aytré (Fig. 1B) the cysta-canth was orientated with its presoma facing the host's cephalic region. Although cystacanth orientation inside the intermediate host would appear to be random in many acanthocephalan species, Wilson & Hubschman (1985) found a significant difference between the number of cystacanths directed anteriorly (66.2%) and those orientated posteriorly (33.8%) in the copepod's haemocoel.

The acanthocephalan reported here is the second helminth parasite to be recorded from harpacticoids of the genus *Halectinosoma* Lang, 1944. McClel-land (1982) tested the possibility that marine copepods may serve as interme-diate hosts of the anisakine nematode *Pseudoterranova decipiens* (Krabbe, 1878). Natural first hosts are marine crustaceans such as mysids, isopods and deca-pods, and second intermediate hosts are marine fish and squid which pass the infection on to the final host (seals and walruses) when eaten. Amongst the twelve species of harpacticoids, used in McClelland's (1982) infection experi-ments with freshly hatched larvae of *P. decipiens*, are two unidentified species of *Halectinosoma*. Both seem to be closely related to *H. neglectum* (Sars, 1904) and one of them is mistakenly labelled *Ameira longipes* Boeck, 1865 in his Fig. 4. *P. decipiens*, commonly called the "codworm", is a serious pathogen of various marine fish such as cod, plaice and smelt, and can cause anisakiasis in man by eating infected raw or pickled fish. The larvae mainly reduce the marketability of the fish because of the unappealing appearance they give to the flesh.

Morphological observations

H. herdmani was first reported from its type locality in the Firth of Forth (T. & A. Scott 1896) but according to the current literature assumes a wide boreo-mediterranean distribution with outliers in the Black Sea and Bay of Bengal. It is conceivable, however, that many of these records are incorrect as various undescribed, morphologically very close species are known to exist in north-west European waters (Clément & Moore, pers. comm.). Since a complete redescription of *H. herdmani* and its related species will be the purpose of a forthcoming paper (Clément & Moore in prep.), we have restricted our exam-ination to a number of morphological details that have been overlooked or misinterpreted in the past.

Perhaps the most distinctive feature of *H. herdmani* is the deeply sinuate pos-terior margin of the cephalothorax (Figs 1A, 5A-B). The wavy indented margin
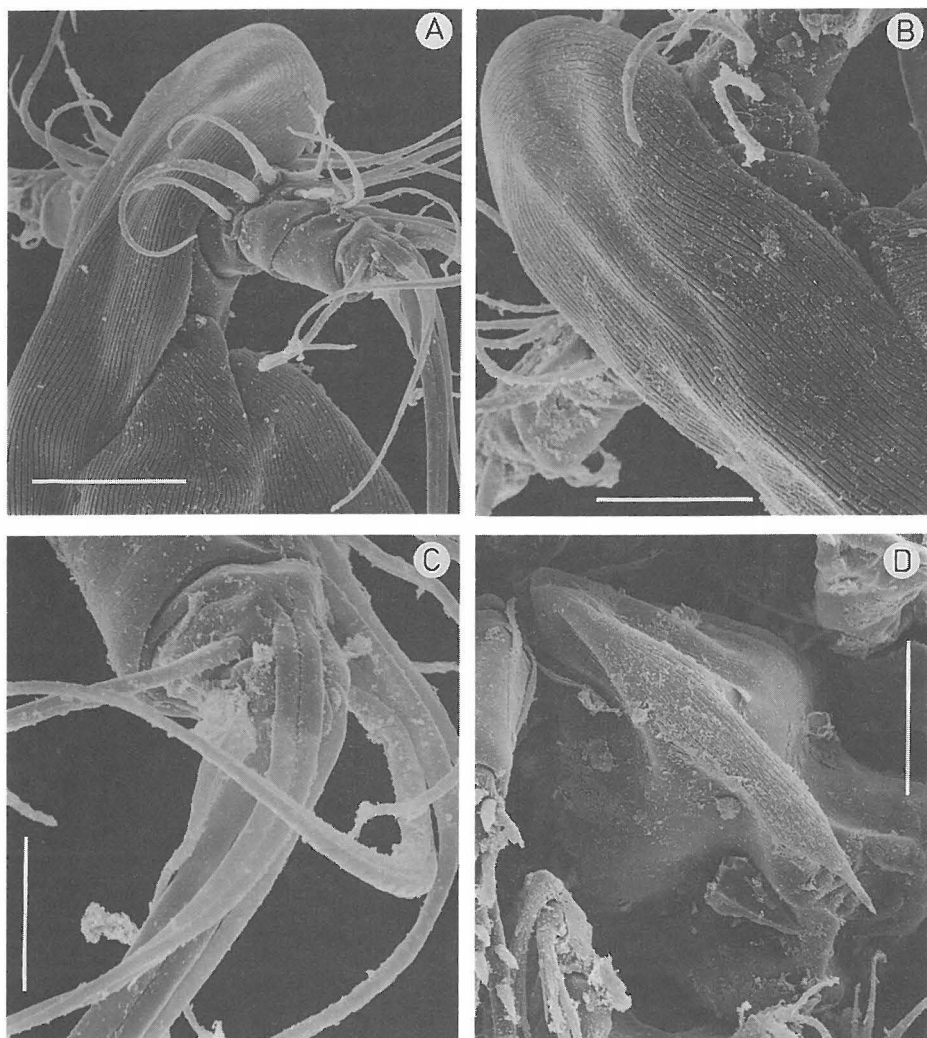
Fig. 4. SEM micrographs of *Halectinosoma herdmani*. (A) Rostrum and right antennule, lateral view. Scale bar: 20 µm. (B) Rostrum, detail showing longitudinal surface furrows. Scale bar: 15 µm. (C) Apical segment of antennule. Scale bar: 75 µm. (D) Labrum. Scale bar: 15 µm.

