CHAPTER 3

The trichocoel: form and function of an unusual type of sensilla present in the carapace of certain cypridinid (Myodocopina) ostracods

(Prepared for Zoomorphology)

Summary Recent extensive trapping of crustaceans off the eastern Australian coast has revealed several species of Cohenia, a new genus of cypridinid ostracods. Species of Cohenia all appear to be scavengers and in places numerically dominate the scavenging guild on the eastern Australian continental shelf. They all possess an undescribed and unusual type of sensilla, which in most species are numerous, and are arranged in a single row parallel to, and near, the anterior, ventral and posterior margins of the external surface of each carapace valve. These sensilla are here termed trichocoels, and consist of an almost spherical cavity within the external carapace exoskeleton. The cavity lies at the base of a circular depression, and the circular depression of each trichocoel lies within a sunken channel on the exterior carapace surface. The opening of the trichocoel cavity bears a

plug, through which only the widened double base of a seta passes. This seta is very fine and stiff throughout most of its length, and exhibits no pores. For much of its length, this seta is orientated parallel to the carapace surface rather than the perpendicular, shielded within the sunken channel. The trichocoel is probably a velocity detector, acted upon by the viscous drag of the surrounding fluid. Its function is possibly to detect vibrations in the substrate; either steady fluid drainage motion or acoustic motion in the surrounding liquid.

A. Introduction

Ostracods are small crustaceans with a body completely enclosed within a bivalved carapace. The carapace, a part of the cuticle which is secreted by the epidermis as a continuous sheet (Harding 1964), often bears numerous sensory setae. These extend from the valve surface through pore canals, and are serviced by dendrites within the non-calcified inner lamella of the carapace (Tsukagoshi 1990; Yassini and Jones 1995). Apart from marginal pore canals, the remaining normal pore canals are distributed over the entire carapace surface. These pore canals are a useful character in taxonomy and phylogenetic studies of podocopid ostracods (Benson 1977; Tsukagoshi 1990).

The myodocopid carapace contains amorphous calcium carbonate rather than the crystalline calcium carbonate found in other ostracods (Sohn and Kornicker 1969), hence

myodocopids do not preserve well as fossils. Consequently, myodocopids have received relatively little attention, compared to podocopids. However, simple pore canals, including setae, are prevalent on both the myodocopin (Myodocopida) and podocopid carapace. The taxonomic value of myodocopin external carapace setae has not been studied.

Ostracods generally operate at low Reynolds numbers (Cohen 1989; also see Koehl and Strickler 1981). Therefore, there is a thick layer of viscous water which surrounds ostracods in motion (see Emlet and Strathman 1985).

Cypridinid ostracods are a diverse marine group, represented at all depths, worldwide, and are largely benthic. They are the dominant macro-scavengers in terms of numbers of individuals and species below about 100m depth off the eastern Australian coast (Jim Lowry, personal communication). One recently described cypridinid genus, Cohenia (Chapter 2), containing several small (1-2mm long) but abundant species, is endemic to Australian seas. Species of Cohenia are often the dominant ostracods collected from baited traps set along the east Australian continental shelf. They probably spend most of their lives buried a few millimetres into the sand substrate of their habitat (as do related taxa; Vannier and Abe 1993). Species of Cohenia bear feeding appendages and putative sensory apparatus typical of other scavenging cypridinids (Chapters 2, 4 and 5).

One feature unique to the genus Cohenia is an unusual type of sensilla, arranged numerously in most species in a row parallel to, and near, the anterior, ventral, and posterior margins of the external surface of both carapace valves (Fig.

1). The ultrastructure of this sensilla, herein termed the 'trichocoel' (from the Greek, meaning hair cavity), is described and its potential functions are discussed.

B. Material and methods

I. Collection of specimens

Specimens of an undescribed species of Cohenia (Cohenia sp. 1) were collected from a baited trap (single chamber; see Keable 1995). This trap was set overnight outside of Bate Bay, New South Wales, Australia (34°44'S 150°39'E), at 25m depth, and recovered the following day (15 January 1991). 1,512 specimens (958 females, 554 males; including the last two juvenile stages) of Cohenia sp. 1 were caught and subsequently fixed in 5% formalin and preserved in 70% ethanol (deposited in the Australian Museum, registration number P45077).

II. Light microscopy

Ten specimens of Cohenia sp. 1 were dissected and their carapaces mounted in glycerol and examined at 1000x magnification under a compound microscope. Trichocoels were photographed.

One specimen of Cohenia sp. 1 was embedded in paraffin wax and longitudinally sectioned at 4μm. Sections were stained using a modified Mallory stain (Frank Crandle, unpublished), a multicomponent stain suitable for crustacean sensory

structures, and again the trichocoels were observed and photographed at 1000x magnification using a compound microscope.

III. Ultrastructure

The dissected carapace of a specimen of Cohenia sp. 1 was placed on a paper label stuck to a glass slide and longitudinal sections (about 0.2mm thick) cut using a razor blade (the blade sank into the paper label, providing a complete cut) (Louis Kornicker, pers. comm.). These sections, together with a complete carapace, were critical point dried using a Denton critical point drier, coated with gold, and examined using an Hitachi 570 scanning electron microscope (SEM). Trichocoels were observed from external views and internal cross-sections.

Two specimens of Cohenia sp. 1 were prepared for the transmission electron microscope (TEM). These were fixed overnight in 2.5% glutaldehyde with 2% paraformaldehyde in 0.1M sodium cacodylate buffer, then washed in 0.1M sodium cacodylate buffer. The specimens were subsequently fixed in 1% osmium tetroxide then dehydrated through an alcohol series and finally 100% acetone. The specimens were embedded in spurr resin and 60nm sections were cut. The sections were stained using lead citrate and uranyl acetate, then examined in a Philips CM10 TEM.

C. Results

Trichocoels are structures based within almost spherical (or areas equivalent to two overlapping spheres, Fig. 2d) invaginations of the carapace epicuticle, forming cavities about 10μm deep, but not reaching beyond the boundary of the endocuticle. Each cavity lies within its own circular depression, or pit. At the cavity entrance there is a plug of material (stains red in modified Mallory stain) with a very different composition to the rest of the cuticle (which stains blue, indicating chitin) (Fig. 3). This plug is a flat, circular plate with a central hole through which a seta passes. This seta arises from inside the cavity, near the plug (Fig. 2e) and bears two basal sections (Fig. 2d), each separately joining with the cavity wall. Just external to the plug (about 2μm from the base of the seta) the two setal base sections fuse (Fig. 4c) and the seta constricts to form a very fine, and stiff distal section (Fig. 2c), about 20μm long, lying almost parallel (usually slightly angled) with the external carapace surface, about 2μm from this surface. There are no pores in the seta. The tip of the seta may reach as far as the adjacent trichocoel cavity (eg. Fig. 2b), but never overlaps or touches the seta of the adjacent trichocoel. The setae of a row of trichocoels are all orientated similarly (Fig. 4a); they lie parallel to the valve margin and point in a ventral or posterior direction, depending on their position on the carapace.

A row of trichocoel pits always occurs in regions of the carapace exhibiting some further type of recess. Along the

rostrum and lower incisure margin, the trichocoel row is at the most sunken part of a depressed area or trough in the carapace. Along the anteroventral, ventral, and posterior carapace margins they lie at the base of a ridge or lip of the carapace margin, which extends about 5μm laterally. These recessed areas form channels, in which the trichocoel pits and setae all lie.

The trichocoel nerve supply enters the cavity through a pore in the cuticle, leading from the carapace epithelium to the cavity. The material occupying the remaining space in the cavity is unknown; one or two "lever-like" structures were occasionally observed within the cavity, joining to a setal base (Fig. 5a). Results from the TEM analysis confirmed the above observations, made from light microscopy and SEM analysis.

Trichocoels always occur near the anterior, ventral, and posterior margins of the carapace; never near the dorsal margins, or far from any margin. They occur in the form described above in both males and females, and adults and the final two juvenile stages.

D. Discussion

I. Functional morphology of a trichocoel

From the reconstructed model (Fig. 5b), it can be concluded that trichocoels bear no morphological resemblance to any other animal sensilla.

The absence of pores in the seta means that the trichocoel is probably not chemosensory, although high power TEMs are required to test further for pores. The long and fine but stiff seta probably acts as a mechanoreceptor. However, the specific distributional pattern of the trichocoels over the carapace surface probably excludes the function of carapace stress reception.

The trichocoel seta lies raised from, but almost parallel to, the carapace surface. This seta is "protected" by its surrounding raised areas of the carapace, unlike the other types of carapace setae which lie perpendicular to the carapace surface (and do not usually emerge from recessed areas of the carapace). Therefore, the trichocoel is probably not tactile (ie. a touch receptor). The possibility that a trichocoel is an acceleration detector (eg. otoliths; see Fletcher 1992) can also be dismissed because of the absence of a dense mass on the free end of its seta. A further functional possibility is that the trichocoels are velocity detectors, acted upon by the viscous drag of the surrounding fluid. The following is presented as evidence for this conclusion.

Cypridinid ostracods probably spend most of their time buried in the sediment, where they retract their appendages and rest (Vannier and Abe 1993). This sediment is loosely compacted and full of water. There are two possible fluid motions of this sediment: one a simple drainage flow, and one an acoustic flow under the influence of sound or vibration. In the first case, the water clearly moves relative to the sand grains of the sediment and to the ostracod's carapace. The second case is less obvious. It can be shown that when a sound

wave propagates through a composite medium, such as the sediment in which the density of the solid particles is different from that of the liquid, there is an acoustic motion of the liquid relative to the solid particles (analogous to the scattering of sound by a bubble in a liquid) (see Fletcher 1992). The amplitude of this motion depends upon the difference in density, but is comparable to the overall acoustic amplitude. The carapace of the ostracod behaves like the solid particles of the sediment because it also has a greater density than water. Therefore, in each case, there is a fluid flow velocity over the carapace that could be detected and provide useful information to the animal.

Consider the flow of water past one of the trichocoel setae (Fig. 5b). There are three possible directions of water flow relative to the ostracod's carapace. For flow in the Z direction, normal to the carapace, the seta is ideally orientated to be deflected by viscous forces. Flow in this direction, however, is impossible because the carapace provides a rigid boundary. For flow in the Y direction, normal to the orientation of the groove in which the trichocoel seta lies but parallel to the carapace, the groove orientation protects the hair from the flow, so there is no response. For flow in the X direction, parallel to the groove, the flowing water can come in contact with the seta and exert viscous drag forces upon it. It is reasonable to suppose that this is what happens, so this latter situation will be examined in more detail.

Flow in the X direction is essentially parallel to the main body of the trichocoel seta and tends to pull it in the

flow direction by the action of viscous forces. Because of the bend near the base of the seta, this drag force is converted to an angular deflection, as well as possibly to a lateral displacement, both of which could stimulate the trichocoel's sensory cells.

The viscous boundary layer adjacent to the surface of the carapace has a thickness of:

$$\sqrt{[\nu/(2\pi f)]}$$

where ν = kinematic viscosity of the fluid (ν is approximately 1.0×10^{-6} m^2s^{-1} for water)

f = frequency involved.

This is about 40 micrometres at 100 hertz, and hence large compared with the size of the trichocoel seta. Within the boundary layer, however, the fluid velocity increases nearly linearly with distance from the stationary surface of the animal. This means that, for an acoustic disturbance, the angular amplitude of motion of the trichocoel seta, assuming it to be freely pivoted at its base and not too massive, is independent of its length. The deflecting torque, however, is proportional to the cube of the setal length. In the trichocoel, since the seta is protected by the "plug", its "root" (the base of the seta, inside the cavity) can probably be very flexible, giving a considerable response without requiring a large torque.

When the trichocoel seta is bent by an external

vibration, the force required to return the seta to its original position is $-F_e$;

$$F_e = -ES\kappa^2 \frac{d^4z}{dx^4}$$

where $\kappa = a/2$ (a = radius of the cross-section of the distal setal section)

$S = \pi a^2$

E = Young's modulus for the material of the seta

$\frac{dz}{dx}$ = angular deflection

If the plug is simply compliant, ie. does not clamp the seta (which is probably the case), then the angular deflection is proportional to the bending moment. Therefore;

$$\frac{dz}{dx} = \mu ES\kappa^2 \frac{d^2z}{dx^2}$$

where μ = angular compliance of the plug

Additionally;

$$\mu_s = l/ES\kappa^2$$

where μ_s = angular compliance of the seta

l = length of the seta

Therefore, the behaviour of the seta is described by the ratio of the plug compliance to the seta compliance;

$$\mu/\mu_s = \mu ES\kappa^2/l$$

For a detailed explanation of how the above equations are derived, see Fletcher (1992). These equations are simplified somewhat by assuming a uniform thickness for the trichocoel seta. This assumption may not be too erroneous because the seta is relatively thin and tapers very gradually.

The setae of a row of trichocoels are arranged so that adjacent setae almost touch (ie. with minimal gaps between setae), therefore the probability of detecting any vibrations is extremely high. Each trichocoel seta has a figure-of-eight sensitivity pattern along the direction of the channel in which it lies, so that the ostracod can judge the direction from which the signal is coming, with an uncertainty of 180 degrees. Therefore, the semicircular arrangement of trichocoels around the carapace margins is all that is required in order to detect signals from any direction.

In a body of water that is large compared with the boundary layer thickness, the deflection of a trichocoel seta will be inversely proportional to the boundary layer thickness. Since species of Cohenia spend most of their time in sediment with an interparticle spacing that is perhaps comparable with the boundary layer thickness, however, this analysis requires some modification.

The trichocoel nervous system may comprise different types of neural transducer cells, each with different mechanical properties and consequently different vibrational responses (see Fletcher 1992). The two basal sections of the seta constrict to form the single long, thin, stiff distal section of the seta; it is uncertain whether the nerves enter this distal section or terminate at its base (probably at

least most nerves terminate at the base of the distal section because of the dramatic reduction in cross-sectional area, and the seta may even become solid distally). If the seta is acting as a lever, when the tip of the seta moves towards the carapace, the "upper" basal section becomes stressed and the "lower" section is relaxed; when the tip of the seta moves away from the carapace, the "lower" basal section becomes stressed and the "upper" section is relaxed.

The "plug", which surrounds the seta near its base and joins with the rim of the cavity (ie. it is the setal mounting, "clamping" the seta in position), is not chitinized. This should be stiff enough to prevent the seta ever undergoing too large an angular displacement. The greater the flexibility of the plug, the smaller the resonance frequency of the seta. If the plug itself is part of the vibrational detection mechanism and is serviced by its own nerve supply, then it should be only moderately stiff, so as to transmit the setal motion to its nerves (Fletcher 1992). However, it seems very unlikely that the plug would be innervated.

The function of the trichocoel cavity, formed by an invagination of the epicuticle, is less apparent. It is spherical (or the result of two overlapping spheres) in shape; this shape would provide the strongest mechanical properties (protection against collapsing) but also maximum dampening of vibrations from within the carapace wall. The layer of epicuticle which surrounds the cavity is also more highly chitinized than the endocuticle, adding further strength to the cavity. If one function of the cavity is to dampen vibrations transmitting through the carapace wall, then a

sphere, as large as possible (and the cavity almost extends to the limits of the endocuticle layer), would be the ideal shape. This adds to the hypothesis that the entire trichocoel detects external vibrations, by excluding confusing vibrations from within the carapace wall caused by movements of the ostracod itself.

The sensory structures most comparable to the trichocoels are the lateral line mechanoreceptors (canal organs) of fish, which are situated at the bottom of a sunken canal in the skin, and are particularly well developed in the head (Jakubowski 1967). Here, hair cell bending is an adequate stimulus, and these lateral line organs also bear dome shaped "cupulas", which are filled with a gelatinous matrix consisting of a finely fibrillar substance (Flock 1971). The lateral line organs detect water motion, including laminar flow, wave eddies, and near field displacement caused by vibrating sources (Harris and van Bergeijk 1962). However, the hairs of a lateral line organ are thicker (about 1.5μm in diameter) and shorter (about 7μm long) than the trichocoel seta, and are also arranged in bundles of about 35, projecting almost perpendicular to the surface of the fish, with tips of adjacent organ setae pointing in opposite directions (Flock 1971). Cephalopods bear cells in the skin (the lateral line system) with setae similar to those of the lateral line organs of fish, and these cephalopod cells respond to local water movements (Hanlon and Budelmann 1987; Williamson 1995). Another consideration here is the difference between the thickness of the boundary layer of an ostracod and a fish (or a cephalopod); this may either explain the morphological

differences between the trichocoel and a lateral line organ of a fish (or cephalopod), or separate the two structures even further in terms of their mechanism of function.

Whatever the function of the trichocoel, its intriguing ultrastructure must attract further attention.

II. Source of the stimuli detected by a trichocoel

Crustaceans react to diverse stimuli from their physical, chemical, and biological environment (Mauchline 1977). The most plausible hypotheses for the function of a trichocoel is the detection of either steady fluid drainage motion or acoustic motion in the surrounding liquid, while the ostracod is buried in the sediment. Therefore, possible sources of vibrations in the water column, such as the fins of fish predators, will not be discussed, although the trichocoel may detect motion in the water column, in the direction indicated by X in Fig 5.

Species of Cohenia scavenge. The rapid sinking of an animal carcass and its impact on the bottom would generate rapidly and widely spread vibrations through the water (Dahl 1979), and consequently through the top layers of sediment. Species of Cohenia could be detecting such vibrations, although it is doubtful that these vibrations could transmit further than the chemicals released by an animal carcass, which are almost certainly detected by species of Cohenia, in which case the detection of vibrations from the carcass would be unnecessary. Also, Vargula hilgendorfii, a cypridinid with a similar morphology to species of Cohenia, buries at an angle

of 45-60 degrees between the longitudinal axis of the carapace and surface of the substratum, anterior end first (Vannier and Abe 1993). Presuming that species of Cohenia behave similarly, the trichocoels would face away from the water column, which is not the ideal position to detect stimuli from the water column or sediment surface (although signals from all directions should be detected, maximum detection would presumably occur from a source nearest the half of the ostracod bearing the trichocoels). For similar reasons, the detection of other sounds created in the water column (see Myrberg *et al.* 1965; Horch and Salmon 1969), or temperature variations (see Altner and Prillinger 1980) may not be the function of the strategically positioned trichocoels.

An explanation for the source of acoustic motion detected by the trichocoels is from prey, such as nematodes (cypridinid ostracods are known to scavenge and feed on detritus, but they may be opportunists, feeding on whatever is available). Alternatively or additionally, the acoustic motion detected may arise from predators, such as certain polychaetes, which burrow through the sediment. Because species of Cohenia probably only bury near the sediment surface, most animals would burrow below these ostracods. Therefore, assuming the above burial posture, the trichocoels would be well positioned to detect the movement of such predators or prey. However, the trichocoels may not provide the accuracy required to capture small prey. Nevertheless, predator evasion is still a reasonable hypothesis.

The detection of predators in the sediment below the burrow of a species of Cohenia is a more reasonable hypothesis

for the trichocoel function. For example, certain carnivorous polychaetes would devour any small ostracods they may find, or the ostracods may get sucked into the mouth of a deposit feeding polychaete, if lying in the polychaete's path. However, if the ostracod had an advanced warning of such a hazard, it could have time to burrow out of the sediment and swim to safety. If the trichocoels detected both predators and prey, they could distinguish between the two by the differences in amplitude and frequency of the vibrations they transmit. These different signals would consequently stimulate different responses of the ostracod; this hypothesis is therefore testable. Males, females, and at least the latter juvenile stages, all possess trichocoels, and would all be expected to employ this early warning system, if such a function of the trichocoel is correct.

Another explanation for the function of the trichocoels is to detect drainage currents through the sand. These currents may tell the ostracod which direction was towards the shallow water. For unidirectional signals such as this there would be no ambiguity, and having an array of sensory hairs would allow the ostracod to localise the direction somewhat exactly.

Acknowledgements Cordial thanks are due to Neville Fletcher (ANU, Canberra) for contributions to the interpretation of the results of this study. I also thank the Australian Museum, Macquarie University and the National Museum of Natural History (Smithsonian Institution) for the use of their

facilities; Noel Tait (Macquarie University, Sydney) and Jim Lowry (Australian Museum) for critical manuscript review, and for discussions on external stimuli detected by the trichocoels, Louis Kornicker and Duane Hope (Smithsonian Institution) for helpful discussions on invertebrate biology and sensilla; Frank Crandle and Cathy Price (Smithsonian Institution) for histology advice. Thanks are also due to the Australian Museum Trust, Macquarie University, and the Smithsonian Institution for the funding of this study.

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Fig. 1 Right valve of Cohenia sp. 1, adult female, lateral view, showing trichocoels (setae not visible at this magnification). Note that the number of trichocoels vary in different species of Cohenia (often less numerous than in the species illustrated, although always more closely spaced anteriorly).

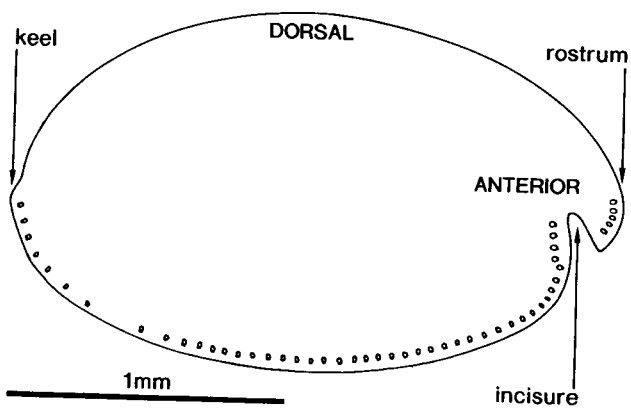

keel
DORSAL
rostrum
ANTERIOR
1mm
incisure

Fig. 2 Light micrographs of trichocoels in the left carapace valve of an adult female Cohenia sp. 1 specimen, medial view. **a** Anterior of valve (below incisure) showing part of row of trichocoels. **b** Two adjacent trichocoels, tip of the left seta arrowed. **c** Trichocoel plug (below, left) and stiff seta (arrowed). **d** Complete cavity and base of seta (the two basal sections are arrowed). **e** Trichocoel plug and base of seta (position where seta appears to join the cavity wall is arrowed).

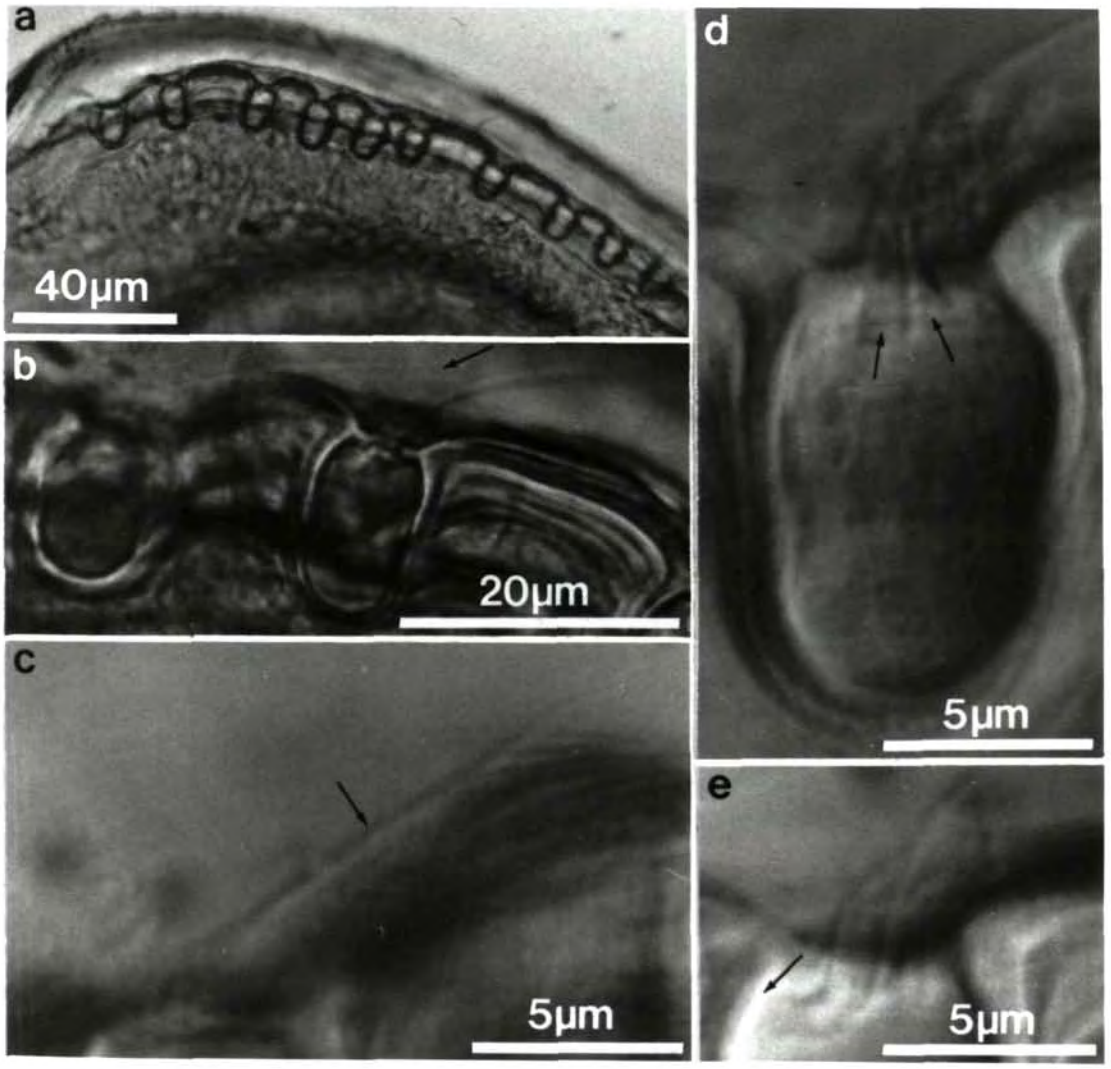

a
40µm
b
20µm
c
5µm
d
5µm
e
5µm

Fig. 3 Light micrograph of a transverse section (4μm thick) of the carapace of an adult female Cohenia sp. 1 specimen, stained with a modified Mallory solution (external surface above): a = epicuticle (stained medium-dark blue); b = endocuticle (laminate, stained pale blue); c = epithelium. The trichocoel plug stained dark red, and appears black in this photograph.

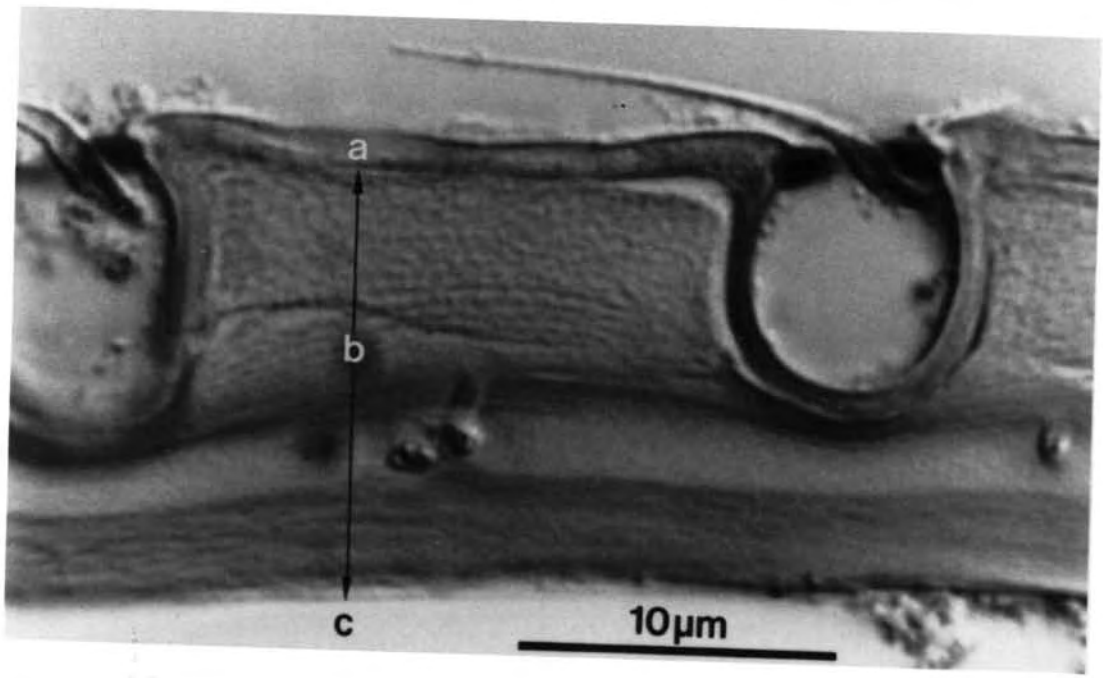

a
b
c
10µm

Fig. 4 Scanning electron micrographs of an adult female Cohenia sp. 1 specimen, left carapace valve. **a** Row of trichocoels (2) at base of lip (L) of ventral margin (edge of valve to the right), also showing pore canal entrances with setae (1, typical for the Cypridinidae). **b** Close up of a dried trichocoel seta (from **a**) and entrance to the cavity at the base of the valve lip (L); plug may have fallen out (possibly after shrinking) during drying. **c** Base of seta (double) arising from trichocoel (close up of **b**); plug probably occupied the space surrounding the setal base. **d** Anterior end of the carapace, anterior view, showing external entrances to trichocoels (in pits) in rows on the rostrum (R), and just below the incisure (L.I.). **e, f** Transverse sections through trichocoel cavities (possible base of seta arrowed in **e**).

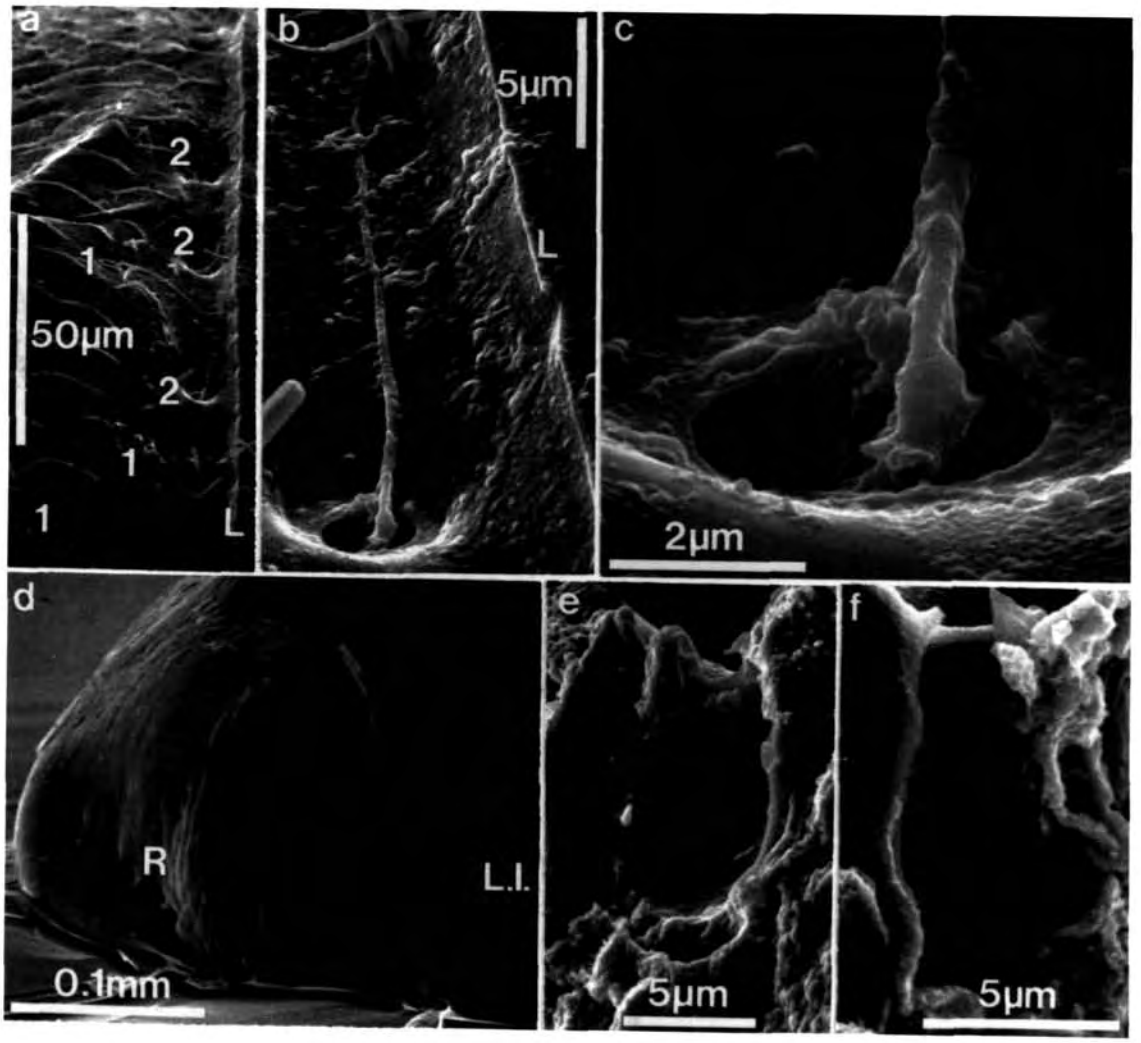
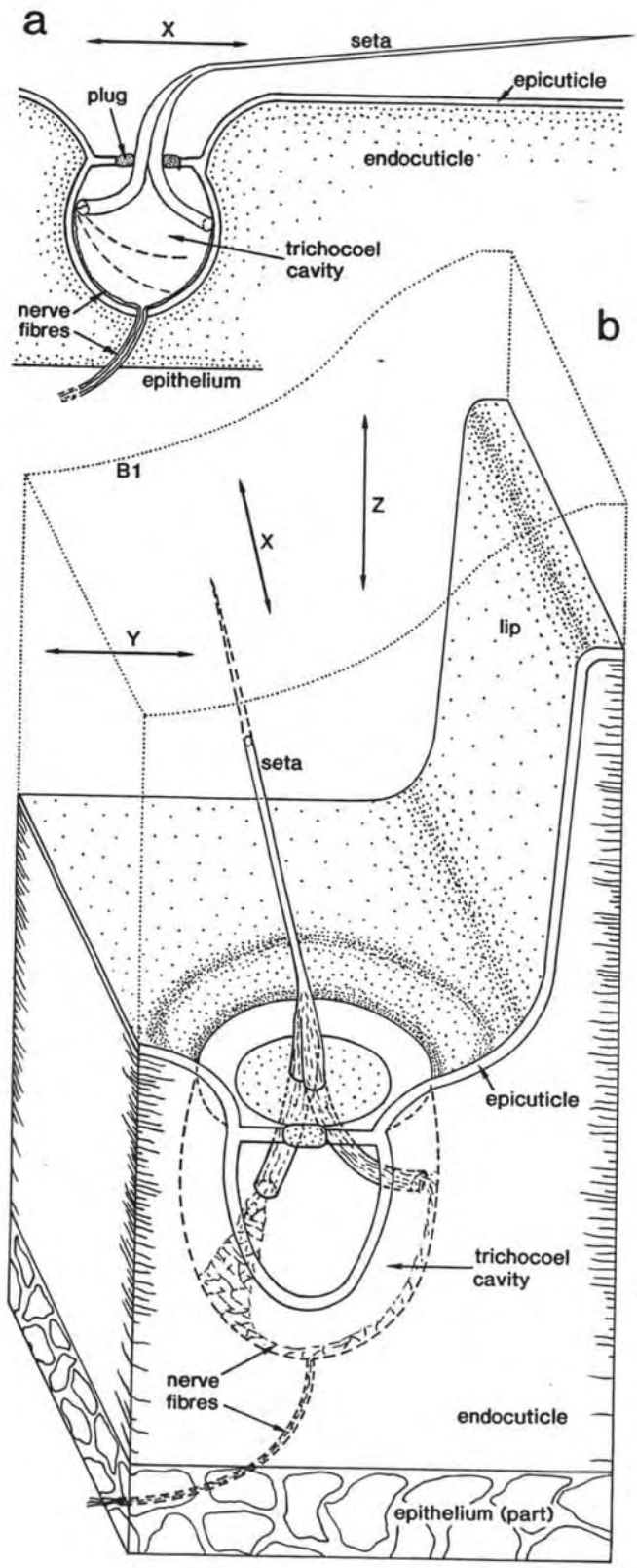

a
2
1
2
50μm
2
1
1
L
b
5μm
L
c
2μm
d
R
L.l.
0.1mm
e
5μm
f
5μm

Fig 5 Generalised diagrams of a trichocoel of Cohenia sp. 1. **a** Longitudinal section through the centre of a trichocoel; dashed lines inside cavity represent two possible structures occasionally observed; X represents the direction of water flow parallel to the groove in which a row of trichocoels lie. **b** Theoretical model of a trichocoel at the base of the lip near the ventral margin of the carapace; trichocoel is sectioned transversely and off centre (near edge of plug); X, Y and Z represent different directions of water flow over the trichocoel seta; B1 represents the proximal part of the boundary layer (of viscous water), usually present with a thickness greater than the length of the trichocoel seta.


a
X
seta
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fibres
epithelium
b
B1
Z
X
Y
lip
seta
epicuticle
trichocoel
cavity
nerve
fibres
endocuticle
epithelium (part)

CHAPTER 4

Functional morphology of the myodocopin (Ostracoda) furca, sclerotized body plate and central adductor muscles

(Prepared for Journal of Crustacean Biology)

ABSTRACT

This study shows that the furca has several major functions in the feeding process of scavenging cypridinid ostracods, which include the cutting and holding of small food sections from an animal carcass, helping to hold the ostracod firmly in position on a carcass and removing small fish scales. These functions are made possible by the circular motion of the furca on a vertical plane, the arrangement of the claws on each lamella and by varying the angle between lamellae. When the furca is undergoing its cutting role, the ostracod is held in position against the food source by the mandibular claws grasping the food and the mandibular muscles locking the limb in one position, and/or the "swimming" towards the food, effected by the second antennae. Many of the cypridinid furcal characters that appear adapted for scavenging may have originally developed for digging, a

process which requires a comparable mechanism.

The central adductor muscles allow areas of the carapace to open differentially. Thus the ostracod's body remains relatively well protected, even during the extension of body parts through the carapace aperture (the carapace may open only in the region necessary for this protrusion). The area of hardened dorsal body wall just anterior to the furca in the Myodocopina is termed the sclerosome and its functions probably include protection for the soft body, exposed when the carapace valves are open, and support for certain furcal muscles. The sclerosome is unique to the Myodocopina.

INTRODUCTION

Ostracoda and the Caudal Furca

The diverse ostracod family Cypridinidae (Myodocopida: Myodocopina) currently comprises 28 genera and is represented in marine environments world-wide, at all depths. The cypridinid furca is a relatively large section of the body, having a length of between about one quarter and one half of the body length, and is joined to the sub-terminal end of the body (the myodocopid anus is just posterior to the furca). It is comprised of a pair of subtriangular plates (lamellae), connected to the body at their anterior margins, each bearing between 4 and 28 dorsal (usually appear ventral, see Fig. 1) claws. Because of this morphology, the cypridinid furca would appear to be a useful scavenging tool. However, the use of the

furca in the feeding mechanism of scavenging cypridinids has not been studied using modern techniques. In fact, little is known about the function of the caudal furca in any crustacean group (Schminke, 1976).

The crustacean telson is regarded as the unsegmented terminal lobe of the trunk that remains after segmentation of the trunk has been completed (Bowman, 1971). The telson may bear paired caudal rami; the telson and caudal rami constitute the caudal furca (Bowman, 1971; Schminke, 1976). The most posterior crustacean trunk somite frequently bears appendages called uropods which often form a caudal fan with the telson (Bowman, 1971). However, the absence of body segmentation and abdominal appendages makes interpretation of the terminal part of ostracods difficult. It has been suggested that the myodocopid furca is a deeply incised telson (Bowman, 1971). Bowman considered an ostracod furca dorsal to the anus to be a telson and a furca ventral to the anus to be a uropod. Kornicker (1975) chose not to continue the use of these terms but used the former situation to characterise the Myodocopa (= Myodocopida) and the latter the Podocopa (= Podocopida).

In cypridinid keys, the furca is often used to separate genera based on the number of claws on each lamella. However, intrageneric, and to some extent intraspecific, variation occur within some taxa. Cohen (1983) illustrates sexual dimorphism of the furca and the differences in the furca of each juvenile stage, including the shape of the lamella, the number of claws and the number and position of claws fused to the lamellae. The most posterior claw (for orientation see Fig. 1A) of the right furcal lamella is always posterior to

that of the left lamella in myodocopins, which is independent of ontogeny or sex (Kornicker & Cohen, 1981: note that in this paper the posterior part of the furca is regarded as anterior, ie. as the furca would appear in its resting position, see Fig. 1B).

The internal furcal sclerites are part of the cypridinid skeletal system (Cannon, 1931). The furcal musculature of Gigantocypris mulleri Skogsberg is described as a series of dorsal, longitudinal muscles attached directly to the carapace at the side of the heart, a powerful pair of muscles running anteriorly, and the pericardio-furcal muscles which comprise 3 broad muscles running anteriorly, dorsally and laterally (Cannon, 1940).

Cypridinid Feeding Mechanisms

Cannon (1931, 1933, 1940) first described in detail the feeding mechanism of modern ostracods, but these studies were made using preserved animals and no behaviourial observations were included. Feeding strategies considered were those of "collectors" (collect detritus from the sediment, Walker, 1972), scavengers and predators, where the cypridinid ostracods Doloria levis (Skogsberg), G. mulleri and a species of Cypridina were used as examples, feeding on large particles of detritus and remains of fish, active animals such as free-swimming copepods and young fish, and small particles of detritus respectively. The myodocopin families Philomedidae, Sarsiellidae and Rutidermatidae are believed to contain predators and collectors (Kornicker, 1975). Kornicker (1975)

classified pelagic members of the Cypridinidae as predators and benthic forms as collectors (similar to, but more selective than, the philomedids). Cannon (1933) suggested that cypridinids do not filter feed (filter particles out of the water column) as do cylindroleberidids (Myodocopina). However, it is now known (Cohen, 1989) that ostracods probably have low Reynolds numbers (eg. Koehl and Strickler, 1981; Emlet and Strathman, 1985) so their movements through water are movements through a viscous medium. Therefore, filter feeding may not occur in ostracods; the term "comb feeding" is more appropriate when referring to the feeding of cylindroleberidids (Cohen, 1989). The fan-like epipodite of the cypridinid fifth limb beats to produce a flow of water through the carapace from the anterior to the posterior end. Food particles kicked up by the mandibular claws are sucked into the carapace on this stream and entangled in the sticky secretion exuded from the upper lip. Large food masses are held directly under the mouth by the mandibular palps where they are torn to pieces by the very powerful claws of the endopodites of the fourth limbs (Cannon, 1931; Kornicker, 1975). Next, the "barrage of claws" on the first and second endopodial joints of the fifth limbs continue the tearing-up of the food, simultaneously moving it towards the mouth (Cannon, 1931). The remaining endites of the fourth and fifth limbs complete the lifting of the triturated food into the oesophagus (Cannon, 1931).

A cypridinid feeding adaptation is seen in the articulation of the mandibles; some articles are relatively long and narrow to allow a high degree of flexing so that food

can be passed directly to the mouth region (Kornicker, 1975). The cypridinid mandibular palps can also be thrust outwards to grasp drifting particles or swimming prey (Cannon, 1940).

Recent trapping of small crustaceans off the east coast of Australia has shown that many genera of cypridinid ostracods occur frequently and abundantly as scavengers (Jim Lowry, personal communication; Keable, 1995). These are present from 5 to 43° south in this region and often in large numbers (up to 75,000 individuals caught in each baited trap). This suggests that the east Australian cypridinids include a high diversity of scavengers (from comparisons of trap and hand collected samples, and literature reports) and may form the dominant macro-scavengers of the east Australian continental shelf (Jim Lowry, personal communication). This contrasts with the situation in the Caribbean (Cohen & Morin, 1990b), where most of the over 50 species of cypridinids recorded from this area do not enter baited traps and, therefore, are probably not scavengers (Anne Cohen, personal communication).

Parasitism has been reported in cypridinids (Wilson, 1913; Monod, 1923; Harding, 1966). Harding found Sheina orri Harding on the gills of the ray Taeniura lymna (Forsskål), and the cat-shark Hemiscyllium oscellatum (Bonnaterre), both bottom dwellers, and Monod reported Cypridina squamosa Mueller from the back, head and in the mouth of the scorpionfish Scorpaena scrofa (Linnaeus). But more surprisingly, Wilson (1913) found Vargula parasitica (Wilson) on the gills and in the nostrils of the hammerhead shark Sphyrna zygaena (Linnaeus), a very active swimmer believed not to rest on the

sea floor, and additionally on the gills of the sea bass Epinephelus adscensionis (Osbeck), and the jack fish Caranx crysos (Mitchill). It has since been suggested that these myodocopins are not parasitic and that they only attached themselves to unhealthy fishes (Cohen, 1983). However, recent evidence suggests that S. orri is an ecto-parasite of H. oscellatum (Bennett & Parker, in prep.).

Cohen (1983) maintained living specimens of the cypridinid Skogsbergia lerneri Kornicker in an aquarium and in small dishes, primarily for the study of reproduction and development but also reported on their feeding behaviour. Cohen suggested that S. lerneri is a scavenger, or preys on restrained and/or injured animals rather than being an active predator. It was noted that the furca (and also the mandibular palps) are used to climb over the food and apparently aid in pushing food towards the mouth. Cohen also described the feeding of instars of live S. lerneri in laboratory conditions, which all appear to scavenge.