is present in both sexes and copepodids and is a very useful characteristic to identify this species without dissection. In the majority of species such as those related to *H. sarsi* (Boeck, 1865) the cephalothoracic margin is linear and smooth (Clément & Moore 1995). Another feature – not restricted to *H. herd-mani* – that is only clearly discernible using SEM is the peculiar surface sculpturing consisting of fine longitudinal furrows (Fig. 5C). These furrows are
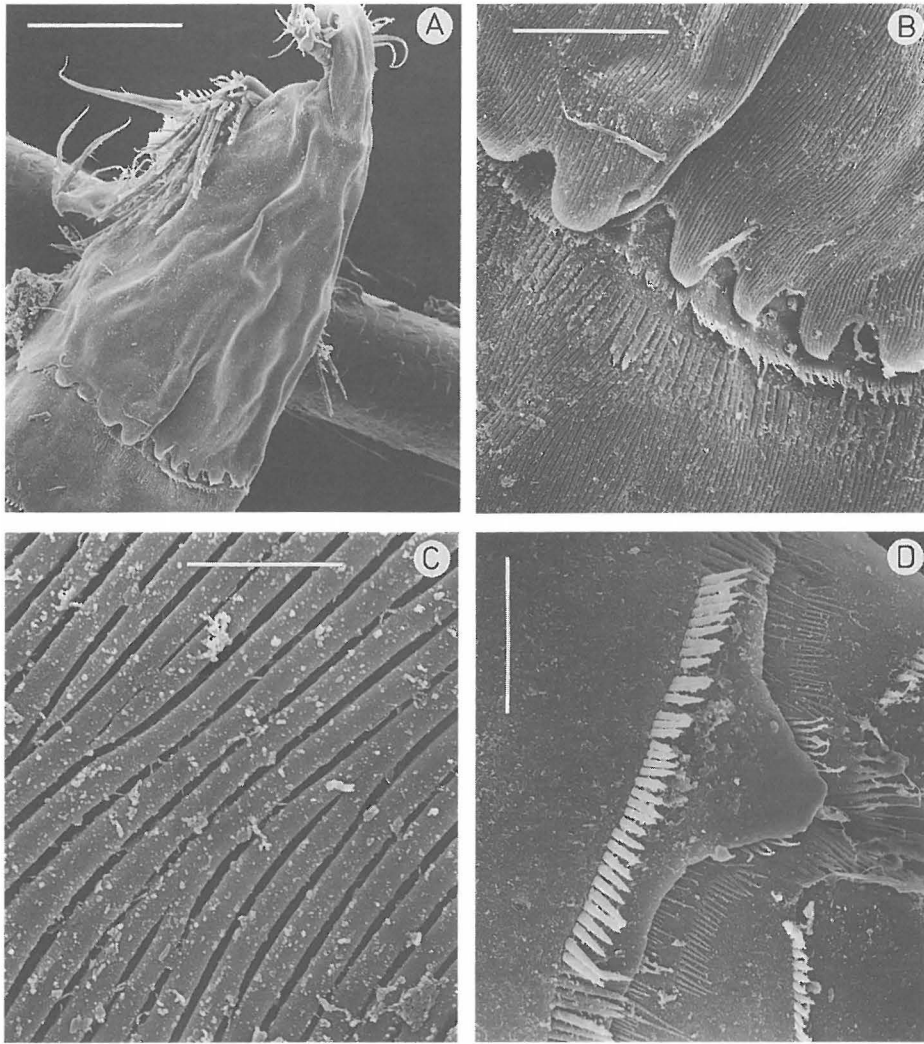
Fig. 5. SEM micrographs of *Halectinosoma herdmani*. (A) Cephalothorax, lateral view. Scale bar: 75 µm. (B) Detail of cephalothorax showing sinuate posterior margin and surface ornamentation of first pedigerous somite. Scale bar: 20 µm. (C) Detail of integumental furrows on first pedigerous somites. Scale bar: 3 µm. (D) Pseudoperculum, dorsal. Scale bar: 20 µm.