The cypridinid ostracod Vargula tsujii Kornicker & Baker is an active predator of Oxyjulis californica (Günther), a wrasse (Collins *et al.*, 1984). These ostracods attack the internal organs of the fish after entering the body cavity via the mouth or the cloaca as well as attaching to the outer integument. The fish were considerably weakened, although still alive, after three hours of exposure to the ostracods. Vargula tsujii and the cirolanid isopod Cirolana diminuta Menzies were responsible for the death of caged adult nearshore fishes within 3 to 4 hours after sunset (Stepien and Brusca, 1985). The ostracods were attracted to chemicals

released by sexually mature fishes, and subsequently the isopods were attracted to chemicals released by the injured fishes after ostracod attack (Stepien and Brusca, 1985). Such crustaceans cause extensive damage to commercial fish catches and consequently economic loss. But all the fish used in these experiments were restrained in cages, as are the fish caught in fishermen's nets, and the ostracods were never found on uncaged fish.

Possible Role of the Ostracod Furca in Feeding

In all the work carried out to date on myodocopin feeding, there has been no mention of the caudal furca as a major scavenging tool, other than aiding in pushing food towards the mouth (Cohen, 1983). However, the feeding mechanism of another scavenging myodocopid, Conchoecia borealis Sars (Halocyprina) was studied (Iles, 1961). Although only preserved material was examined, the possible feeding mechanism of this species was discussed in detail and compared to that of the cypridinid genus Cypridina, where a difference in the function of corresponding limbs was proposed, but a similar diet presumed. This work lead Lochhead (1968) to publish his observations on living Conchoecia. Under a stereoscopic microscope, Lochhead observed the caudal furca of Conchoecia spinirostris Claus to lift food away from the mouth during feeding on small dead crustaceans (mostly copepods). Boluses formed by Sepia ink particles trapped in the sticky secretion of the marginal carapace glands appeared to be steered away from the body by the furca, although the

mandibles and the fourth and fifth limbs tended to push the boluses toward the mouth. Perhaps the furca was attempting a similar role. Lochhead concluded that his feeding observations differed from those made by Iles only in the constant shifting and rotation of the food, a task partially accomplished by the furca.

More recently, behaviourial studies using video recordings have been conducted by ostracod workers. Some examples are the underwater recordings of bioluminescent display patterns of certain cypridinids (eg. Morin and Cohen, 1988) and laboratory recordings of Vargula hilgendorfii (Mueller) in a thin (5 mm wide) plexiglass container to study functional morphology (Vannier and Abe, 1993). Vannier and Abe (1993) found that "the furcae facilitated the penetration into the sediment and assisted rotations in a vertical plane, on or within the substratum", and suggested that the furca is used to support the ostracod resting on, and to push the ostracod away from, the substrate.

While studying the east Australian scavenging cypridinid fauna, the genera Cohenia Parker (Chapter 2) and Lowrya Parker (Chapter 2), containing many described and undescribed scavenging species, were identified on the basis of the morphology of the furcae, including the presence of an unusually large fourth claw and similarly shaped small (anterior) claws. The identification of this large fourth furcal claw initiated this study on the function of the furca in these scavengers. The relatively large cypridinid Azygocypridina lowryi Kornicker, was also caught in abundance in baited traps set off the New South Wales (Australia) coast

and therefore can be considered to be a scavenger, a previously unreported behaviour for members of the genus Azygocypridina Sylvester-Bradley. When examining a large sample of A. lowryi, it was noticed that all the specimens, including all juvenile stages, exhibited small pieces of food (the fish bait) firmly attached to their furcae in addition to the feeding appendages (the claws of the mandibles and the claw-like setae of the fourth and fifth limbs).

Functional Analyses Made During this Study

This study presents an analysis of video recordings of living animals and comparative morphology to examine the mechanism of feeding in scavenging cypridinid ostracods. This includes: the role of the furca, mandibles and second antennae; the central adductor muscles; and the hardened section of dorsal body wall, which I term the sclerosome.

MATERIALS AND METHODS

Collection of Specimens

Four baited traps were set in shallow water off New South Wales, Australia, during August to December, 1993. These traps were designed by Keable (1995) and consisted of a 30 cm length of PVC pipe 11 cm in diameter with a funnel at one end (7.5 mm opening). The other end of each trap was covered by 0.5 mm mesh, allowing water to circulate inside the trap, and a 4 mm

mesh was placed over the entrance to prevent large snails entering and blocking the funnel. Inside each trap was placed a small pilchard, itself contained within a smaller jar with 0.5 mm mesh secured over the entrance to prevent ostracods from feeding on the fish. Each trap was attached to a chain and an anchor, and by an appropriate length of rope to marker buoys at the surface. These traps were set overnight and recovered the following day.

The first trap, set in Watsons Bay, Port Jackson, NSW, Australia (33° 50.85′ S, 151° 16.80′ E), at a depth of 4m on a fine sand and gravel substrate, yielded undescribed species of the cypridinids Skogsbergia sp. 1, (about five hundred specimens) and Vargula, sp. 1, (about twenty specimens). The second trap was set off Grotto Point, Port Jackson (33° 49.05′ S, 151° 15.92′ E), at a depth of 10-12m. Three undescribed species of cypridinid were caught; Skogsbergia sp. 2, and Lowrya kornickeria (Chapter 2) and Lowrya sp. 1. About five hundred individuals were caught in total. The third trap was set in Jervis Bay, NSW, Australia (35° 06.5′ S, 150° 46.40′ E), at about 20 m depth. Four undescribed cypridinid species were caught; Vargula sp. 2, Skogsbergia sp. 3, Cypridinodes sp. 1, and Paradoloria sp. 1. A total of about three hundred individuals were caught. A fourth trap was set off the coast at Wollongong, NSW (34° 31.48′ S, 151° 13.22′ E), at 200 m depth. About fifty specimens of the cypridinid A. lowryi were caught. See Table 1 for species used during this study.

The ostracods were removed from the traps and immediately transported to the laboratory in aerated, fresh sea water. Behavioural observations were carried out within 4 hours,

during which time they appeared to be in a healthy condition.

Video Recording

Males and females of all the species of Skogsbergia, Vargula, Cypridinodes, Paradoloria and Lowrya collected (Table 1) were observed feeding in a glass Petri dish (10 cm in diameter, 2 cm deep) within two hours of being retrieved from their traps. The Petri dish was filled with fresh sea water and a small piece of pilchard placed in the centre. Both light and dark fields were used, illuminated from above (and below with the light field) with fibre optic illumination. About three ostracods were placed in the Petri dish at one time and filmed using a Panasonic F10 video camera connected to an Olympus SZH stereo microscope and an NEC video recorder. The specimens were observed on a monitor and recorded on BASF E-240 Premium High Grade chrome video cassettes at 40 to 64x magnification (Fig. 2A).

A male and a female Skogsbergia sp. 1 specimen and a female Vargula sp. 1 specimen were transferred to cavity slides with a few drops of sea water containing minute food particles and a cover slip placed on top. The specimens were examined under an Olympus BH2 compound microscope connected to a Panasonic CL350 video camera and the above video recorder and tape. The ostracods were observed on a monitor and videoed at 60 and 100x magnification in order to observe whether comb feeding was occurring (Fig. 2A). Only light field illumination from below the slide was used. Green and orange filters were also used to improve the contrast of the picture. Ostracods in

these cavity slides were restrained, and hence under unnatural conditions.

A few specimens of Vargula sp. 1 were filmed feeding in a flow through aquarium using a Broadcast Television Systems LDK 91 camera mounted on tracks and controlled with a separate control panel with monitor (Fig. 2B). This was to observe the ostracods feeding in more natural conditions than in a Petri dish, although filming was made unavoidably difficult, although still possible, by the regularly changing depth of field caused by the ostracods moving over the food source (fish section) in many directions. The results of this filming were compared to that of the more extensive filming of the ostracods in a Petri dish to test whether the feeding behaviour was normal under the restrained conditions of a Petri dish and a cavity slide.

The resultant video recordings were viewed at normal speed and also slowed down for frame by frame analysis.

Photography

On completion of filming, some of the Skogsbergia sp. 1 specimens were photographed alive in cavity slides containing fresh sea water with a cover slip on top to demonstrate the various furcal positions exhibited. Pictures were taken on Ilford FP4 Plus, ISO 125, black and white film using a Zeiss stereo microscope connected to a Wild camera.

Scanning Electron Microscopy

Scanning electron micrographs were taken of A. lowryi with and without food and carapace to observe the different positions of the furcal claws, and of a dissected specimen of Cohenia sp. 1, also a scavenger, to demonstrate the feeding parts. The cylindroleberidid Tetraleberis brevis (Mueller) and philomedid Euphilomedes sp. 1 (undescribed), within the Myodocopina, and the halocyprin Conchoecia belgicae Mueller (all from Australian Museum collections), were examined after removal of their carapaces to compare furcae between more distantly related myodocopids. All specimens were fixed in 5% formalin, preserved in 70% ethanol, and the specimens observed without food were cleaned using 5 half-second exposures to ultrasound. All of these specimens were critical point dried using a Bio Rad CPD 750, coated with gold, and examined using a Cambridge Instruments S120 scanning electron microscope.

Light Microscopy

An adult female specimen of Cohenia sp. 1, fixed in 5% formalin then preserved in 70% ethanol, was embedded in paraffin wax and 4μm thick longitudinal sections were cut. These sections were stained using a modified Mallory stain (Frank Crandle, unpublished) and the pivoting point (fulcrum) of the furca on the body and furcal musculature (masked externally by membranous folds) was observed and photographed. An adult female specimen of A. lowryi, fixed in Bouin's solution (to facilitate the sectioning of this larger, more

heavily calcified ostracod) then preserved in 70% ethanol, was embedded in paraffin wax, but 4μm thick transverse sections were cut and observed for a different perspective.

Dissections

Two specimens (male and female) of both A. lowryi and Skogsbergia sp. 1, fixed in 5% formalin then preserved in 70% ethanol, were dissected in glycerol. The muscles associated with the furca were examined.

Literature Comparisons

Illustrations of furcae from different cypridinid genera were obtained from the literature and compared with regard to the relative size and shape of their lamellae and claws to demonstrate the possible taxonomic value of the furca. The furcae of known scavenging and non-scavenging cypridinids were compared to identify the presence of characteristics of the furcae unique to scavenging ostracods. The furcae of cypridinids were also compared with those of other myodocopids, including T. brevis, Euphilomedes sp. 1 and C. belgicae (and additional examples from the literature).

A literature search to document the occurrence of the sclerosome in ostracods was also conducted.

RESULTS

Behaviourial Observations

From video recordings, all cypridinid specimens trapped (ie. scavengers) and observed feeding clearly used their furcae in obtaining small, workable sections of fish (eg. a sphere of diameter similar to the longest furcal claw length) from a larger piece of fish. This was achieved by holding the fish with the mandibular claws and quickly slicing into the fish with the furca in an anterior to posterior direction (Fig. 3A). The dorsal body wall was seen to move significantly in an anterior to posterior plane within the carapace during such a cut, which accounted for the furcal movement in this plane. The movement of the furca in a dorsoventral plane was made possible by the furca itself pivoting on, and moving independently to the body (Figs. 3B and 4). Between each cut, a recovery stroke was made by the furca to bring it back to the anterior (starting) position. This was made possible by moving the dorsal body wall anterodorsally and pivoting the furca to a dorsal (of body) position, thus raising the claws from the food source. Up to about ten of these cutting/recovery strokes could be made per second, and the furcal movement often ceased after several cuts. When feeding on a corner edge of a large fish section, for which the ostracods tended to show a preference, the furca often removed a section using only its first (most posterior) or first and second claws. The fish is again held in the ostracod's mandibular claws and an anterodorsal to posteroventral furcal

movement is used.

When making a cut, often involving several cutting cycles, the furca begins as a knife-like arrangement with the lamellae held flat against each other, and claws of opposite lamellae interlocked or lying side-by-side. Then the lamellae (and claws) gradually separate along their dorsal margin, either during one cutting cycle or throughout a group of cycles, to tear very small sections of flesh from the large fish section.

Sometimes the furca cut into the fish and remained there, anchoring the ostracod while the other feeding limbs (mandibles, and fourth and fifth limbs, see Fig. 5) continued the feeding process. These other feeding limbs appeared to work as previously stated in the literature, but an accurate account of this process could not be made due to the poor contrast of these limbs against the body.

When a section of fish was eventually removed, the ostracod moved away from the larger piece of fish and began feeding from this smaller section. Tiny fish pieces were then scraped off with the mandibular claws and passed to the "claws" of the fourth and fifth limbs while the furca firmly held the fish section. When a small fish section, onto which Skogsbergia sp. 1 was holding with its furca, was moved through the water using forceps, the furca did not let go of the fish, implying a relatively strong furcal grip.

The same ostracod specimens also moved towards small sections of fish that were drifting freely in the water. These sections were positioned between the furcal lamellae and then the lamellae were closed together to give a strong hold on the

food.

Small pieces of fish were sometimes grasped from the water and passed to the fourth and fifth limbs by the furca, without the mandibles being used. Occasionally the mandibles held on to the fish while the furca pushed the ostracod away, tearing off a section of food in the grip of the mandibular claws. The furca was also used to help rotate the food bolus.

During these observations, the ostracods swam very rapidly using their second antennae. The second antennae also appeared to have a function in balancing the ostracods which were attached to the fish, especially against currents created by other ostracods swimming nearby or movement of the Petri dish itself (analogous to currents present in the ostracod's natural habitat), and in pushing the animal against the water and onto the fish while the furca is making a cut and effectively pushing the ostracod away from the fish. This counterbalancing role of the second antennae was determined by judging the swimming direction of the oar-like exopodites during a frame by frame analysis of the video recordings.

When the ostracods were viewed on the fish from above and below, each carapace was seen to open and close, altering the aperture, x, between carapace margins on the ventral surface (Figs. 3, C and D, and 6). However, this aperture varied irregularly at different positions along the ventral carapace margins, ie. the carapace was not opened and closed uniformly (eg. Fig. 6C: the anterior margins of the carapace are open, yet the posterior margins are closed).

When feeding on the outer surface of the fish, the furca removed the scales individually by pushing each scale towards

the posterior end of the ostracod until the scale was forced off. The ostracod then continued to feed on the exposed flesh.

The ostracods on the cavity slides (Skogsbergia sp. 1 and Vargula sp. 1) were observed to draw minute food particles into the anterior carapace aperture on a stream created by the beating of the fan-like epipodial plate of the fifth limb. These particles also appeared to leave the ostracod via the posterior aperture of the carapace in the same stream. The fourth and fifth limbs were used to tear up small food particles, larger than the minute particles passing out through the carapace, and pass them towards the mouth. The seventh limbs continuously flexed and moved over the body, possibly performing a cleaning function (Vannier & Abe, 1993). The role of the sixth limbs could not be determined, due to their poor contrast against the body. The ostracods on the cavity slides were very restrained (under unnatural conditions) and therefore may not have behaved naturally.

Throughout these observations, males and females, and the last two juvenile stages of Skogsbergia sp. 1, behaved similarly.

Anatomy

On examination of electron micrographs (comparison of Fig. 6, micrographs B and F) the furcal lamellae are seen to be compressed together or separated to varying degrees. This compression and separation is synchronised with the opening and closing of the ventral margins of the carapace, which is controlled by the several central adductor muscles. These run

horizontally through the body as a group attaching, at their ends, to both carapace valves. However, the separation of the furcal lamellae is controlled by anterior transverse furcal muscles (see Figs. 7, 8A and 9) which join the lamellae at their anterior ends.

The furcal lamellae may close together further than shown in Fig. 3C, because the large, most posterior, claws of some species (eg. Cohenia, Fig. 3; C and D) are arranged so as to slot together both at their bases and throughout the claw lengths (staggered arrangement), allowing for a partial interlocking effect. There appears to be a recess in the ventral margin of each lamella, between claws, into which the opposite claw could fit. The smaller anterior claws may show side by side alignment. This interlocking of the large claws creates a knife-like arrangement of the furca, useful for slicing through flesh.

The muscles associated with the dorsal body wall are probably responsible for moving the furca in an anterior-posterior plane. However, both A. lowryi and Cohenia sp. 1 showed two major groups of longitudinal muscles. One dorsal muscle group (appears as two muscles in A. lowryi, Fig. 7) attaches to the anterior edge of the furcal lamellae and the ventral edge of the sclerosome (see below) of the dorsal body wall. The other more ventral muscle group attaches to another, undetermined, part of the ostracod (the dorsal muscles appear broader and longer in both A. lowryi and Cohenia sp. 1). These two groups of muscles are responsible for the furcal movements in a dorsoventral plane, independent of the body movement. With the ostracod in its resting position (Fig. 1B), when the

ventral muscle was pulled with forceps the posterior end of the furca moved towards the body, dorsally, and when the dorsal muscle was pulled the anterior end of the furca moved away from the body, ventrally (Fig. 3B). This dorsal-ventral movement of the furca was made possible by pivoting on the internal sclerites (see Rome, 1969; Kornicker, 1975) and the flexibility of the body wall connecting to the furca. Each furcal lamella is connected to the body along its anterior margin, but the body wall in this region displays folds (Figs. 3E, 5A, 8B, and 9) when in the resting position, which become stretched out in different areas when the furca is moved.

The above folds only occupy a small region of flexible membrane near the terminal end of the body; adjacent (anterodorsal) to this is a relatively large area of much harder body wall, here called the sclerosome. This approximately symmetrical hard plate is positioned along the posterodorsal edge of the body (posteroventral when the ostracod is in its resting position), and is the external part of the body making direct contact with the environment when the carapace is opened (Fig. 10C). In A. lowryi and Skogsbergia sp. 1, the longitudinal muscles (although possibly not the ventral group) running from the anterior edge of the furca attach to this hard plate at its ventral edges (as with the furca, the ventral edge of the hard plate appears dorsal when the ostracod is in its resting position). Muscles running to other parts of the body also attach to the ventral edges of this hard plate (one large, longitudinal muscle of the dorsal body section, attaches to the internal side of the dorsal ridge of this plate, anteriorly), although the parts these

muscles are servicing could not be determined in this study (more suitable preparation techniques would be required).

All of the above anatomical observations refer only to the cypridinids caught in baited traps. However, the hard sclerotized plate adjacent to the furca is also present in a similar form in other myodocopin families: in the philomedid Euphilomedes sp. 1, and in the cylindroleberidid T. brevis (the latter bears a row of long setae, see Fig 11B). The sclerosome does not occur in C. belgicae (Halocyprina) (Fig. 11C). A literature search revealed that the sclerosome is confined to the Myodocopina.

On comparison of the furcae of known scavenging cypridinids and cypridinids known not to scavenge (Fig. 12), there appears to be no significant morphological adaptations of the furca to aid feeding in scavenging cypridinids. The major differences in cypridinid furcal morphologies, such as the number, size and arrangement of claws on the lamellae, occur between the two subfamilies Cypridininae and Azygocypridininae. With few exceptions (eg. Sheina orri Harding, see Fig. 12) the furcae belonging to species within the same subfamily are morphologically similar, although vary in the number of claws on their lamellae.

There may be significant sexual dimorphism of the furca, such as in Sheina orri (Harding, 1966).

DISCUSSION

The Furca as a Scavenging Tool

The furca is shown to have a major role in the feeding process of scavenging cypridinids. Its main function appears to be the removal of small, workable sections of flesh from a food source. If the food source is a small fish, the fish scales are also sometimes removed by the furca.

The fact that the mandibles could tear away a section of fish in its grip while the furca pushed the ostracod away illustrates the strength of the mandibular muscles in locking the mandibles in one position. This may be useful in holding the ostracod in position while the furca makes its cut, so preventing the ostracod's body from being pushed away from the fish and the furca only scratching the surface of the food. The synchronization between the opening of the carapace and furcal lamellae means that the carapace is always open minimally during any activity requiring an open carapace. Thus, the ostracod's body is maximally protected against the environment by the carapace.

Ostracods are probably surrounded by a viscous medium due to their low Reynolds number. Therefore, the knife-like configuration of the furca provides a good design for the reduction of drag while cutting or digging and allows for a faster, more efficient, movement. Because the lamellae are only joined at their anterior ends, the interlocking of at least some claws would increase the structural stability and, therefore, the robustness of the furca. In some scavenging

cypridinids (eg. Cohenia sp. 1) the large second and fourth most posterior claws (often fused with the lamellae) may be designed to take most of the pressure during cutting because theoretically these claws would reach furthest into the food source on each cutting stroke, and therefore make the initial cut into tough flesh.

The cypridinids are very successful, and probably the only, Australian marine scavenging ostracods (Jim Lowry, personal communication). The feeding limbs of the cypridinids demonstrate an increased adaptation towards scavenging compared to those of the other extant myodocopin families (Philomedidae, Rutidermatidae, Sarsiellidae and Cylindroleberididae). However, the major function of the furca for many cypridinids is probably digging (Vannier and Abe, 1993). In fact the basic mechanism for digging into sediment or flesh is very similar. Therefore, a cypridinid furca modified for cutting would still permit efficient digging. The whole process is a compromise that reflects the versatility of the organ. The fact that the furcal lamellae are hinged on their anterior margins may also be a useful adaptation for digging, in varying the distance between the claws on opposite lamellae to suit sediments of different particle size and in holding sediment between lamellae to be ejected from the burrow. Therefore, members of other myodocopin families, and non-scavenging benthic cypridinids, may also exhibit this adaptation.

The genus Conchoecia Dana (Myodocopida: Halocyprina), which includes scavengers (Illes, 1961), exhibits an altogether different design of furca to the Myodocopina (eg.

Fig. 11D). Its species are planktonic (Illes, 1961) and therefore do not dig. This is reflected in a less robust furca and the occupation of a different scavenging niche to that of the cypridinids: Conchoecia would be outcompeted by the "heavyweight" cypridinids for the feeding on the rapidly decaying carrion (eg. Vader and Romppainen, 1985) in warm shallow waters.

Reasons for Sexual Dimorphism

Cohen and Morin (1990a) suggest reasons for sexual dimorphism in secondary sexual characters of valves, eyes and limbs. Collectively the dimorphism of the mandibles, fourth and fifth limbs, and the furcae of many myodocopins (Kornicker, 1981) are thought to be "related to copulation, female brooding, and/or differences in diets" (Cohen and Morin, 1990a). A difference between the male and female diet and/or habitat (ie. sediment type) would account for sexual dimorphism of the furca (as would diet differences for the mandibles, fourth and fifth limbs). However, the furcae are involved in the mating process of Skogsbergia sp. 1 (Chapter 7).

The Function of the Central Adductor Muscles

The central adductor muscles have a double function; closing the two carapace valves and suspending the body (which "floats") within the spherical carapace (Cannon, 1940). However, these central adductor muscles exist as a group of

muscles rather than one large muscle, and so are arranged in various patterns on their attachment to each carapace valve as seen in the muscle scars (Fig. 7). This arrangement may allow for different areas of the ventral carapace margin to be open to different degrees, as a single muscle would only permit a uniform opening and closing of the carapace. This allows appendages to be protruded through a gap in the carapace in one area, while the carapace can remain closed, or more realistically only slightly open, in other areas, thus providing increased protection from the environment for the soft body lying within the hardened carapace. The selvage, a thin, flexible, flap-like continuum of the anterior/ventral carapace margins (seen in Fig. 6, E and F), may also contribute to this protection.

The central adductor muscles are a useful phylogenetic character when preserved in fossil specimens, and the scars appear as a pattern of stripes (eg. Fig. 7) and/or spots on the carapace valves. Myodocopids with more highly derived characters (Siveter & Vannier, 1990) tend to have patterns of spots; perhaps these provide a more precise opening and closing of specific areas of the ventral carapace margins than do stripes, making spots a functionally and evolutionary advanced character.

The Sclerosome

The myodocopin body is unsegmented and bears a flexible outer membrane throughout most of its length, displaying the contours of the muscle bands lying just interior to the dorsal

body wall (eg. Fig. 10; B, E and F). However, posterior to these muscle bands, just anterodorsal to the furca, lies a region of hard (sclerotized) outer body wall (eg. Fig. 10C). This hardened plate has never previously been named or considered as a functional unit, yet it provides a strong attachment point for the muscles running to the furca in a similar manner to the individually termed internal sclerites. Therefore, I term this hardened (sclerotized) plate of the myodocopin dorsal body wall the 'sclerosome', from the Greek, meaning hard body.

The sclerosome is separated from the furca only by a small region of thin, flexible, sub-terminal body wall, allowing the furca to pivot on the internal sclerites of the body. The sclerosome is inarticulate (although it bears a fold near and parallel to its ventral and anterior margins), rigid, and does not represent the boundary of a body segment, nor, probably, any remnant of segmentation. When the carapace valves are opened, the sclerosome occupies the area of the body wall which comes into direct contact with the ostracod's environment, and hence provides protection for the body (for example against sediment particles or fish scales while the ostracod is digging or feeding on a fish, activities which require an open carapace).

The muscles running dorsally between the anterodorsal margin of the furca and the body (ie. the longitudinal muscles, responsible for moving the furca in a dorsal to ventral direction, in the ostracod's resting position, Fig. 7) attach to the ventral edges of the sclerosome (although the ventral muscles may attach elsewhere). Therefore, the high

degree of structural strength of the sclerosome provides the foundation for the powerful cutting and/or digging action of the furca. Additionally, the sclerosome provides an attachment point for muscles servicing other parts of the body, including the dorsal body section.

The sclerosome is approximately symmetrical along its longitudinal axis (dorsal ridge, appearing ventral when the ostracod is in its resting position) and occupies a length of the body similar to the entire length of the furca (about one-fifth to one-half of the body length). In some cypridinids, such as Cohenia sp. 1, the sclerosome may bear a dorsal patch of maroon pigment. The sclerosome is absent in halocyprins. Many halocyprins are planktonic and probably do not require such a high degree of body protection against their environment as myodocopins, most of which are benthic. This would explain the absence of a sclerosome, for example, in C. belgicae. In fact, the sclerosome is exclusively and always present within the Myodocopina (including Triadocypris spitzbergensis Weitschat, known only from fossils from the Lower Triassic, Weitschat, 1983).

CONCLUSION

The cypridinid furca plays an important role in removing flesh from an animal carcass. The sclerosome is a relatively large sclerotized plate of the dorsal body wall, almost adjacent to the furca. When the carapace is opened, the sclerosome is directly exposed to the environment, and

therefore provides protection for the soft ostracod body, for example from the rough surface of a food source. The central adductor muscles allow the carapace to open minimally during the extension of body parts through the carapace aperture. Therefore, the minimum area of body surface is exposed to the environment during such extensions.

The functional morphologies of the furca, sclerosome and central adductor muscles combine to permit cypridinids to successfully radiate into scavenging niches.

ACKNOWLEDGEMENTS

I thank the Australian Museum, Macquarie University, Smithsonian Institution, Manly Oceanarium and Coral Sea Television Pty Ltd for the use of their facilities, Noel Tait and Jim Lowry for critical manuscript review, Ray Cameron for his help with video techniques, Geoff Avern for his advice with electron-microscopy and photography, and Louis Kornicker and Wim Vader for their general advice on manuscript drafts. I also thank Frank Crandle and Kathy Price for making histological sections and staining, and Duane Hope for photographic guidance. Thanks are due to the Australian Museum Trust and the Smithsonian Institution for funding this project.

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Fig. 1. Generalized diagrams of myodocopin ostracods (carapaces indicated by dashed lines) with anterior end to the right and dorsal surface above, showing orientation of the furca (boundaries labelled); A, fully stretched position, depicting the furca as posterior to the body; B, resting position with the furca folded beneath the body (in which the ostracod spends most of its life).

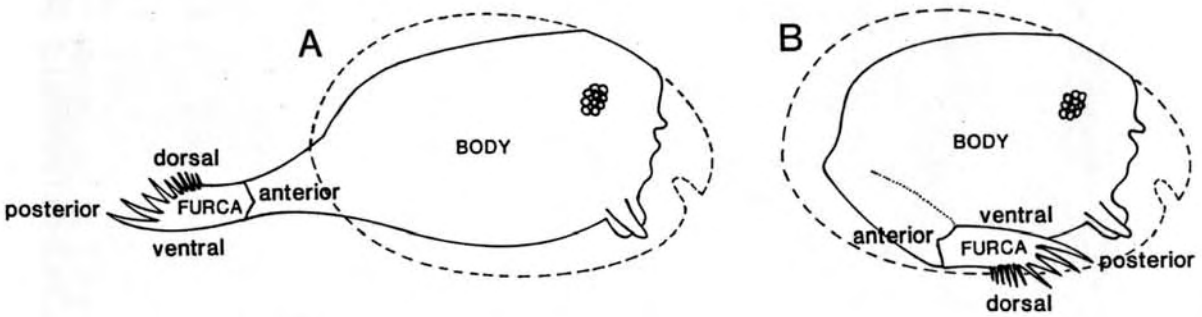
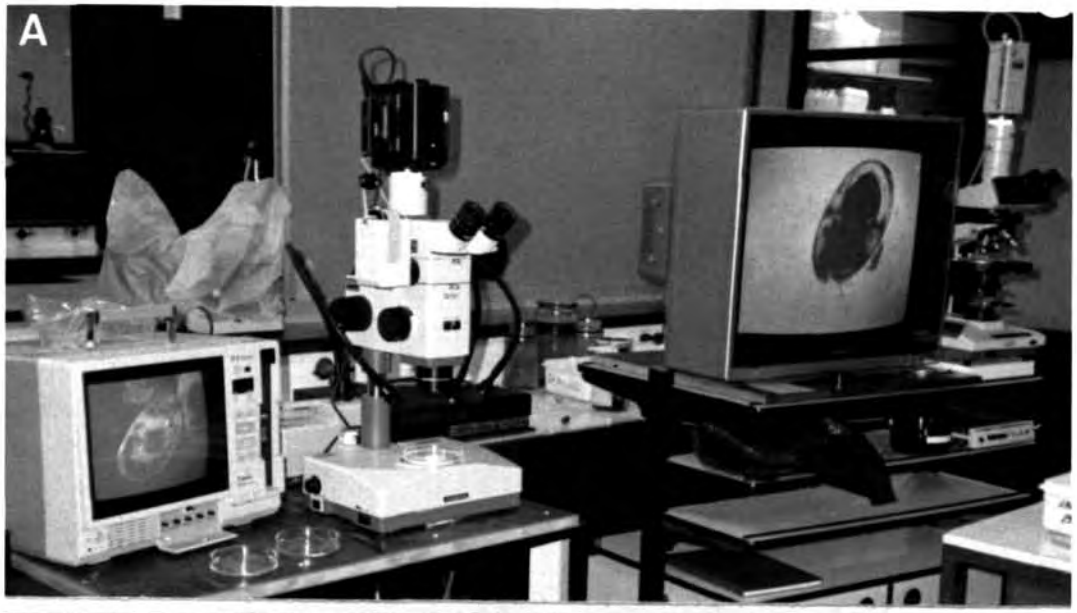

A
BODY
dorsal
posterior
FURCA
anterior
ventral
B
BODY
ventral
anterior
FURCA
posterior
dorsal

Fig. 2. Apparatus used to video ostracods feeding. A, stereo (left) and compound microscopes connected to video cameras (ostracods viewed in a Petri dish and cavity slide respectively, providing a dorsal view); B, Broadcast Television Systems camera, mounted on tracks (ostracods viewed in a flow through aquarium, providing a lateral view).


A

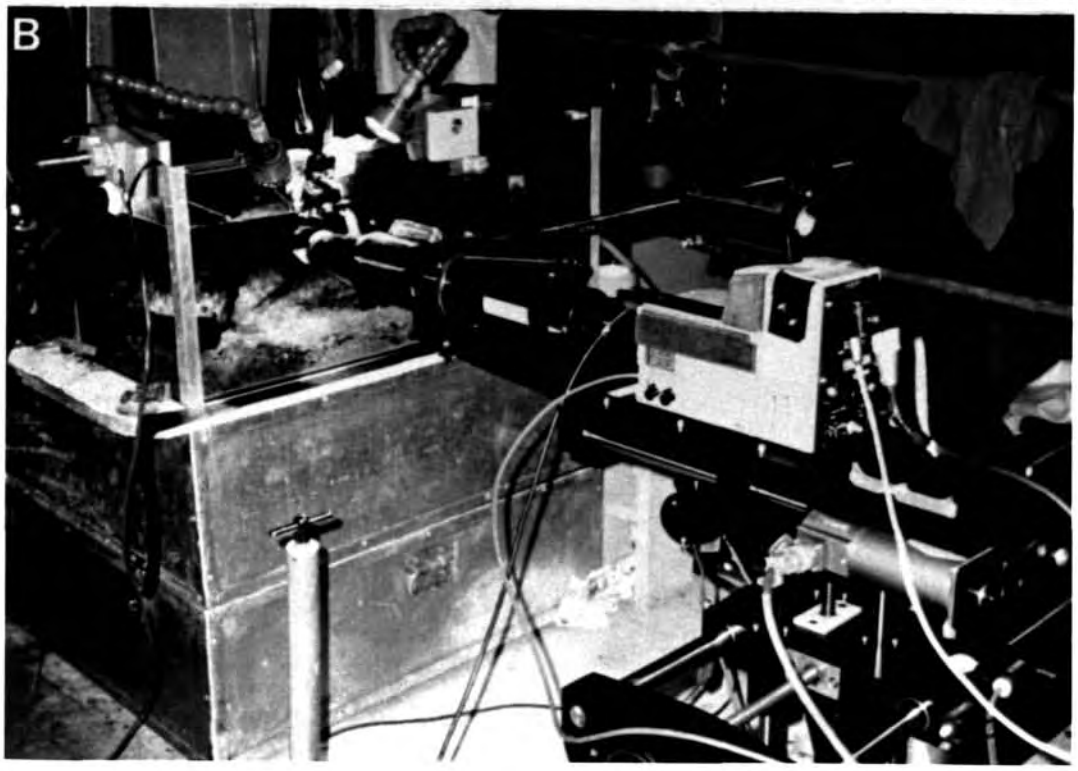
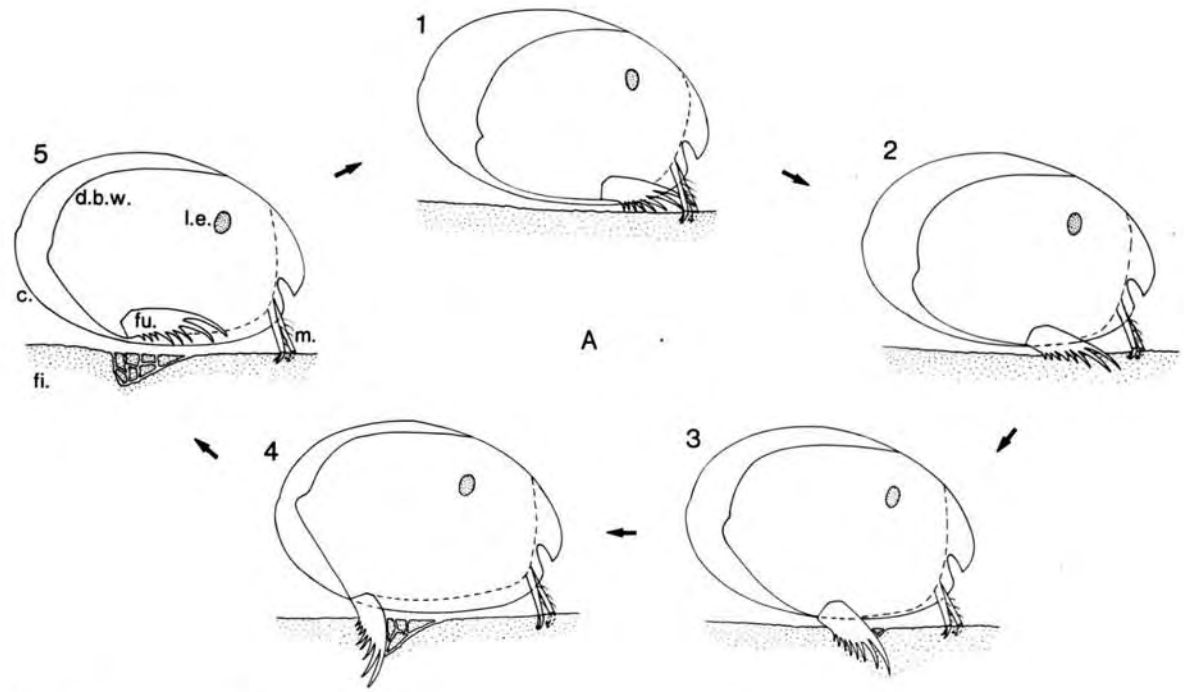
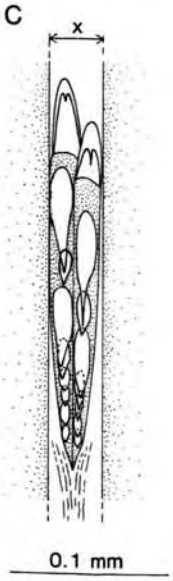
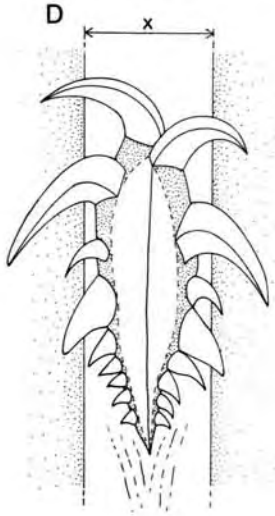
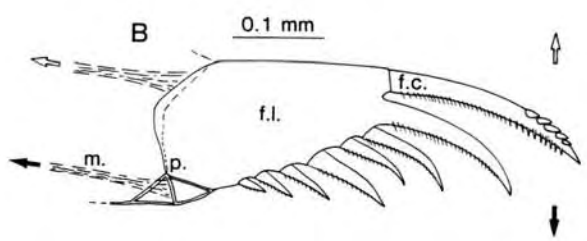

B

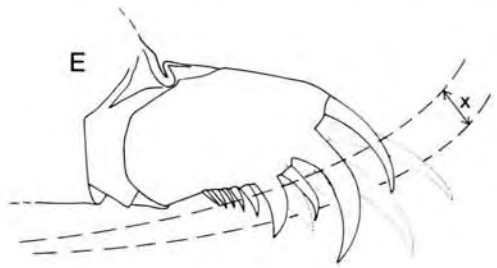
Fig. 3. A, generalized diagram of the cutting cycle of scavenging cypridinids, right carapace valve removed, showing left carapace valve (c.), dorsal body wall (d.b.w.), fish section (fi.), furca (fu.), lateral eye (l.e.) and mandibular palps (m.), position 5 shows part of recovery stroke; B, left furcal lamella (f.l.) of Skogsbergia sp. 1 (medial view) showing furcal claws (f.c.), longitudinal muscles (m., dorsal muscles below, ventral muscles above) and pivoting point or fulcrum (p.). C-E: Cohenia sp. 1; C, ventral view of furca protruding through narrow carapace aperture; D, ventral view of furca protruding through wide carapace aperture; E, lateral view of right furcal lamella, first three claws of left lamella dotted, position of ventral margins of carapace valves (displaying wide aperture) dashed. C and D illustrate the synchrony between the opening of the carapace aperture and the furcal lamellae. x = carapace aperture.











0.1 mm

0.1 mm

Fig. 4. A-D, light micrographs of Skogsbergia sp. 1, adult females, illustrating some different positions of the furca (f) relative to the body, first antennae (a1) and mandibular palps (m) also displayed. Sclerosome (s) is protruded through carapace aperture in D; body is contained within the carapace in A-C. Scale = 1 mm.

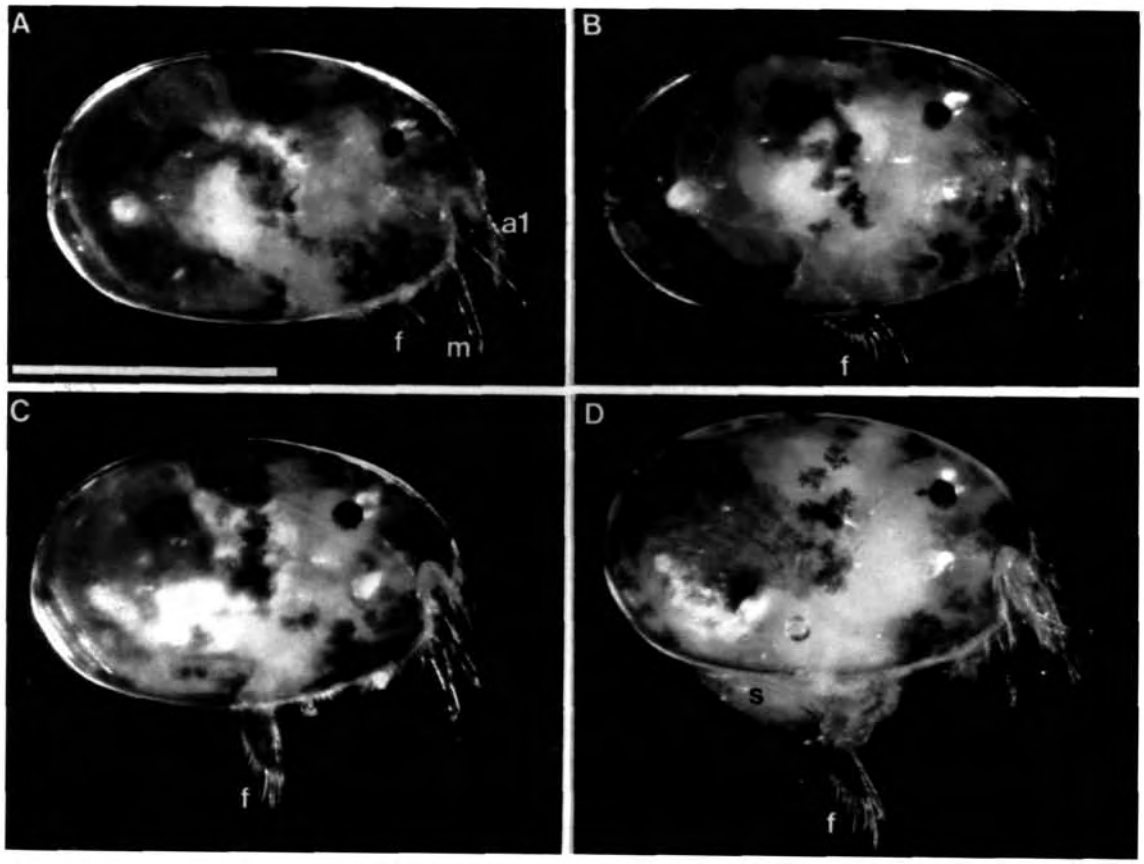

A
a1
f
m
B
f
C
f
D
s
f

Fig. 5. Scanning electron micrographs of the feeding parts of Cohenia sp. 1: A, lateral view of furca; B, dorsal view of furca; C, claws of left mandible, lateral view; D, posterior view of peg, teeth (1st article), a- and b-setae (2nd article) of fifth limb endopodite; E, ventral view of upper lip showing pores (example of a pore arrowed). Scales: A, B and E = 100μm; C and D = 20μm.

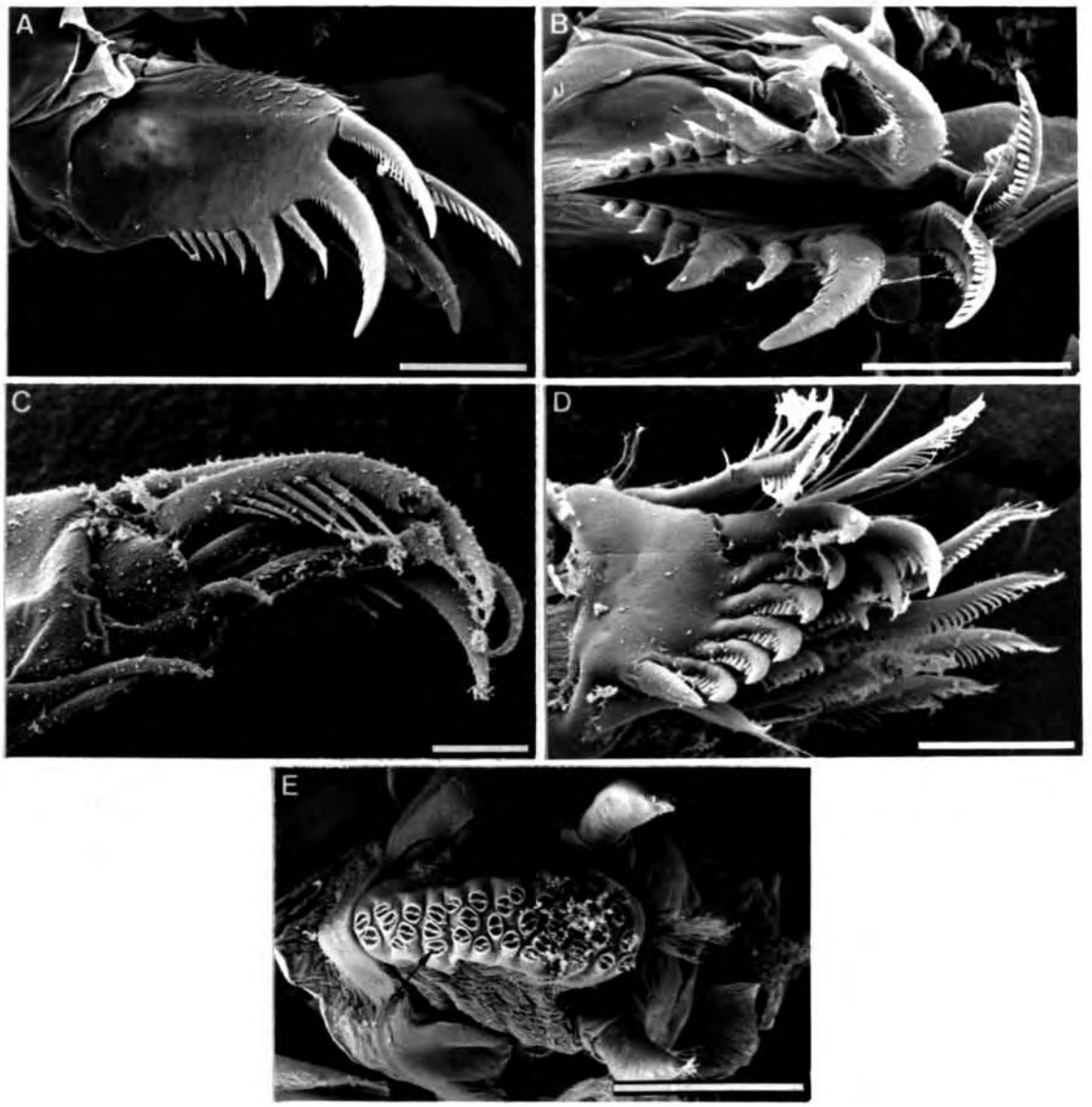

A
B
C
D
E

Fig. 6. Scanning electron micrographs of Azygocypridina lowryi, juvenile females, in resting position: A, lateral view, left carapace valve removed, showing furca (f), central adductor muscles (c), first antennae (a1), second antenna (a2), mandibular claws (m), epipodial plate of the fifth limb (e), seventh limb (s), dorsal body wall (d), sclerosome (sc) and right carapace valve (ca); B, ventral view, carapace removed (showing dorsal view of furca); C, anterior view of whole animal; D, anterior view of whole animal with food (fish section, arrowed) being held by the furca; E, anterior view of furca protruding through carapace; F, ventral view of furca protruding through carapace. E and F illustrate the synchrony between the opening of the carapace aperture and the furcal lamellae (when carapace is almost closed, lamellae are closed), thus maximum protection of the body is provided. Scales: A-D = 2 mm; E and F = 0.5 mm.