present on the cephalothorax and pedigerous somites (Fig. 5A-B) and extend onto the rostrum (Fig. 4A-B) and labrum (Fig. 4D). The integument of the abdominal somites is smooth and provided with a characteristic pattern of transverse spinule rows and finely incised hyaline frills (Fig. 1C). Females of *H. herdmani* can be readily distinguished by the form of the transverse chitinous rib marking internally the original segmentation of the genital double-somite

(Fig. 1C). The rib is almost continuous all around the ventral and lateral sides of the double-somite and consists of individualized thickenings dorsolaterally. The pseudoperculum is weakly developed and rounded (Fig. 5D). The presence of a pseudoperculum is a typical feature for harpacticoids that have a medially cleft anal somite (and therefore have lost the anal operculum), and represents a family diagnostic for the Paranannopidae and Ectinosomatidae. The absence of a medially cleft anal somite and pseudoperculum in *Halectinosoma* sp. 1 illustrated by Bodin (1970) on the basis of a single male from Châtelaillon suggests that the specimen was an immature female, most probably a CV stage of *H. herdmani*.

There exists some confusion over the segmentation of the female antennule in *Halectinosoma* Lang, 1944. Moore (1974) described the antennule of *H. pterinum* Moore, 1974 as 8-segmented and after re-examination of *H. herdmani* and *H. propinquum* (T. & A. Scott, 1896) [= *H. chrystalli* (T. Scott, 1894)] suggested an emendation of the generic diagnosis to include this character state as a generic diagnostic, considering previous observations of 5 or 6 segments as incorrect. The twelve species recently (re)described in great detail by Clément & Moore (1995) all have a 6-segmented antennule in the female, the apical segment being completely defined but largely concealed beneath the penultimate one. In *H. herdmani* the antennule is clearly 5-segmented (Fig. 4A) and the apical segment shows an incomplete surface suture along the posterior margin and a membranous insert anteriorly (Fig. 3A-B), probably indicating the plane of fusion between segments 5 and 6 expressed in *H. sarsi* and related species, and allowing for a certain degree of telescoping into the fourth segment (compare Fig. 4A, C). The acrothek on the apical segment consists of 3 long swollen setae which are distinctly fused at the base forming a minute pedestal which could be mistaken for an extra segment as in the original description of *H. pterinum*. General features of the setae on the antennule are their flaccid appearance and the presence of an apical pore on almost all of them (Fig. 3B). Similar setae have been observed on other cephalic appendages such as the mandible, maxillule and maxilla (Fig. 3C-D).

One of the characters that is traditionally used to distinguish *Halectinosoma* from *Pseudobradya* Sars, 1904 is the condensed maxillary endopod in the former. Although the endopod has retained its basic 3-segmented condition as in *Pseudobradya*, the precise arrangement of the various setae is difficult to unravel. According to Clément & Moore's (1995) description of the maxilla in *H. pseudosarsi*, the basis [here called allobasis following Huys & Boxshall (1991)] has 2 slender setae near the apex, and the first 2 segments of the endopod are each armed with a thick geniculate seta whereas the third segment has 1 lateral and 3 distal confluent setae. Our observations on *H. herdmani* revealed that the allobasis has only 1 distal seta, the proximal endopod segment has 1 long bare seta plus a geniculate one, the second segment a short bare seta and a geniculate one and the distal segment 4 setae (Fig. 3C-D).

The genus *Halectinosoma* is the largest in the family, currently encompassing 62 valid species. Although the detailed morphology is quite conservative within the genus some of its species have obviously been misplaced and should be referred to other genera. One of them is *H. porosum* Wells, 1967, originally described from Inhaca Island, Mozambique (Wells 1967). Species of *Ectinosoma* Boeck, 1865 can be identified on the basis of their quadratic caudal rami, the presence of large subrectangular integumental pores on the cephalothorax and free thoracic somites, and the presence of four marginal setae on the P5 exopod of both sexes. All these features are displayed by *H. porosum* and hence, we formally transfer the species to *Ectinosoma* as *E. porosum* (Wells, 1967) comb. nov.

COPEPODS AS INTERMEDIATE HOSTS FOR ACANTHOCEPHALA

Thus far copepods have been found to serve as intermediate hosts for members of the Eoacanthocephala only. All of them are exclusively freshwater inhabiting species belonging to the Calanoida (Diaptomidae), Cyclopoida (Cyclopidae) and Harpacticoida (Canthocamptidae). With the exception of Sharma & Wattal (1976), determination of the intermediate host was achieved by experimental infection of a range of potential freshwater crustaceans from the definitive host's habitat.

Calanoida

Hubschman (1983, 1987) and Wilson & Hubschman (1985) demonstrated that the limnetic calanoid *Skistodiaptomus pallidus* (Herrick, 1879) [as *Diaptomus pallidus*] serves as an intermediate host for *Tanaorhamphus longirostris* (Van Cleave, 1913) in Caesar Creek Lake, a man-made freshwater reservoir in southwestern Ohio. Adult *T. longirostris* (Neoechinorhynchidae) occur in the intestine of the gizzard shad *Dorosoma cepedianum* (Le Sueur, 1818) but immature specimens have been reported in at least four other freshwater fish species (Hubschman 1983, 1987). Cystacanths were found in both adult calanoids and their copepodid stages. Wilson & Hubschman (1985) suggested that shelled acanthors may remain dormant in the lake until the autumn or spring overturn, thus making them accessible to limnetic filter-feeders as other materials are known to circulate through the water column during this period. Hubschman (1983, 1987) examined also 15 other crustaceans (cladocerans, calanoids, cyclopoids) of the Caesar Creek Lake plankton community, but *S. pallidus* seemed to be the only carrier.

Cyclopoida

According to Cable & Dill (1967), *Tropocyclops prasinus* (Fischer, 1860) serves as an intermediate host for *Paulisentis fractus* Van Cleave & Bangham, 1949 in

northwestern Indiana. The definitive host for this helminth is the creek chub *Semotilus atromaculatus* (Mitchill, 1818), which is widely distributed east of the Rocky Mountains from Canada to the Gulf Coast. Cable & Dill (1967) reported that at 11 days development inside the copepod is complete, and by the 13th day the juvenile is infective for the creek chub. This is probably the shortest development time ever reported.

Keppner (1974) described a closely related species *Paulisentis missouriensis* from Missouri creek chubs, and suggested that *Acanthocyclops vernalis* (Fischer, 1853) [as *Cyclops vernalis*] is the most likely intermediate host. The life history of *P. missouriensis* is very similar to that of *P. fractus*. Developing juveniles in the cyclopoid are only infective for the definitive host by the 16th day, however, many factors could account for this time difference between the two related species (Keppner 1974).

Another neoechinorhynchid, *Pallisentis* (*Farzandia*) *nagpurensis* (Bhalerao, 1931), typically utilizes the cyclopid *Cyclops strenuus* Fischer, 1851 as an intermediate host in freshwater ponds in India (George & Nadakal 1973). The life cycle of *P.* (*F.*) *nagpurensis* involves the fish *Channa striatus* (Bloch, 1794) [as *Ophiocephalus striatus*] as the definitive host. Freshwater copepods form one of the major food items during the early development of *O. striatus*, but George & Nadakal (1973) also listed a number of facultative paratenic hosts including *Macropodus cupanus* (Cuvier & Valenciennes, 1831), *Oryzias melastigma* (McClelland, 1839) [as *Aplocheilus melastigma*], *Barbus* sp. and *Channa gachua* (Hamilton-Buchanan, 1822) [as *Ophiocephalus gachua*]. Additional paratenic hosts such as *Heteropneustes fossilis* (Bloch, 1797), *Rana tigerina* Daudin, 1802 and *Wallago attu* (Bloch, 1801) were reported by George & Nadakal (1984).