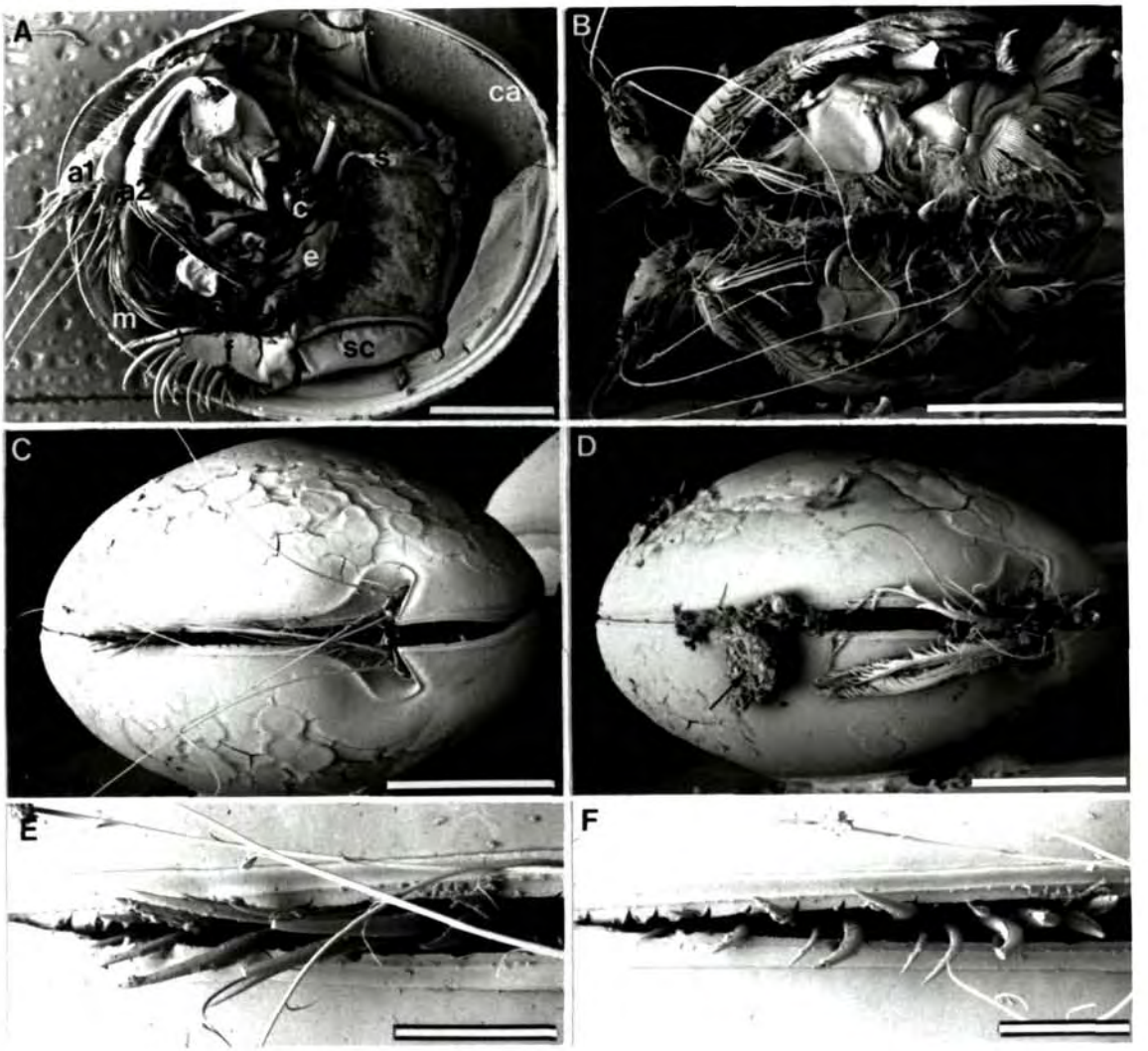
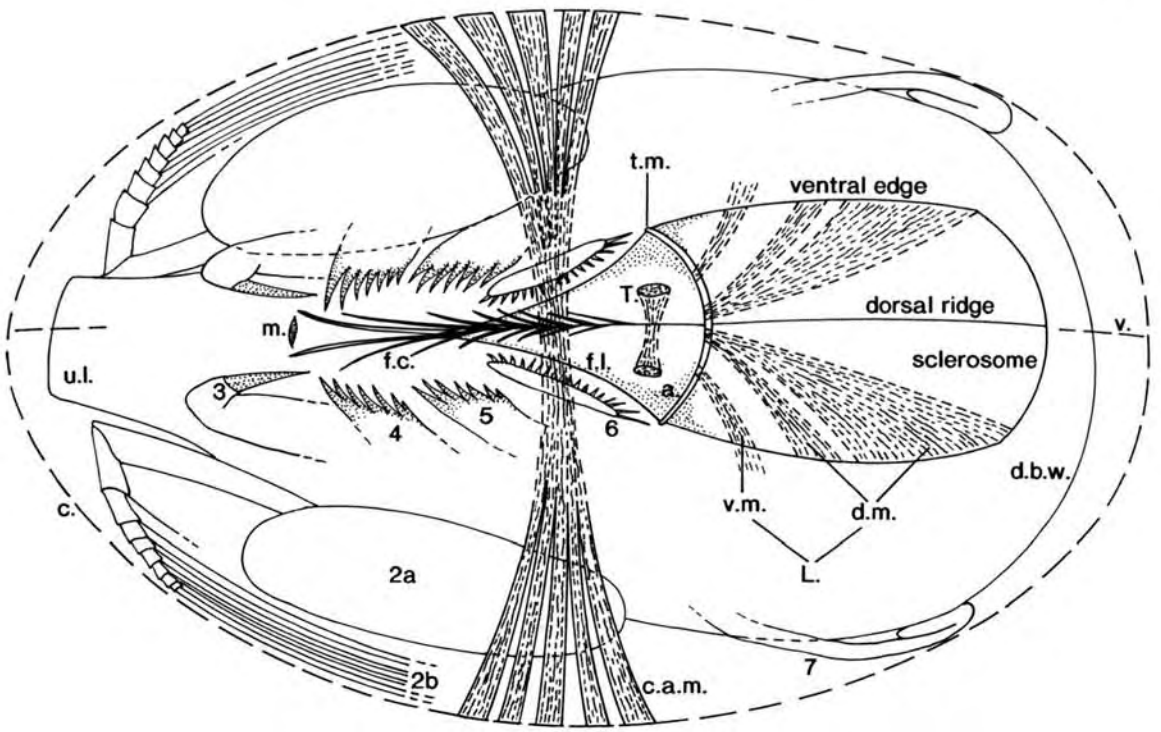

A
ca
a1
a2
s
c
e
m
sc
B
C
D
E
F

Fig. 7. Generalized ventral view of Azygocypridina lowryi, adult female, in resting position, carapace removed (position of carapace dashed), anterior is to the left. Furcal muscles and central adductor muscles (c.a.m.) are illustrated, including a lateral view of the scars left by the c.a.m. on the right carapace valve at their points of attachment (below). L. = longitudinal furcal muscles (v.m. = ventral muscles; d.m. = dorsal muscles); T. = transverse furcal muscles; f.l. = furcal lamella; f.c. = furcal claws; a. = anterior margin of furcal lamella; t.m. = thin membrane; c. = position of carapace; v. = position of ventral carapace margins when carapace is closed; u.l. = upper lip; m. = mouth; d.b.w. = dorsal body wall; 2a = protopodite of second antenna (encompassing natatory muscles); 2b = natatory setae of second antenna; 3 = mandibular claws; 4 = claws of fourth limb; 5 = claws of fifth limb; 6 = sixth limb, end article; 7 = seventh limb.



c.a.m. scars
(on right carapace valve)

3 mm

Fig. 8. Light micrographs of a longitudinal section of the edge of the furca and body of Cohenia sp. 1, stained with a modified Mallory solution: A, showing pivoting point (fulcrum) of the furca on the body and musculature (furca is to the left); B, area of flexible body wall where the body joins with the anteroventral margin of the furca. Scales: A = 0.1 mm; B = 10μm.

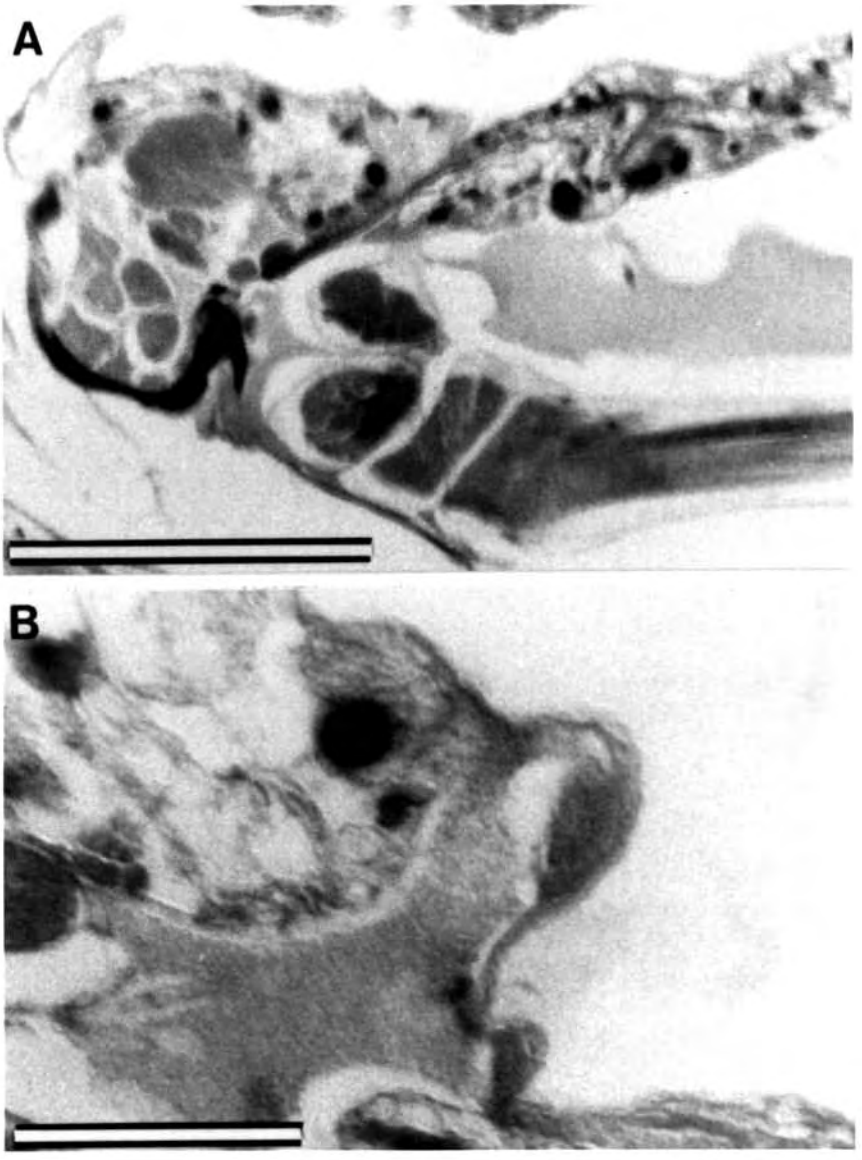

A
B

Fig. 9. Diagram of a longitudinal section of the edge of the furca and body of Cohenia sp. 1. Posterior end of the ostracod is to the left. This gives an explanation of Fig. 8A, also showing region of micrograph 8B.

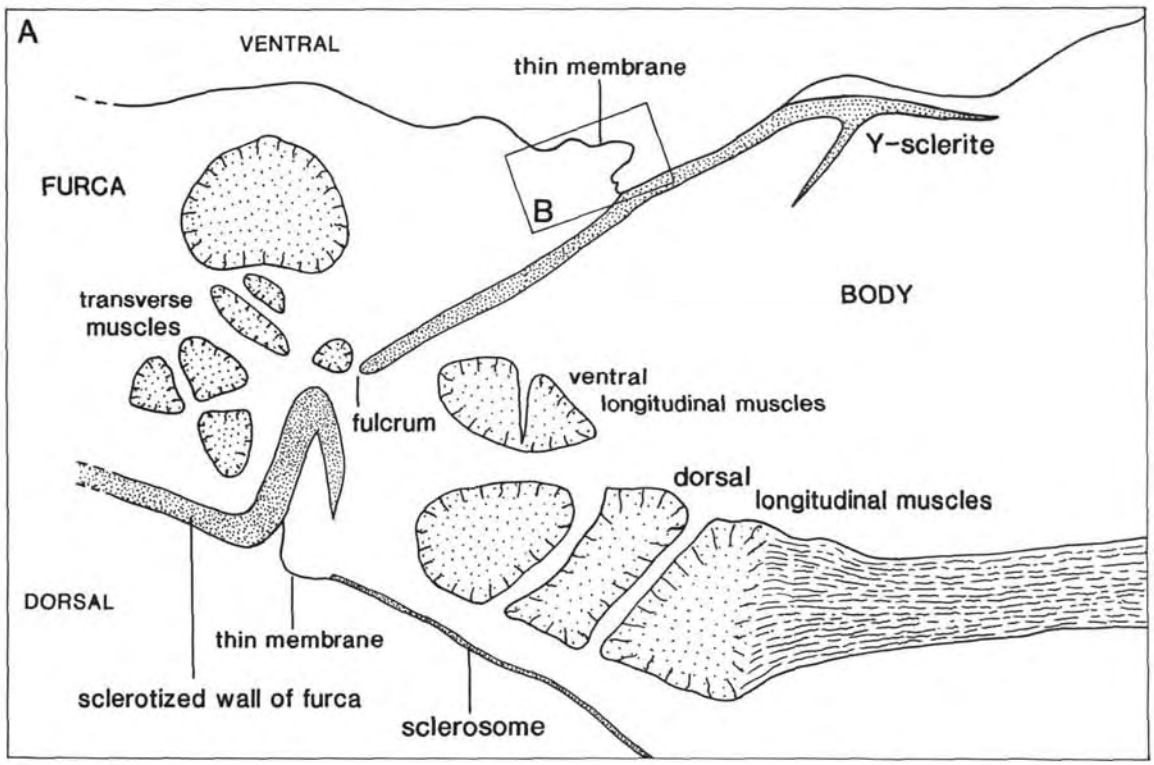

A
VENTRAL
thin membrane
Y-sclerite
FURCA
B
BODY
transverse
muscles
ventral
longitudinal muscles
fulcrum
dorsal
longitudinal muscles
DORSAL
thin membrane
sclerotized wall of furca
sclerosome

Fig. 10. Scanning electron micrographs of Skogsbergia sp. 1. A and B, adult male, right carapace valve removed, resting position, lateral view; A, whole animal, B, section of dorsal body wall (relatively well stretched). C, A-1 juvenile stage, carapace removed, resting position, ventral view of animal, showing dorsal view of furca and sclerosome. D and E, adult female, right carapace valve removed (left carapace valve distorted during drying process), stretched position, lateral view; D, whole animal, E, section of dorsal body wall (displaying folds due to compression; sclerosome does not compress), showing anterior part of sclerosome. F, A-2 juvenile stage, resting position, carapace removed, dorsal body wall and anterior part of sclerosome, lateral view (similar features to adult). Anterior of ostracods is to the right in A-E, and below in F; s = sclerosome, f = furca, c = carapace, m = mandibular palps. Scales: A and D = 0.5 mm; B = 50μm; C and F = 0.2 mm; E = 0.1 mm.


A
c
m
D
s
c
f
B
s
E
s
C
s
F
s

Fig. 11. Scanning electron micrographs of the dorsal sections of non-cypridinid ostracods in their resting positions, carapaces removed, lateral views. A, sclerosome of Euphilomedes sp. 1, furca (f) to the left, dorsal surface above. B, Dorsal body wall of Tetraleberis brevis showing gills (g, only occur in cylindroleberidids), and sclerosome (s, bearing a dorsal longitudinal setal row), furca (f) is to the left, dorsal surface above. C, Dorsal body wall of Conchoecia belgicae (adult female), furca (f) below, dorsal surface to the right (sclerosome is absent). D, Furca of C. belgicae (adult female). Scales: A = 0.1 mm; B = 0.5 mm; C and D = 0.2 mm.

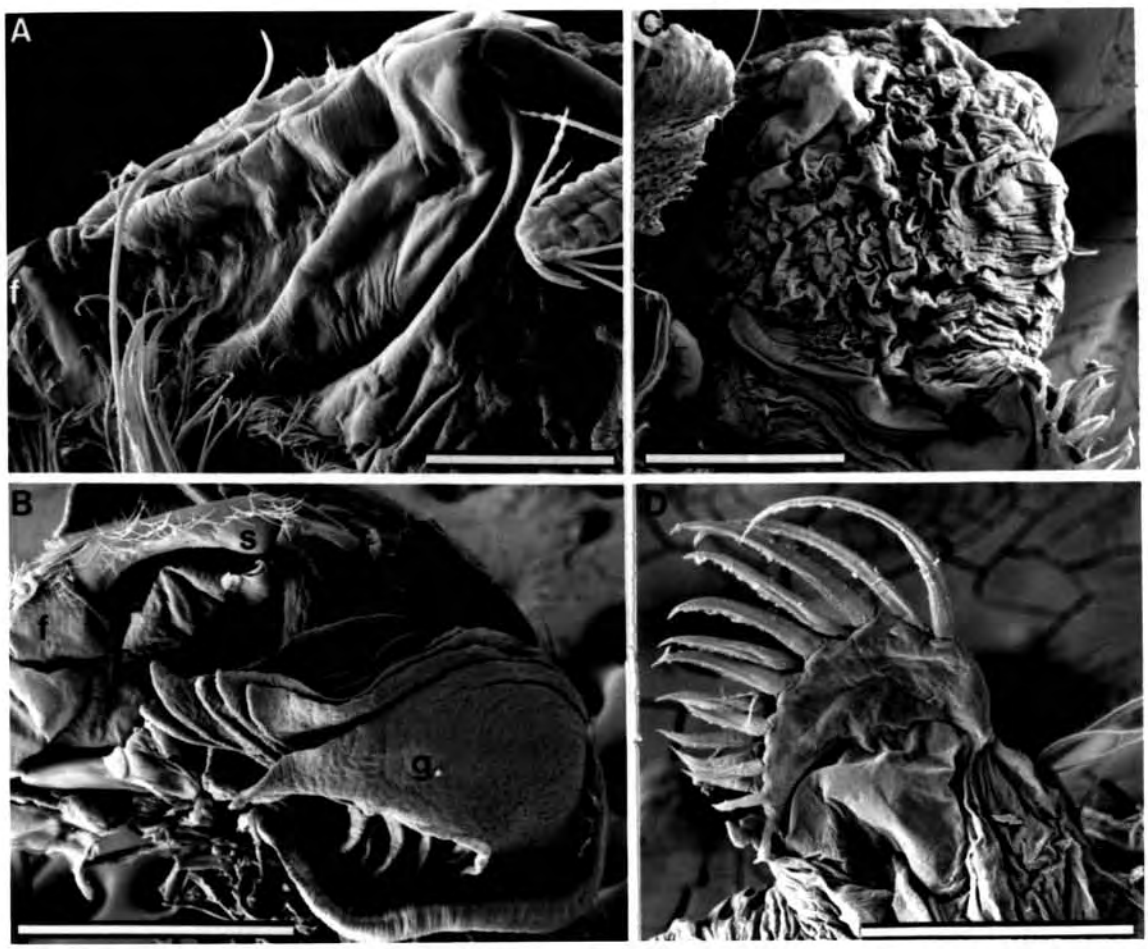

A
f
C
B
s
f
g
D

Fig. 12. Representative furcae of different cypridinid genera, lateral views; A, E-H, J-N, P, R, S, U and V from Poulsen (1962), B from Harding (1966), C from Sars (1928), I, O, Q, T and X from Kornicker (1975) and D from Kornicker (1979). Most species have only been caught from unbaited benthic sampling, therefore feeding mode is unknown (unless otherwise stated). There are intrageneric and age differences, and sexual dimorphism of the cypridinid furcae.