In the course of a survey of freshwater cyclopoids in perennial ponds in Delhi, Sharma & Wattal (1976) discovered several specimens of *Mesocyclops leuckarti* (Claus, 1857) infected with juvenile stages of *Acanthogyrus* (*Acanthosentis*) *dattai* (Podder, 1938). The known definitive hosts for *A.* (*A.*) *dattai* are two species of freshwater fish, *Puntius ticto* (Hamilton-Buchanan, 1822) [as *Barbus ticto*] and *P. sophore* (Hamilton-Buchanan, 1822) [as *Barbus stigma*] from West Bengal. Sharma & Wattal (1976) observed that the cystacanths could leave the cyclopoid anteriorly and suggested that they could survive as free stages in the water, presumably till they are picked up by the final host. This observation, however, is doubtful and requires confirmation.

Harpacticoida

The only previous record for this order is that of Dill (1975) who experimentally elucidated the life cycle of the neoechinorhynchid *Atactorhynchus verecundus* Chandler, 1935, and discovered that *Cletocamptus deitersi* (Canthocamptidae) is utilized as an intermediate host. Adults of *A. verecundus* are known to live in the alimentary tract of the sheepshead minnow *Cyprinodon variegatus*

Lacépède, 1803. The development in *C. deitersi* from ingestion of the egg to infective juvenile takes 14 days.

THE DEFINITIVE HOST

Orecchia et al. (1988) collected the host mugilids in the Adriatic somewhere in the Bay of Kotor (Montenegro) whereas the presumed intermediate copepod hosts came from the French Atlantic coast. *Liza aurata*, commonly called the golden grey mullet (mulet doré), assumes a wide distribution along the Atlantic coast from Natal (South Africa) northward to the British Isles and southern coasts of Norway and Sweden (but not the Baltic), and the whole of the Mediterranean and Black Sea (Ben-Tuvia 1986). Schools of *L. aurata* occur mostly in shallow water, especially coastal lagoons and reservoirs of varying salinity. They can enter the lower arms of rivers and estuaries for feeding but rarely move into freshwater. Their food consists of minute benthic organisms, detritus and occasionally insects and plankton. In view of the dietary preferences of the final host it is conceivable that epibenthic harpacticoids living in the upper cm of the sediment such as large-sized Ectinosomatidae are suitable intermediate hosts. The harpacticoid community of the intertidal mudflats at Châtelaillon is dominated by Cletodidae and Ectinosomatidae which together account for over 80% of the total abundance (Bodin 1970). The two most abundant species in this area are *Enhydrosoma propinquum* (Brady, 1880) (Cletodidae) and *Halectinosoma cooperatum* Bodin, Bodiou & Soyer, 1970 (Ectinosomatidae) which apparently are not utilized as intermediate hosts by *A.* (*A.*) *lizae*. *H. herdmani*, a congener of the second most abundant species, was found in much lower numbers except for restricted areas characterized by a higher sand content. The fact that only this harpacticoid (out of 46 species in total) was infested and moreover, at two different sites which are about 10 km apart, suggests that the intermediate host spectrum of *A.* (*A.*) *lizae* might well be restricted to *H. herdmani*.

At least in the Mediterranean Basin *Liza aurata* serves also as host for a number of parasitic copepods such as the poecilostomatoids *Ergasilus lizae* Krøyer, 1863 (Ergasilidae) and *Colobomatus mugilis* Raibaut, Caillet & Ben Hassine, 1978 (Philichthyidae), and the siphonostomatoids *Eubrachiella mugilis* Kabata, Raibaut & Ben Hassine, 1971 (Lernaeopodidae), *Caligus pageti* Russel, 1925 and *Pseudocaligus apodus* Brian, 1924 (Caligidae), *Lernanthropus mugilis* Brian, 1898 (Lernanthropidae) and *Lernaeenicus neglectus* Richiardi, 1877 (Pennellidae) (Raibaut & Ben Hassine 1977, Raibaut et al. 1978).

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