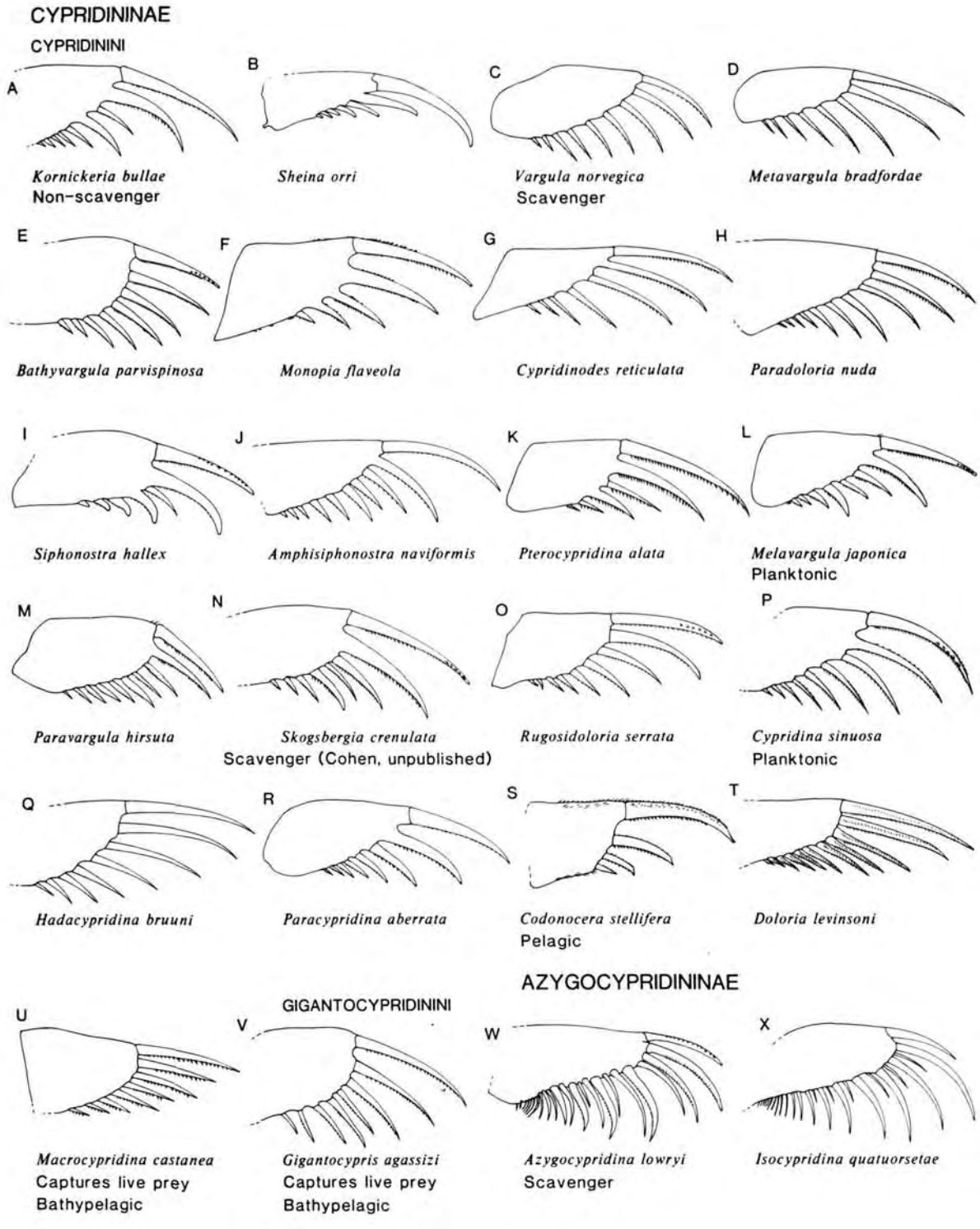

CYPRIDININAE
CYPRIDININI
A
B
C
D
Kornickeria bullae
Non-scavenger
Sheina orri
Vargula norvegica
Scavenger
Metavargula bradfordae
E
F
G
H
Bathyvargula parvispinosa
Monopia flaveola
Cypridinodes reticulata
Paradoloria nuda
I
J
K
L
Siphonostra hallex
Amphisiphonostra naviformis
Pterocypridina alata
Melavargula japonica
Planktonic
M
N
O
P
Paravargula hirsuta
Skogsbergia crenulata
Scavenger (Cohen, unpublished)
Rugosidoloria serrata
Cypridina sinuosa
Planktonic
Q
R
S
T
Hadacypridina bruuni
Paracypridina aberrata
Codonocera stellifera
Pelagic
Doloria levinsoni
AZYGOCYPRIDININAE
GIGANTOCYPRIDININI
U
V
W
X
Macrocypridina castanea
Captures live prey
Bathypelagic
Gigantocypris agassizi
Captures live prey
Bathypelagic
Azygocypridina lowryi
Scavenger
Isocypridina quatuorsetae

Table 1. Cypridinid specimens used in this study. Material deposited in the Australian Museum.

Species	Registration Number	Locality
Skogsbergia sp. 1	AM P45068	Watsons Bay, NSW, Australia
Vargula sp. 1	AM P45069	Watsons Bay, NSW, Australia
Skogsbergia sp. 2	AM P45070	Port Jackson, NSW,Australia
Lowrya sp. 1	AM P45071	Port Jackson, NSW,Australia
Lowrya kornickeri	AM P45072	Port Jackson, NSW,Australia
Vargula sp. 2	AM P45073	Jervis Bay, NSW, Australia
Skogsbergia sp. 3	AM P45074	Jervis Bay, NSW, Australia
Cypridinodes sp. 1	AM P45075	Jervis Bay, NSW, Australia
Paradoloria sp. 1	AM P45109	Jervis Bay, NSW, Australia
Azygocypridina lowryi	AM P45076	Wollongong, NSW, Australia
Cohenia sp. 1	AM P45077	Bate Bay, NSW, Australia
Tetraleberis brevis	AM P45110	Lizard Is., Qld., Australia
Euphilomedes sp. 1	AM P45111	Lizard Is., Qld., Australia
Conchoecia belgicae	AM P45112	Macquarie Is., Australia

CHAPTER 5

Exoskeleton and position of the flexible setules on the myodocopin (Crustacea: Ostracoda) first antenna

(Prepared for Journal of Crustacean Biology)

ABSTRACT

Halophores are setules with an unique exoskeletal ultrastructure comprising a layer of very fine rings, with walls approximately circular in cross-section, covered by an outer, probably elastic, layer or sheath. There is a single pore at the halophore tip. This organization allows for great flexibility. If dendrites innervate halophores, the flexibility may aid in sampling for water-borne chemicals or mechanoreception. The s-seta (formerly the sensory seta) is a seta arising from the fifth article of the myodocopin first antenna that frequently possesses numerous long halophores. The s-seta is always and only present in the Myodocopina. The collective halophores distributed over the whole of a first antenna are termed the halothalium.

INTRODUCTION

The ostracod sub-order Myodocopina, within the order Myodocopida, comprises five families; Cypridinidae, Cylindroleberididae, Philomedidae, Rutidermatidae and Sarsiellidae (Kornicker, 1975). Myodocopins occur in marine or brackish environments world-wide at all depths (Cohen, 1982). Most (including juveniles) can swim but are benthic or epibenthic (only 3-6 of the 26 described cypridinid genera are wholly or mostly planktonic) for much of their lives (Cohen, 1982). They all exhibit sexual dimorphism (Cohen & Morin, 1990). They are "filter-feeders" (Kornicker, 1975), or more accurately comb-feeders because they typically operate at low Reynolds numbers (Cohen, 1989), scavengers, active predators, "collectors" (collect detritus from the sediment; Walker, 1972) or detritus feeders (Cannon, 1933; Kornicker, 1975).

Previous terminology

The first antenna (antennule) of the Myodocopina includes about seven long terminal and subterminal setae of previously unconfirmed function (Fig. 1). The first antenna of Vargula hilgendorfii Poulsen (Cypridinidae) was observed to extend when resting on the substrate. Thus the function of at least some of the first antennal setae was believed to be tactile (Vannier & Abe, 1993). In addition, the function of the seta arising from the fifth article has long been designated as sensory (eg. Skogsberg, 1920; Sars, 1922). However no such evidence has been presented to substantiate these sensory

claims. Presumably, based on morphological similarities, original assumptions were made from comparisons with homologous or convergent structures in other crustacean taxa. Poulsen (1962) followed the terminology for myodocopin limbs as established by previous myodocopin workers but remained unconvinced of the implication about their function.

Morphology of the myodocopin first antenna

The myodocopin first antenna consists of eight articles (some occasionally fused); the more proximal articles bearing various (often short) setae, three of the four distal articles (namely 5, 7 and 8) with about seven relatively long setae (Fig. 1). It is these longer setae that project through the anterior end of the open carapace and probably reach out beyond the boundary layer (ostracods typically operate only at low Reynolds numbers, eg. Koehl & Strickler 1981). These setae are historically termed: the sensory seta (arising from the 5th article); a- (usually short), b- (usually mid-long) and c-setae (from 7th article); and the d-, e-, f- and g-setae (from 8th article; Fig. 1). Some are missing in a few myodocopin taxa. Most are annulate, and may bear spines, setules, or "suckers" (the last in males only). The "sensory" seta of the fifth article usually appears morphologically distinct. This mid-long seta is sometimes widened (or bulbous) at the base or has a separated basal section, and usually has at least six long thin flexible setules. These setules, previously unconventionally termed filaments (see Watling, 1989) have been described as unringed although figures in the literature

often illustrate them shaded using dots, giving them a granular appearance (eg. Poulsen, 1962) which is how they appear below about 250 times magnification.

This study shows the setules of the b- to g- and the "sensory" myodocopin first antennal setae to share the same unique ultrastructure and all are termed 'halophores' herein. The "sensory" seta is termed the 's-seta'. The collection of halophores on one first antenna is termed the 'halothalium'. The terms halophore, s-seta and halothalium (designated in this study) are used hereafter to avoid unnecessary confusion (an explanation of these terms can be found in the Discussion).

Myodocopin first antennal nervous system

The nervous supply of the first antenna of the cypridinid Doloria levis Skogsberg arises from two swellings on the ventral side of the fore-part of the nerve ring, marking the deuterocerebral part of the brain (Cannon, 1931). The antennulary basal ganglion is the largest in the body of D. levis and occupies most of the basal article. What appear to be motor nerves pass directly through the ganglion to the muscles, but other antennulary nerve fibres terminate in cells in the postero-medial corner of the ganglion. From here other fibres extend to the distal end of the ganglion, passing out as a bundle running to the tip of the limb. Between these two bundles of nerves lie a group of four or five bipolar cells, giving rise to medium-sized giant fibres (Cannon, 1931). The antennulary nerves are similar in the cypridinid Gigantocypris

mulleri Skogsberg (Cannon, 1940). However, nothing more detailed regarding the precise innervation of the first antennal setae has been published.

The aim of this study is to describe the morphology of the halophore exoskeleton. Techniques suitable for the study of nervous structures are not employed.

MATERIALS AND METHODS

Specimens examined

Living specimens of Azygocypridina lowryi Kornicker were collected in single chamber baited traps designed by Keable (1995). These were set overnight at depths of 200 m (34°31.48'S 151°13.22'E) and 300 m (34°31.80'S 151°15.60'E) off the Wollongong (New South Wales, Australia) coast. The ostracods were removed from the traps and immediately transported to the laboratory in aerated, fresh sea water. Behavioural observations were carried out within 4 hours, during which time they appeared to be in a healthy condition.

Preserved museum specimens (fixed in 5% formaldehyde and preserved in 70% ethanol) of ostracods and other crustaceans were examined (Table 1).

Anatomical study

For scanning electron microscope examination, preserved museum

specimens were cleaned using five half-second exposures to ultrasound, critical point dried using a Bio Rad CPD 750, then coated with gold. These specimens were examined using a Cambridge Instruments S120 scanning electron microscope.

Accidentally broken halophores were studied to view the internal architecture of their exoskeletons. In some cases, the rings of the halophores themselves were broken, and the internal architecture of the individual rings was examined.

The setae and setules of myodocopin limbs other than the first antenna were also examined under the scanning electron microscope in search of structures with similar external morphologies. Azygocypridina lowryi was mainly used in this investigation due to its relatively large size (carapace length about 11 mm), although preserved museum specimens of species from other ostracod taxa and crustacean classes (Table 1) were compared.

Behaviourial study

Video recordings were made of living A. lowryi in a large Petri dish to determine the movement and action of the first antennal setae. Behaviourial observations were recorded using an Olympus SZH stereomicroscope connected to a Panasonic F10 video camera.

Literature comparisons

Illustrations of first antennae and s-setae from different myodocopins were obtained from the literature. These were

compared to demonstrate the morphological variation in halophores, and their arrangements on the first antennae.

RESULTS

Exoskeletal morphology

Of the material examined in this study (Table 1) only the myodocopins exhibited setules, confined to the b- to g- and s-setae of their first antennae, with the same unique exoskeletal morphology as illustrated in Fig. 2. These setules, or halophores, arising terminally or non-terminally on the first antennal setae, are composed, throughout most or all of their length, of a series of rings (circular in cross-section) lying side-by-side (Fig. 4, A). There is a minute pore at the tip of each halophore (Fig. 3, E). The rings of the halophores range from about 110 to 670 nm in thickness within the Myodocopina (eg. Fig. 5; Table 2) and are themselves hollow or contain a less dense material to that of the outer section (Fig. 4, B). The bases of the halophores are not finely annulate where they do not arise terminally on a seta. Each halophore bears a thin outer layer of a material (sheath) (Fig. 2; Fig. 3, F), which follows the grooved external contours of the halophore set by the rings. Some myodocopins bear first antennal setae (other than the b- to g- or s-setae) with unringed setules, although these setules are evenly tapered and much thinner than halophores (almost appearing like long spines, though sometimes flexible).

Conchoecia belgicae Mueller (Myodocopida: Halocyprina) bears terminal first antennal setae with "wrinkled" surfaces which may indicate the presence of fine rings beneath, although these setae appear to have collapsed walls, not seen in halophores when observed under the same conditions (see ultrastructure section of materials and methods).

The b-, c-, f-, g- and s-setae (and the "bases" or shafts of the d- and e-setae) show walls comprising large connected sclerotized rings (with walls approximately rectangular in cross-section). A few setules on the b- and c- first antennal setae of male cypridinids bear "suckers" (see Kornicker, 1983); these setules are annulate with ring widths greater than 1 μm. The coarsely annulate first antennal setae and setules are quite rigid when compared to the flexible halophores.

Internal structures

In addition to confirming the ring-type construction of the exoskeleton, broken halophores revealed thin interior structures, of unknown ultrastructure, running approximately centrally through the halophores (Fig. 6).

Movements of cypridinid first antennal setae

Video recordings of the first antenna of a living A. lowryi specimen show that the c- and s-setae move equally and opposite to the f-seta. The g-seta also exhibited slight movement. At rest, the s- and c-setae lie parallel and

separated from the f-seta by an angle of about 30°. Upon contraction of the muscles attached to the 6th, 7th and 8th articles, these setae move towards each other so that all become parallel, then quickly return to their original resting positions (Fig. 7). This cycle takes less than half a second to complete. As the long rigid setae move uniformly, their halophores flex quite readily subtending a much greater arc and consequently pass through a larger volume of water.

Variation of the s-seta (general)

Halophores occur in all myodocopins and the s-seta is present on the fifth article of the first antenna of all myodocopin taxa, although its form shows much variation. The s-seta usually appears by the third instar (Fig. 8, C and D; Kornicker & Iliffe, 1989). Although present in both sexes, the s-seta (and other parts of the myodocopin first antenna) is sexually dimorphic to different degrees and may also show slight variation between that of the right and left limbs (Fig. 9, D).

The s-seta varies markedly among the Philomedidae and is a useful character in subfamily determination and phylogenetic studies (Kornicker, 1978). However, convergence must be considered when comparing the s-setae of different myodocopin families (represented in separate clades; Kornicker, 1986). For example one form of s-seta appears in both the Philomedidae and Sarsiellidae, but is considered convergent because these two clades do not have an immediate common ancestor (Kornicker, 1978, 1986).

The s-seta is confined to the Myodocopina. However comparable structures exist within the Halocyprina (Myodocopida). Halocyprins frequently possess groups of long thin walled setae ("filaments") on the first antennae which may be finely annulate (Angel, 1970; Martens, 1979). For example, species of Euconchoecia (Halocyprina) have a pad of setae on the fifth article of the first antenna. This is probably a parallelism because halophores are setules and therefore cannot be homologous. In any case, these setae exhibit a different external morphology to halophores in C. belgicae; if fine rings are present in the setal walls of this halocyprin then they probably have a different composition to halophore rings. Podocopid ostracods bear no structures comparable with the s-seta.

Detailed morphological variation of the s-seta and the distribution of halophores on the first antenna

Cypridinidae. The shaft of s-seta is often widened proximally usually with two groups of halophores: several long halophores joined to the setal shaft proximally (sometimes as a double row) and fewer halophores (often short) joined more distally and sparsely. Halophores usually appear slender and not tapered. In most cypridinids, the male s-seta is similar to that of the female or comprises a few more halophores, although the shaft and halophores may be slightly wider in the male. A typical s-seta for this family exists in Cypridina acuminata Müller (Fig. 8, E). However, notable exceptions occur in some genera such as Bathyvargula (Fig. 8, G and H)

and Metavargula where the male s-setal halophores differ from those of the female in that they appear much broader and flattened, and the shaft of the male s-seta may have an almost bulbous base. The cypridinids are the myodocopins with the oldest fossil record (McKenzie, 1972), and Kornicker (1978) suggests that their s-seta is the primitive type.

In some genera, such as Cypridina (Fig. 8, E) the c- and f-setae are unusually long and, therefore, their halophores are capable of reaching further out when the antenna is extended.

An exception to the general arrangement of halophores making up the halothalium within the Cypridinidae is shown by the male first antennae of Skogsbergia (Fig. 8, B), Pterocypridina, Heterodesmus, Siphonostra and Paravargula. The males only of these genera typically have numerous (long in most genera) halophores arising from the widened bases of the f- and g-setae. Therefore in the males of these genera the greatest proportion of the halothalium occurs on the f- and g-setae (as opposed to the s-seta bearing the most dense collection of halophores in other cypridinids).

Cylindroleberididae. A high degree of sexual dimorphism of the s-seta is usually exhibited (Fig. 9, A and B). The female s-setal shaft is quite stout bearing four to ten terminal halophores and up to nine situated more proximally (shorter). The male s-setal shaft is often stouter with numerous halophores arising throughout its length, giving a plumose appearance. Exceptions occur in the genus Homasterope where the male s-seta is similar to that of the female (Fig. 9, C).

Also the female s-seta is bare (no halophores) in the genus Microasteropteron; the d- or e-seta of the eighth article of the first antenna is also missing in this genus.

Philomedidae. The s-seta is without long halophores in females with numerous long halophores in males. The fifth joint of the first antenna (from which the s-seta arises) is well developed and rectangular or trapezoid in the female and small and triangular in the male (Fig. 9, E and F).

Kornicker (1978) divided the male philomedid s-seta into two types: type 1, with an elongated widened proximal (one-third to two-thirds of the total length) shaft region bearing long halophores (Fig. 9, I); type 2, with a bulbous proximal (about one-fifth of the total length) shaft segment bearing the halophores, with the proximal edge of the bulb projecting backwards (Fig. 9, E and G). The male s-seta of the genus Paraphilomedes (Fig. 9, H) appears transitional between the two types but is assigned to type 1 as the bulbous shaft section does not strictly project backwards (Kornicker, 1978). Kornicker (1978) uses this character in part to define two subfamilies: Philomedinae (type 1 s-seta) and Pseudophilomedinae (type 2 s-seta).

Kornicker (1978) considered the type 1 s-seta to be plesiomorphic within the Philomedidae, as it appears intermediate between the male cypridinid s-seta and the type 2 s-seta, and considered the type 2 s-seta to be a synapomorphy.

Rutidermatidae. The female s-seta is either bare (presumably secondarily lost the halophores) or possesses two short

proximal and two terminal halophores. The male s-seta is stout with numerous long halophores, appearing plumose.

The male s-seta is most similar to the type 1 s-seta of the philomedid male (Kornicker, 1978). Males of Rutiderma and Scleraner can be distinguished by the extent of coverage of the broad proximal part of the s-setal shaft by halophores; in Scleraner (Fig. 9, J) halophores occur throughout the length of this part, in Rutiderma (Fig. 9, K) they are confined to the distal third of this length or less (Kornicker, 1994).

Sarsiellidae. The female s-seta is either bare (presumably secondarily lost the halophores) or with two or three short halophores. The male s-seta exhibits a proximal bulbous shaft segment bearing numerous halophores.

The male s-seta resembles the type 2 s-seta of the male Philomedidae, although the two are considered to be convergent (Kornicker, 1978).

DISCUSSION

Myodocopin first antennal setae and setule nomenclature

This study shows that in all of the myodocopins examined (Table 1) all of the setules (except those bearing "suckers" in male cypridinids) of the b- to g- and s- first antennal setae exhibit the same unique exoskeletal morphology, which includes a layer of very fine rings (Fig. 2). Therefore, they probably have a similar function. I term an individual setule

of the myodocopin b- to g- and s- first antennal setae (except those bearing "suckers" in male cypridinids) a 'halophore' (from the Greek, meaning ring-bearing). The Greek word "halo" meaning ring is used rather than the more appropriate "annulus" (Latin for ring) in this nomenclature to avoid confusion with most of the terminal and subterminal first antennal setae which are described as annulate. The rings of these setae are much wider than those of the halophores and have thicker walls of approximately rectangular cross-section. Halophores may branch off a seta terminally (ie. at the terminal end of many b- to g- and s-setae), where the seta-setule interface occurs at the position where the fine annulations of the halophores begin, or may branch off non-terminally. The d- and e- setae, which were each previously thought to be one long bare seta, are actually each composed of a short setal shaft (with approximately parallel margins) constricting slightly at the shaft tip where the base of the long terminal halophore arises (eg. in A. lowryi the halophore of the d-seta is about six times the length of the setal shaft; Fig. 1). Myodocopin first antennal setae may bear more than one halophore terminally (eg. Fig. 9, C), and usually bear most halophores non-terminally (eg. Fig. 9, G-K). Non-terminal halophores exhibit bases without finely-ringed walls (eg. Figs. 5 and 3, C). This is probably to provide increased structural strength at the area most vulnerable to breakage.

Halophores occur on most of the terminal and subterminal myodocopin first antennal setae and so it appears inappropriate to term only one of these setae as "the sensory seta" (inferring a function), as in previous nomenclature.

This has also lead to confusion in discussion of this seta. Therefore I term this seta, arising from the fifth article of the myodocopin first antenna, the 's-seta' (the "s" of the previous terminology "sensory" is retained for historical value while the single letter designation of the other long terminal and sub-terminal first antennal setae is followed). The s-seta is so termed even if it lacks halophores (probably a secondary loss); it usually consists of a shaft plus halophores. The s-seta is always and only present in the Myodocopina.

I term the collective halophores distributed over the whole of one first antenna the 'halothalium' (from the Greek, meaning abundance of "halophores") (plural 'halothalia').

Functional morphology of the halophores

Long thin structures penetrate each halophore. These are possibly dendrites or enveloping cells, however, transmission electron microscopy is required to identify these structures. Halophores exhibit a terminal pore through which water-borne molecules can enter and may be detected, if chemosensory cells exist within the halophores. Setae with a terminal (or subterminal) pore are likely to be chemosensory (Dahl, 1973; Guse, 1978; Hindley & Alexander, 1978; Altner *et al.*, 1983), although the presence of a terminal pore alone does not designate a chemosensory function. However, mechanoreceptive and chemoreceptive sensory cells are often present in the same sensillum (Schmidt & Gnatzy, 1984). Therefore, halophores could be bimodal chemosensory/mechanosensory sensilla.

The unusual annulations of the halophores allows for great flexibility and a relatively large arc for the tip of a halophore to pass through during flexion, probably increasing their ability to detect chemical and/or physical stimuli. The halophores are initially moved when the setae from which they arise move (due to contraction of the muscles of the 6th, 7th and 8th articles. The s-seta is probably moved by the movement of the 6th article against it (see Fig. 7). Such setal movement may also be affected by the surrounding boundary layer, which may prematurely halt the movement of certain setae as setae approach each other or drag otherwise sedentary setae along with the setae moving as a consequence of articular movement. The setae move freely at their joints and are not individually controlled due to the absence of specialised setal musculature (as in all Crustacea).

The thin outer layer (sheath) that covers the rings of a halophore probably has some elastic properties and allows the rings to separate to a relatively high degree and enable the halophore to maintain integrity (Fig. 10, A). However, when halophore rings separate during flexion, the sheath can be "straightened out" to become smooth rather than following the grooved contours set by the rings (Fig. 10, A). If every adjacent ring is separated by an angle where the sheath is linear (but not stretched) along one side of a halophore, then the halophore could still exhibit great curvature. Therefore, the halophore sheath may not have to exhibit great elastic properties; only enough to resume its "resting" position (following the ring contours) after flexion. However, in Fig. 10, A, where $\underline{x} = 12°$, the sheath must exhibit some stretching,

although an angle, x, where stretching of the sheath is required may not be necessary. The sheath must also have significant tensile strength and be responsible, either wholly or in part, for the binding together of the individual rings.

Analogies with other myodocopin flexible structures

The halophore ultrastructure is most similar to the ultrastructure of the setae of the seventh limb (Fig. 11) within the Myodocopina. These setae are used for cleaning and stirring free embryos within the female carapace (Vannier & Abe, 1993); functions which require structural flexibility. The seventh limb setae tend to be approximately linear when "rested" (where the straight adjoining edges of adjacent rings lie parallel; Fig. 10, B), springing back to this resting position after flexing. However, the rings found in the walls of these seventh limb setae are approximately rectangular in cross section and so probably have limited flexibility compared to the thinner rings with walls of circular cross-section of the halophore (Fig. 10). This is because adjacent rings with walls of circular cross-section have an adjustable pivoting point or fulcrum, f (Fig. 10, A), where the whole seta or setule structure is stable when f is in any of a range of positions (ie. the walls of the adjacent rings "roll over" each other), eg. in Fig. 10, A, the fulcrum moves from point f when "resting" to point f' during flexion. However, adjacent rings with walls of rectangular cross-section have a fulcrum, f (Fig. 10, B), which is fixed; consequently these adjacent rings may "slip" from their finely balanced positions when

their angle of separation, x (Fig. 10, B), is anything but very small. Therefore, this type of structure becomes more unstable as x (ie. setal flexion) increases. Also, when the walls of the rings have a rectangular cross-section, the surrounding sheath must stretch during ring separation, making setal flexion additionally dependent on the elastic properties of the sheath.

This general ring-type construction appears successful in allowing both flexibility (to different degrees) and strength and its analogy may be the result of selection pressures because the same physical properties may be required of different structures even though their functions vary.

Comparable crustacean structures

At low magnification halophores appear similar to aesthetascs (Leydig, 1862) common throughout the Crustacea, resembling those described by Laverack & Ardill (1965) and Laverack (1968) in their filamentous, thin-walled appearance. However, aesthetascs show a very different ultrastructure without the finely annulate walls present in halophores (Ghiradella *et al.*, 1968, a & b); the typical marine aesthetasc is a long and slender filament (Ghiradella *et al.*, 1969). The aesthetascs of Cancer productus Randall (Crustacea: Decapoda) do show transverse folds in their outer walls which may contribute flexibility to the filaments (Ghiradella *et al.*, 1969). Similarly, aesthetascs of some cirripede cyprids exhibit a wrinkled external morphology (Glenner *et al.*, 1989).

The aesthetasc "Y", present in certain podocopid

ostracods, bears two distinct regions of different external cuticle morphology, one smooth, one with transverse folds. Perhaps these different morphologies provide different selective properties of the cuticle (Anderson, 1975). Therefore, the cuticle of the aesthetasc "Y" probably has a different function to the more uniform halophore cuticle, which is reflected in the greater flexibility of the halophore.

Antennal setae with fine helical sections of exoskeleton have been described in Mysidacea (Crustacea) (Crouau, 1981). In addition to their number and type of innervating dendrites, the different cuticular structures of Mysidacea setae correspond to functional differences. The regions of first antennal setae with fine helical cuticle in Antromysis juberthiei Bacesco (Mysidacea) are flexible, and are innervated by chemoreceptor and mechanoreceptor cilia (Crouau, 1981). Therefore, these setae would detect turbulences in the environment. However, halophores differ from these Mysidacea setae in that they are annulate rather than helical, with annulations continuing to the very tip of the structure, setules not setae, and they sometimes curve in any direction.

The s-seta is comparable to the callynophore found among the eucaridan and peracaridan crustaceans (Lowry, 1986). The thin-walled sensory hairs of the callynophore, innervated by dense bundles of nerve fibres and terminating at a pore (Dahl, 1979), constitute this brush-like organ, and are also termed aesthetascs (Lowry, 1986). However, the s-seta differs quite markedly from the callynophore in that its halophores arise from a setal shaft, whereas, the aesthetascs of the

callynophore arise from the articles (possibly fused) of the first antenna themselves.

ACKNOWLEDGEMENTS

I thank Dr. Jim Lowry (Australian Museum, Sydney) and Dr. Noel Tait (Macquarie University, Sydney) for critical manuscript review and advice, Dr. Louis Kornicker (NMNH, Smithsonian Institution, Washington D.C.) for advice on ostracod morphology, and Dr. Duane Hope (NMNH, Smithsonian Institution) for advice on sensory structures and photography. Thanks are also due to Mr. Geoff Avern (Australian Museum) for SEM micrograph production, Dr. Frank Crandle and Ms. Kathy Price (Smithsonian Institution) for making histological sections and staining, and Mr. Ray Cameron (Macquarie University) for help with filming. For the opportunity to study the many, often difficult to obtain, crustaceans used in this study I am indebted to Dr. Jim Lowry and Dr. Penny Berents (Australian Museum). I am also grateful to the Trust of the Australian Museum for providing travel money and the Smithsonian Institution for funding of photography and histology.

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Fig. 1. Azygocypridina lowryi Kornicker, adult female left first antenna, medial view (eighth article not in view). New terminology (for explanation see Discussion) is used in the labelling; traditional terminology (where appropriate) is bracketed.

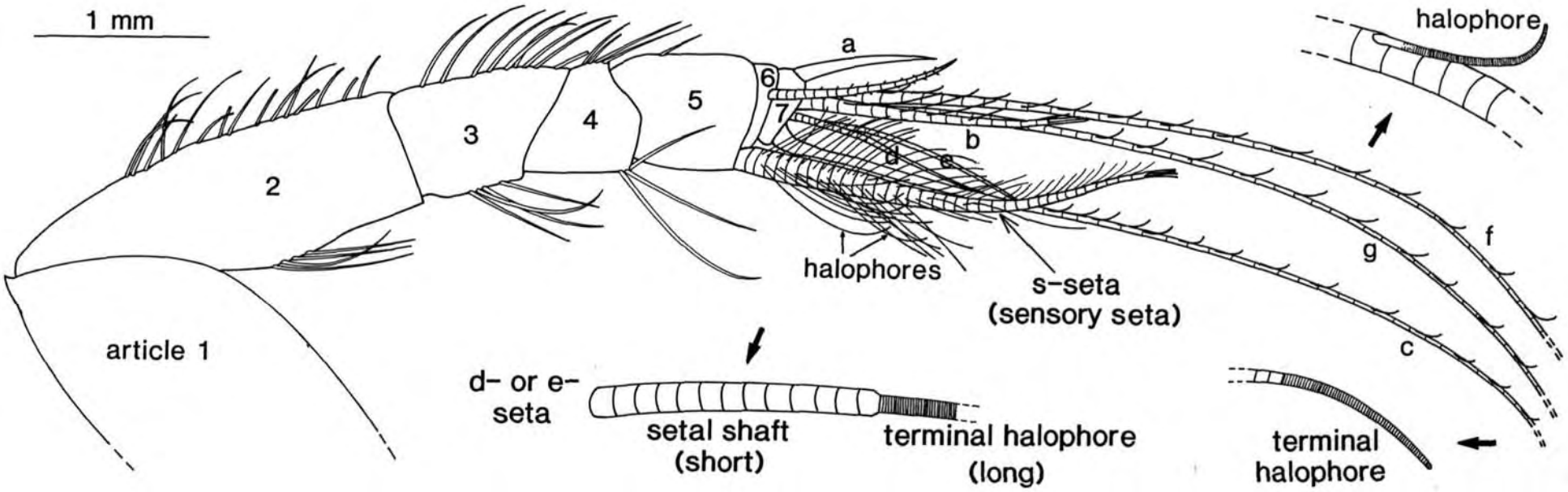

1 mm
halophore
a
6
7
5
4
3
2
b
d
e
f
g
c
halophores
s-seta
(sensory seta)
article 1
d- or e-
seta
setal shaft
(short)
terminal halophore
(long)
terminal
halophore

Fig. 2. Diagrammatic sections of the halophore exoskeleton.-A. Longitudinal-section (shaded areas represent cross-sections of the walls of the rings - circular shaped).-B. Cross-section through t-t.

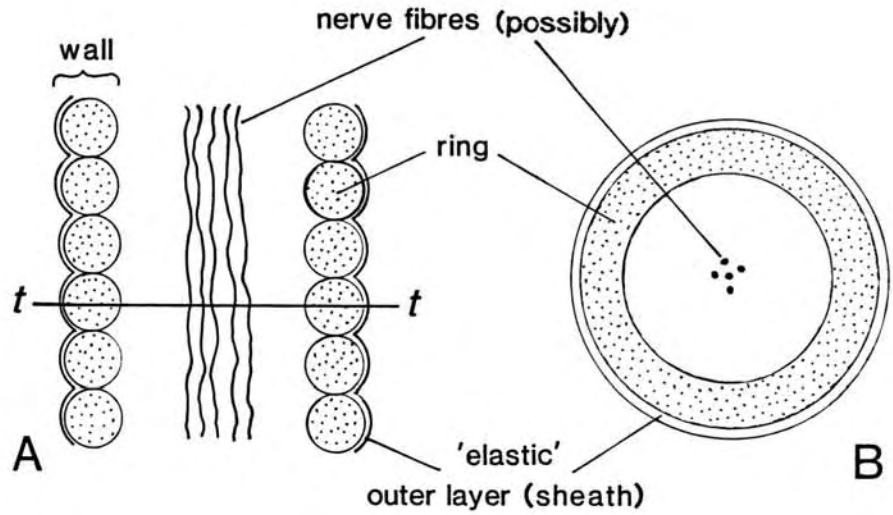

nerve fibres (possibly)
wall
ring
t
t
A
B
'elastic'
outer layer (sheath)

Fig. 3. Azygocypridina lowryi, adult female.-A. Whole animal, left carapace removed: a1 = first antenna; 7th = seventh limb.-B. Tip (articles 5-8) of right first antenna, medial view: s = s-seta.-C. Bases of halophores of the s-seta (most proximal sections without fine annulations).-D. Mid-section of halophores of the s-seta.-E. Tip of a halophore of the s-seta showing pore (arrowed).-F. Split (or dried) halophores of the s-seta showing outer layer (probable elastic-type material, sheath, covering rings, arrowed). Scales: A = 2 mm; B = 500 µm; C-F = 10 µm.

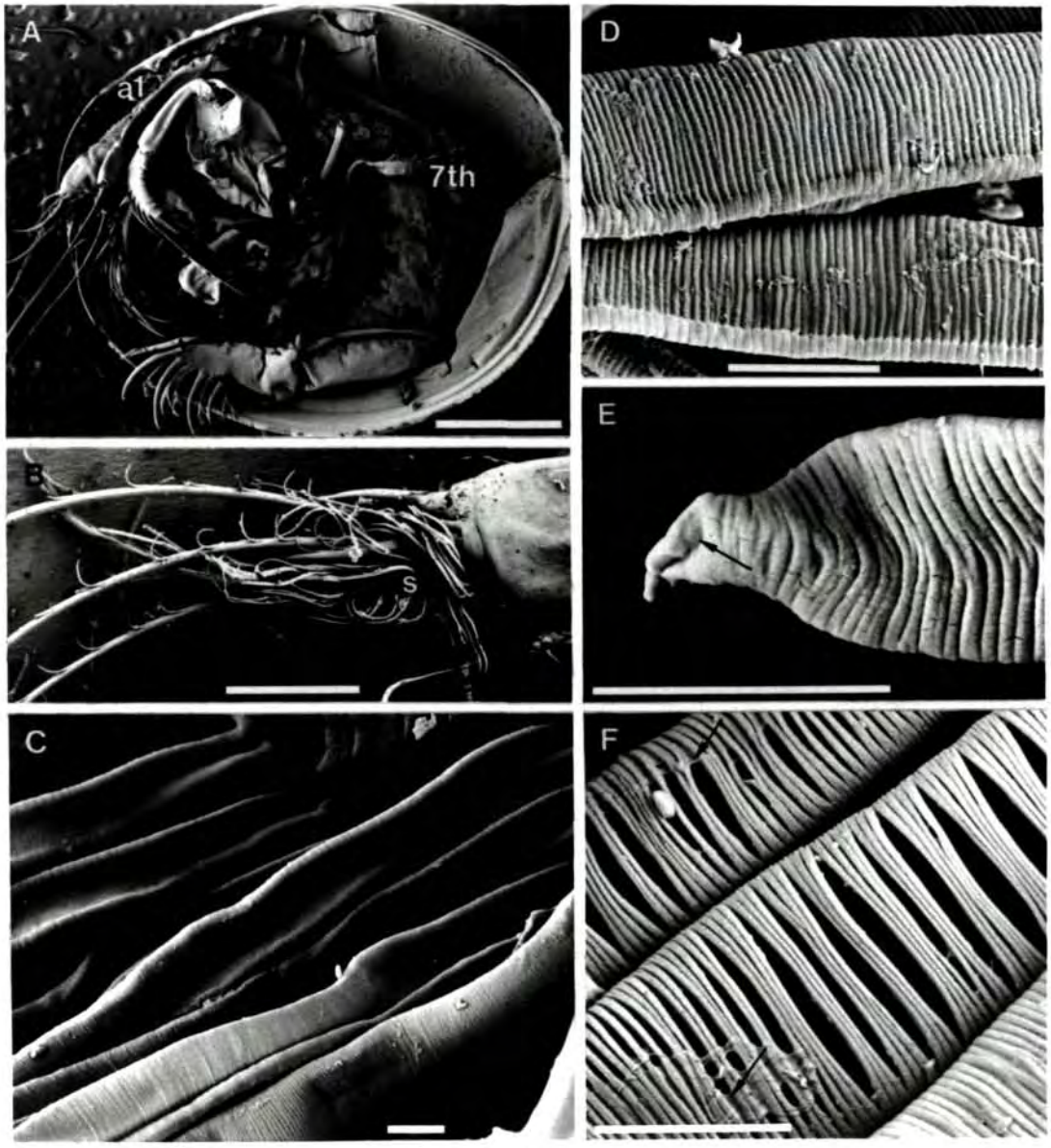

A
at
7th
B
s
C
D
E
F

Fig. 4. Halophores of adult myodocopins in the families Cypridinidae (A-D) and Cylindroleberididae (E).-A. Azygocypridina lowryi, broken halophores of the s-seta showing ring construction.-B. Broken halophore of the s-seta showing a broken ring (ring appears hollow).-C. Paradoloria sp., halophore of the s-seta, rings thinner than in A. lowryi.-D. Male Skogsbergia sp., halophores arising from the f-seta (the halophores of the male f- and g-setae are themselves branched in this species; the female f- and g-setae more closely resembles that of A. lowryi).-E. Archasterope sp., halophores of the s-seta. Scales: A,B,C and E = 2 μm; D = 20 μm.

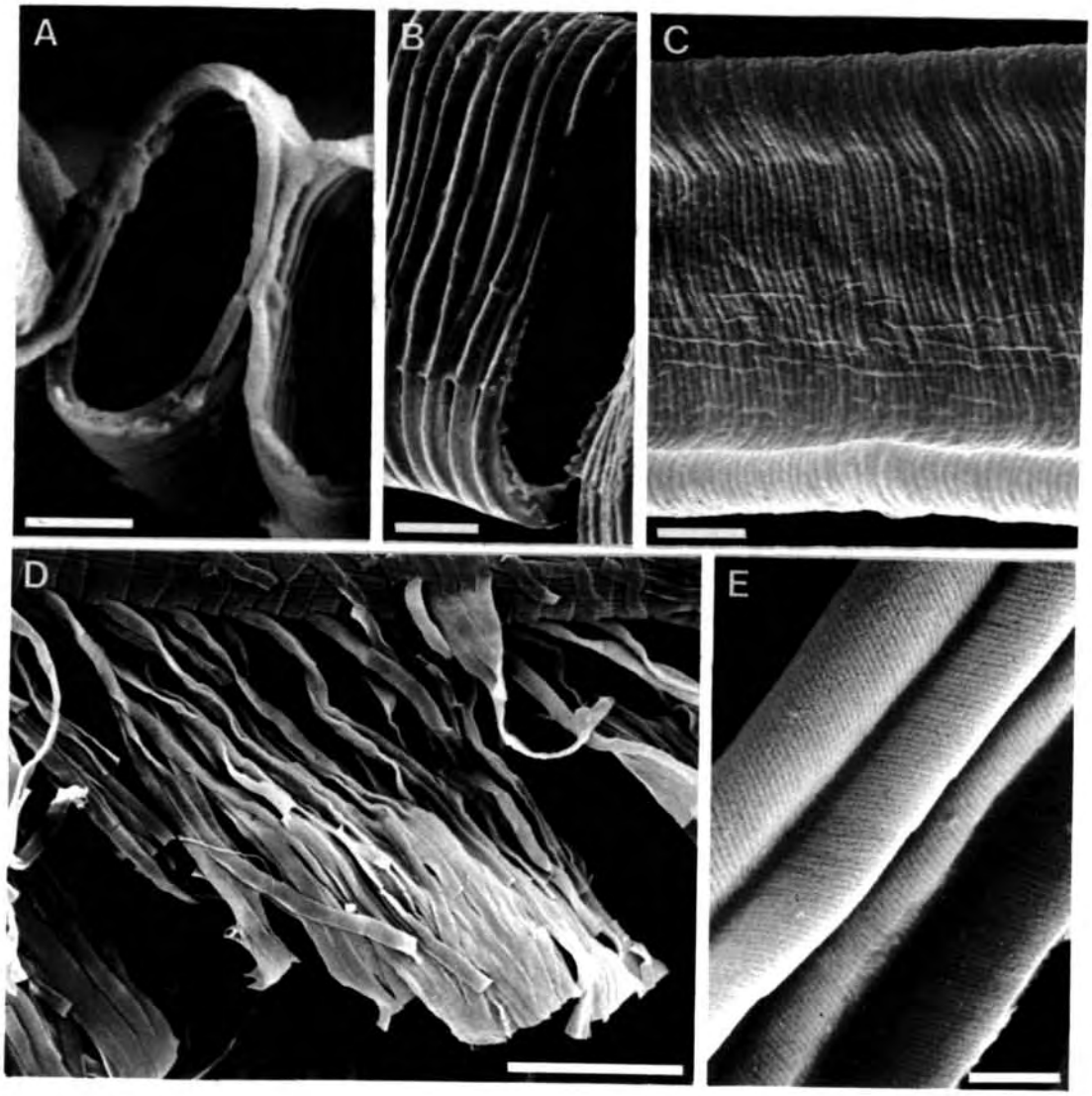
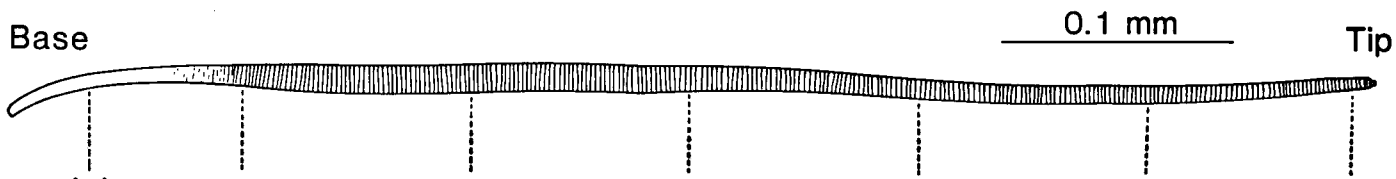

A
B
C
D
E

Fig. 5. Azygocypridina lowryi, halophore of the s-seta of an adult female showing the width of the rings at various positions along the halophore, of length L.



Location of rings on halophore	(0)	1/6 L	1/3 L	1/2 L	2/3 L	5/6 L	(L)
Width of individual rings (nm)		490	530	570	640	550	430
= w	0	430	510	570	550	670	480
(three adjacent rings measured)		480	520	560	570	570	410

Fig. 6. Paravargula sp., adult male, broken base of third most proximal halophore of the left s-seta showing interior structures (attached to the s-seta at the left of the picture). The fact that the presumed dendrites run into the halophore would seem to indicate that its function might be chemoreception, but unless the interior structures are bundles of axons their number would indicate otherwise. Scale = 5 μm.

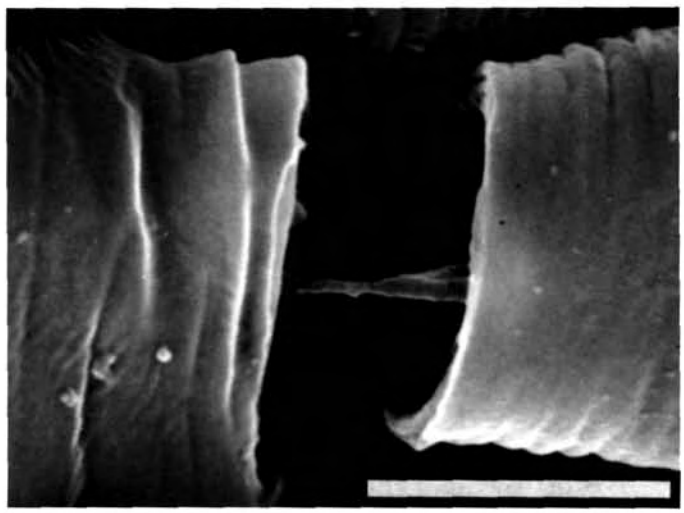


Fig. 7. Diagrammatic terminal part of the first antenna of Azygocypridina lowryi from video recordings (no halophores illustrated). Dotted lines represent positions to which the terminal and subterminal setae move during flexion, solid lines represent resting positions (only setae making significant movements are illustrated). 5 = fifth article; c, f, g and s represent corresponding setae.

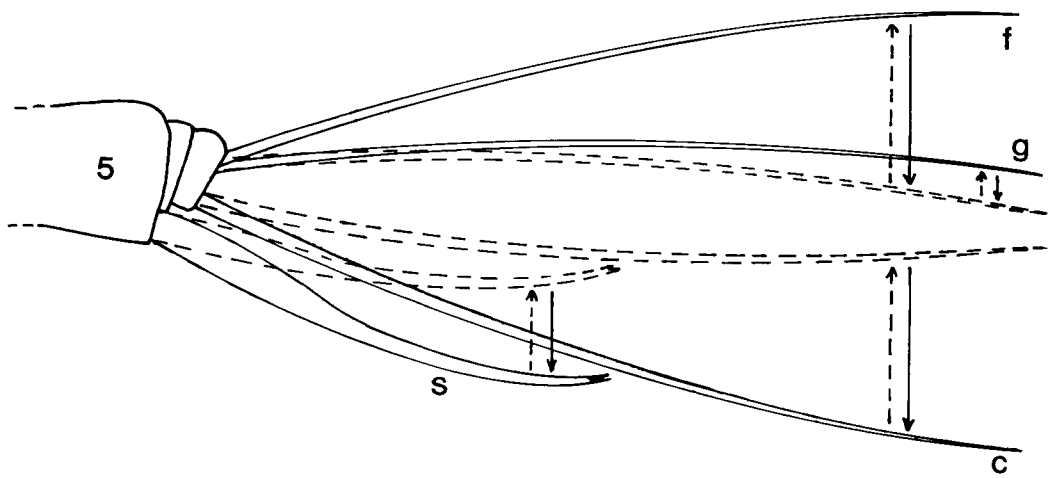

5
f
g
s
c

Fig. 8. Cypridinidae first antennae and s-setae.-A. Skogsbergia minuta Poulsen, female left first antenna, lateral view.-B. S. minuta, male left first antenna, medial view (many halophores present on f- and g-setae).-C. Gigantocypris agassizi Müller, first instar, first antenna (halophores only present on d- and e-setae, terminally).-D. G. agassizi, third instar, first antenna (many halophores present).-E. Cypridina acuminata Müller, male left first antenna, medial view.-F. Pterocypridina sex Kornicker, male left s-seta, medial view.-G. Bathyvargula parvispinosa Poulsen, male right s-seta, medial view.-H. B. parvispinosa, female right s-seta, medial view. Sub-figures all from Poulsen (1962), except F. from Kornicker (1983). 4 = fourth article; a-g and s represent corresponding setae. Scales: A, B and E = 0.1 mm; C = 0.5 mm; D = 1 mm; G and H = 0.2 mm.

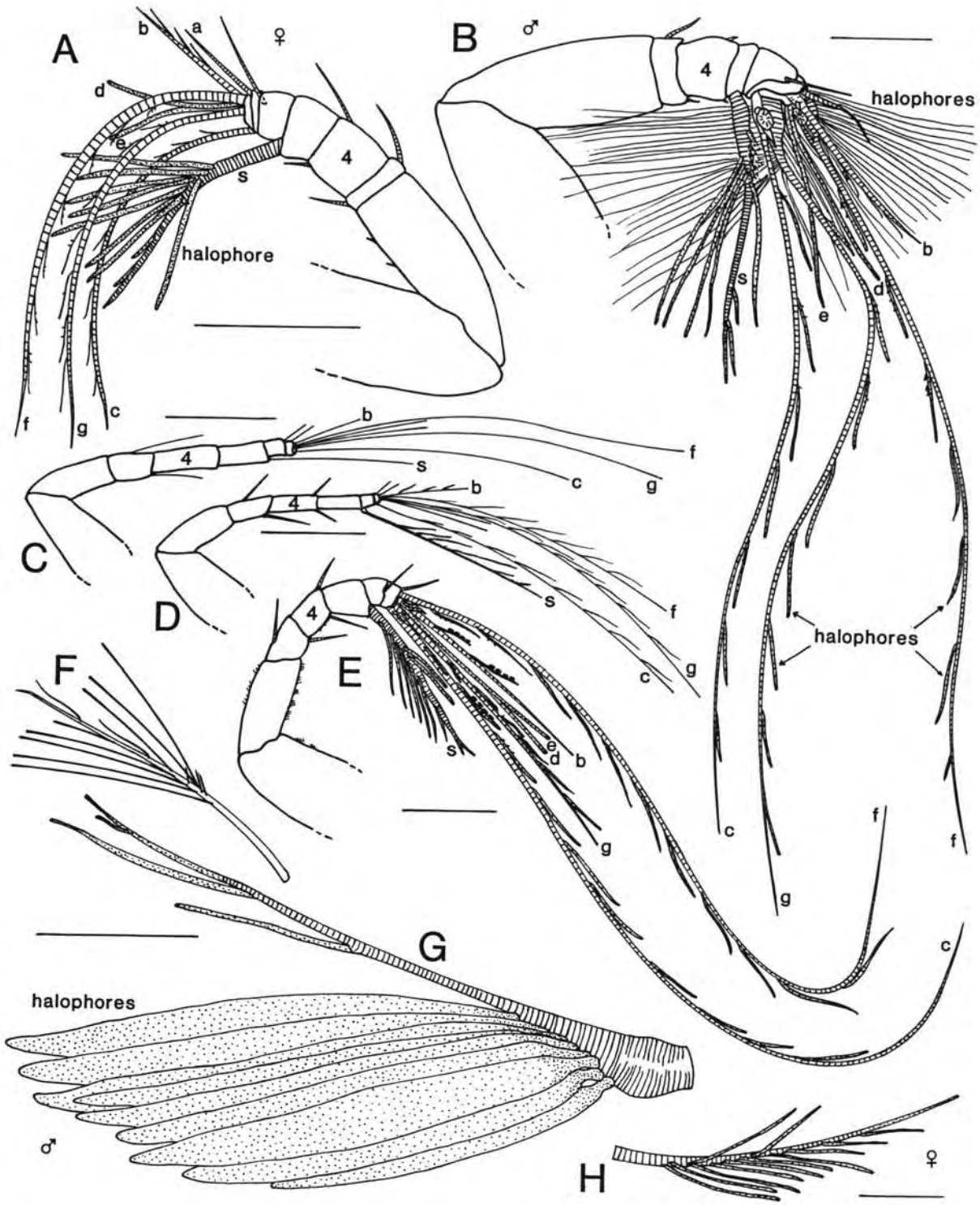

A
♀
B
♂
halophore
halophores
C
D
E
F
G
H
halophores
♂
♀
4
a
b
c
d
e
f
g
s

Fig. 9. Cylindroleberididae (A-D), Philomedidae (E-I) and Rutidermatidae (J and K) first antennae and s-setae.-A. Diasterope grisea Brady, tip of male left first antenna, lateral view (not all setae shown).-B. D. grisea, tip of female left first antenna, medial view (not all setae shown).-C. Homasterope maccaini Kornicker, male and female s-setae.-D. Skogsbergiella spinifera Skogsberg, s-setae of left and right female first antennae.-E. Harbansus paucichelatus Kornicker, male left first antenna, medial view.-F. H. paucichelatus, female left first antenna, medial view.-G. Harbansus dayi Kornicker, male s-seta.-H. Paraphilomedes unicornuta Poulsen, male s-seta.-I. Scleroconcha arcuata Poulsen, male s-seta.-J. Scleraner trifax Kornicker, male s-seta.-K. Rutiderma species B Kornicker, male s-seta. Sub-figures A-D from Kornicker (1975); E-I from Kornicker (1978); J and K from Kornicker (1994). 4 = fourth article; a-g and s represent corresponding setae; l = left; r = right. Scales = 100 μm.

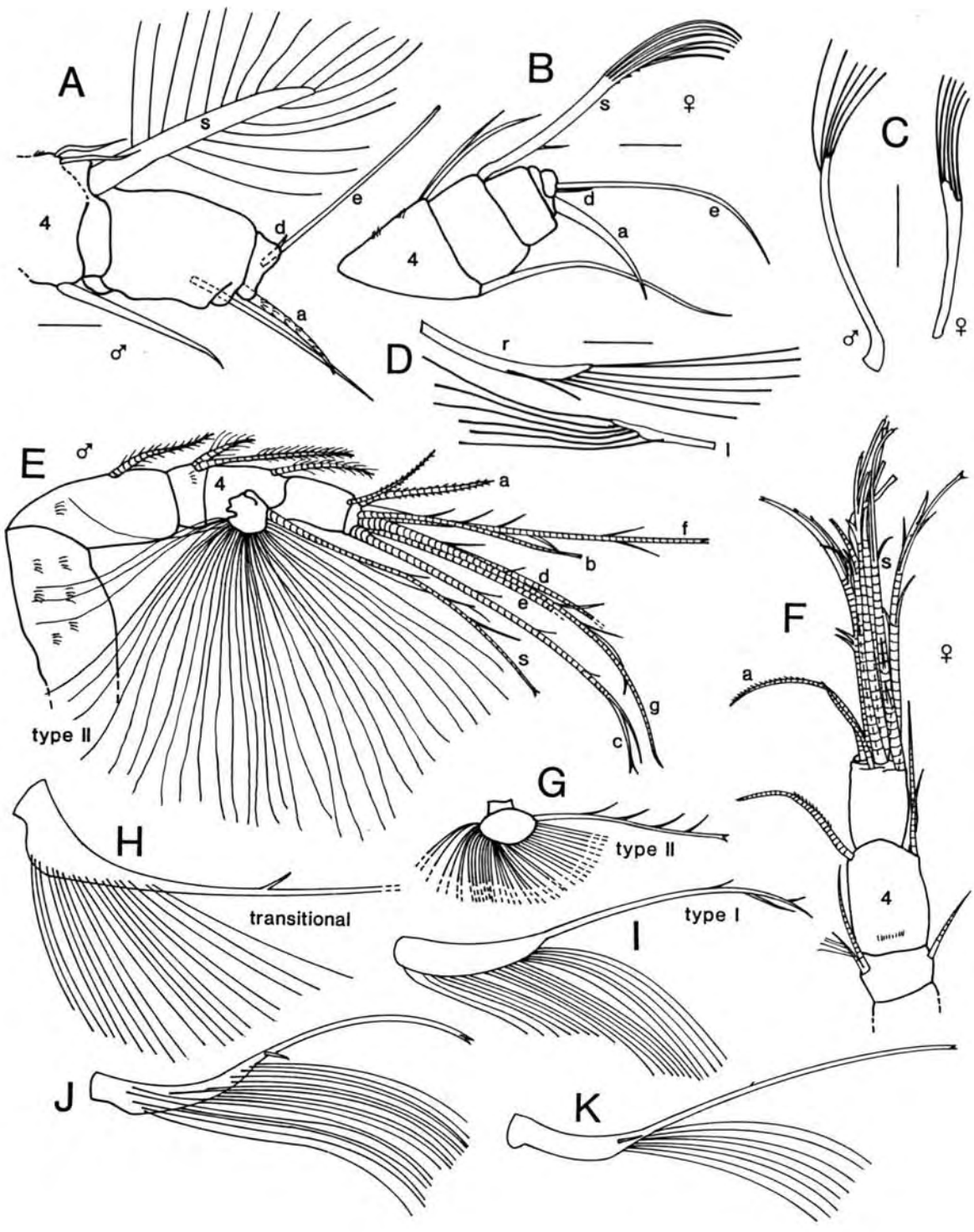

A
s
4
d
e
a
♂
B
s
♀
d
e
a
4
C
♂
♀
D
r
l
E
♂
4
a
f
b
d
e
s
g
c
type II
F
s
♀
a
4
G
type II
H
transitional
I
type I
J
K

Fig. 10. Diagrammatic longitudinal sections of two adjacent rings of an annulate seta or setule at "rest" (linear) and during flexion.-A. Seta (or setule) containing rings with walls of circular cross-section, eg. a halophore.-B. Seta (or setule) containing rings with walls of rectangular cross-section, eg. a myodocopin seventh limb seta. At "rest", $\underline{x}$ = 0; during flexion, $\underline{x}$ = 12°. $\underline{f}$ = pivoting point (fulcrum) of adjacent seta or setule rings when "rested" and/or during flexion; $\underline{f'}$ = adjusted fulcrum of adjacent halophore rings during flexion; $\underline{x}$ = angle subtended by adjacent rings during seta or setule flexion; $\underline{y}$ = 1/2 angle subtended by adjacent rings to provide maximum separation of rings with no sheath stretching; $\underline{z}$ = distance of sheath "extension" required during a separation of adjacent rings of $\underline{x}$°, to be accounted for by stretching.

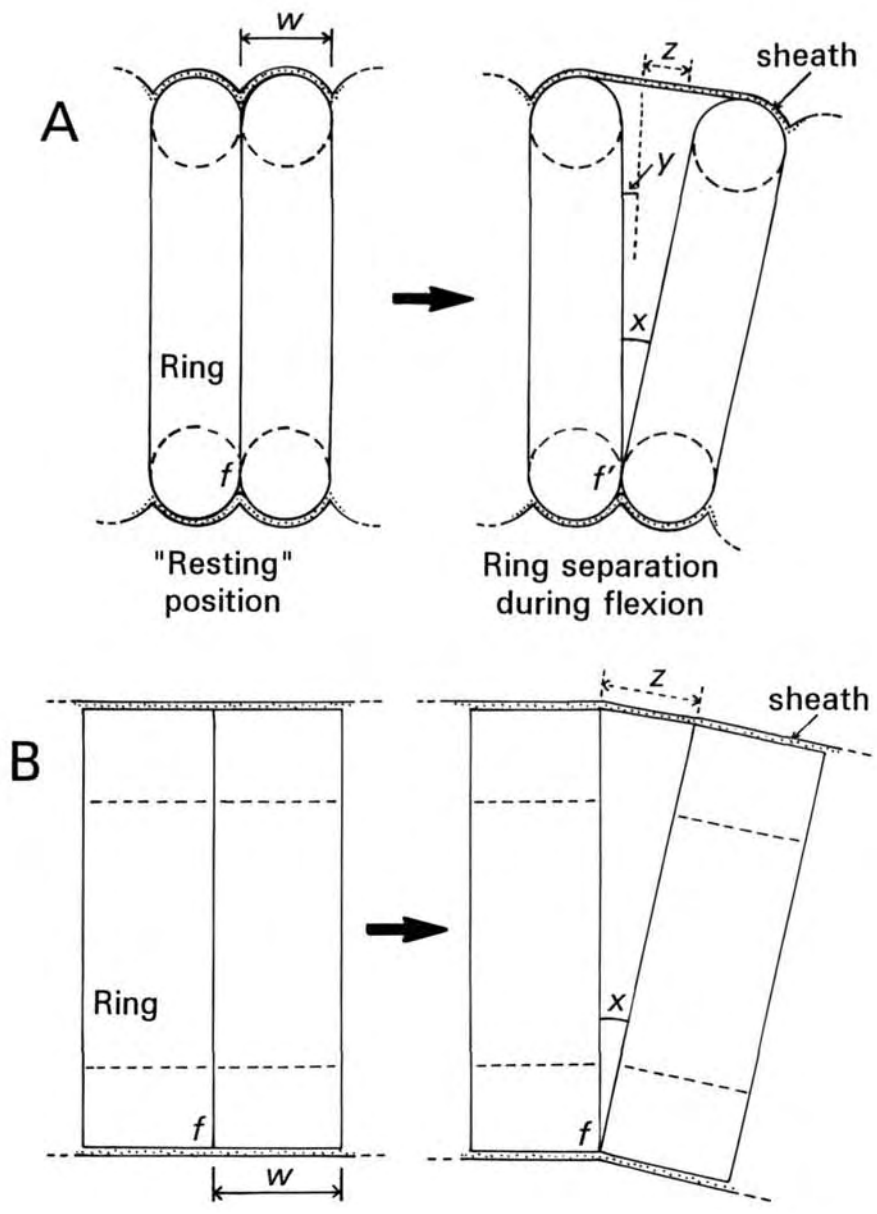

A
w
Ring
f
"Resting"
position
z
sheath
y
x
f'
Ring separation
during flexion
B
Ring
f
w
z
sheath
x
f

Fig. 11. Azygocypridina lowryi, adult female seventh limb.-A. Section near tip showing setae.-B. Mid-section of a seta showing ring-type construction with thin continuous outer layer. Scales: A = 50 μm; B = 5 μm.

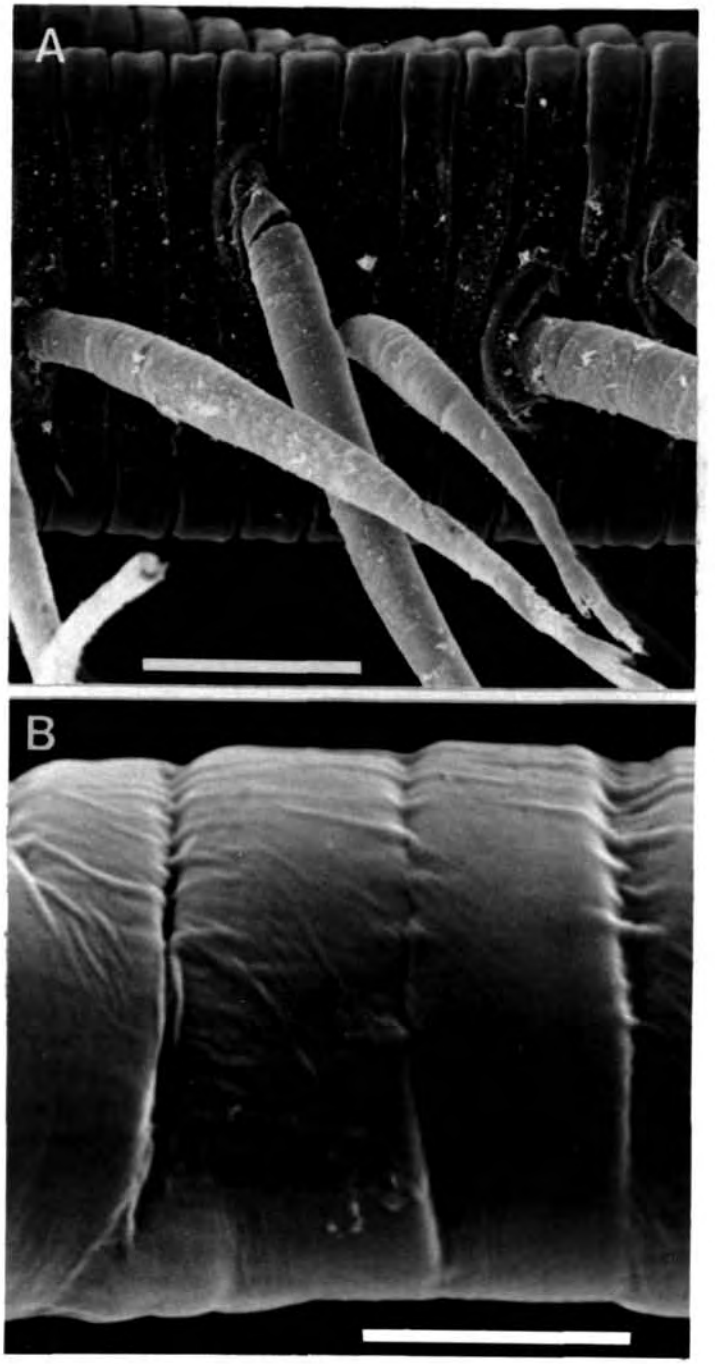

A
B

Table 1. Material examined (museum specimens fixed in 5% formaldehyde and preserved in 70% ethanol). AM represents Australian Museum (Sydney); NMNH represents National Museum of Natural History (Washington D.C.)

Ostracoda	
Myodocopida: Myodocopina	
Cypridinidae	
Azygocypridina lowryi	AM, eastern Australia
Cypridina sp.	AM, eastern Australia
Gigantocypris sp.	AM, eastern Australia
Paradoloria sp.	AM, eastern Australia
Skogsbergia sp. (♂ & ♀)	AM, eastern Australia
Vargula sp.	AM, eastern Australia
New genus sp.	AM, eastern Australia
Cylindroleberididae	
Archasterope sp.	AM, eastern Australia
Philomedidae	
Euphilomedes sp.	AM, eastern Australia
Sarsiellidae	
Sarsiella sp.	AM, eastern Australia
Rutidermatidae	
Rutiderma gerdhartmanni	NMNH, Chile (41°48'S, 75°53'W)
Myodocopida: Halocyprina	
Conchoecia belgicae	AM, Macquarie Island, Australia
Podocopida	
Eucypris splendida	AM, Lake Cooper, Australia
Australocypris robusta	AM, Lake Gnotuk, Australia
Branchiopoda	
Conchostraca	
Limnadopsis brunneus	AM, Australia
Notostraca	
Apus cancriformis	AM, Europe
Copepoda	
Caligus sp.	AM, eastern Australia
Sapphirina sp.	AM, eastern Australia
Malacostraca	
Decapoda	
Chaceon bicolour	AM, eastern Australia
Dardanus sp.	AM, eastern Australia
Oplophorous spinosus	AM, eastern Australia

Stomatopoda	
Gonodactylus smithii	AM, eastern Australia
Mysidacea	
Gnathophausia calcarata	AM, eastern Australia
Cumacea	
Diastylus helleri	AM, Antarctica
Tanaidacea	
Whiteleggia stephensoni	AM, eastern Australia
Isopoda	
Aatolana sp.	AM, eastern Australia
Amphipoda	
Stephonyx pirloti	AM, eastern Australia
Waldeckia australiensis	AM, eastern Australia

Table 2. Width of three individual adjacent rings (w) of a halophore, at different regions along its length (L), from the s-seta in three cypridinid (Myodocopina) taxa.

	Vargula sp.	*Paradoloria* sp.			*Skogsbergia* sp.	
					1/2L	
	1/2L	1/3L	1/2L	2/3L	Male	Female
w (nm)	297	206	137	317	110	148
	282	254	125	291	110	161
	335	271	112	304	110	156

Table 3. General morphology of s-setae and halothalia in myodocopin families

family	s-seta	halothalium
Cypridinidae	Typically as in Fig. 9, E; males often with few more similar halophores, exceptionally males with larger halophores as in Bathyvargula.	Most dense on s-seta, exceptionally on f- and g-setae as in Skogsbergia.
Cylindroleberididae	Mostly very sexually dimorphic; males typically plumose, females typically with mainly terminal halophores (no halophores in female Microasteropteron). Exception in Homasterope: little sexual dimorphism.	Most dense on s-seta, especially in males (except Homasterope). Distributed irregularly in some females.
Philomedidae	Very sexually dimorphic. Without long halophores in females, numerous long halophores in males. Males with a type 1 (eg. Fig. 10, I) or type 2 (eg. Fig. 10, E and G) s-seta; intermediate in Paraphilomedes.	Most dense on s-seta in males. Distributed irregularly in females.
Rutidermatidae	Very sexually dimorphic. Bare or with 2 or 3 short halophores in females, similar to philomedid type 1 s-seta in males.	Most dense on s-seta in males. Distributed irregularly in females.
Sarsiellidae	Very sexually dimorphic. Bare or with 2 or 3 short halophores in females, similar to philomedid type 2 s-seta in males.	Most dense on s-seta in males. Distributed irregularly in females.