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The coelotrich: form and function of an unusual sensillum in *Lowrya* (Ostracoda: Myodocopina: Cypridinidae)

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This study reports a previously undescribed and unique sensillum. Some species of *Lowrya* Parker 1998 (Ostracoda: Cypridinidae) possess sensillae of an unusual type 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 coelotrichs, and are each centred within an almost spherical cavity in the carapace. The cavity forms at the base of a depression, and the depression in turn lies within a sunken channel on the exterior carapace surface. The opening of the coelotrich cavity bears a 'plug', through which only the widened, divided base of a seta passes. The seta is very fine and stiff throughout most of its length, and exhibits no pores. For most of its length the seta is orientated parallel to the carapace surface, shielded within the sunken channel. The coelotrich is probably a velocity detector, acted upon by the viscous drag of the surrounding fluid. Its function is probably to detect vibrations in the substrate, such as acoustic motion in the surrounding liquid, or steady fluid drainage motion.

Keywords: coelotrich; mechanoreceptor; ostracod; *Lowrya*; viscous boundary layer

1. INTRODUCTION

The carapace of Ostracoda 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). Apart from marginal pore canals, the remaining normal pore canals are distributed over the entire carapace surface. Simple pore canals, including their innervating setae, are prevalent in both Myodocopina (Myodocopa) and Podocopa.

Ostracods generally operate at low Reynolds numbers (Cohen 1989). Therefore, there is a thick layer of viscous water that surrounds ostracods in motion (see Emlet & Strathman 1985).

Cypridinid ostracods probably spend most of their lives buried a few millimetres into the sand substrate of their habitat (Vannier & Abe 1993). Species of *Lowrya* Parker 1998, bear feeding appendages and putative sensory apparatus typical of other scavenging cypridinids (Parker 1998).

One unique feature of some species of *Lowrya* is an unusual structure composed of sensillae arranged in a row parallel to, and near, the anterior, ventral, and posterior margins of the external surface of both carapace valves (figure 1). This appears as a row of circles at $\times 100$ magnification (e.g. figure 1), as illustrated in the taxonomic publication of *Lowrya taiti* (Parker 1998). The aim of this study was to determine the morphology, although not the nervous innervation, of this structure. From this information the response of the structure to environmental fluctuations is analysed.

The structure under examination is here termed the 'coelotrich' (from the Greek, meaning cavity of hair).

2. MATERIAL AND METHODS

Specimens of *L. taiti* Parker 1998 were obtained from collections at the Australian Museum (AM P45077). They had been caught in a baited trap set overnight outside of Bate Bay, New South Wales, Australia ($34^{\circ}44' S$, $150^{\circ}39' E$), at 25 m depth, and subsequently fixed in 5% formalin and preserved in 70% ethanol.

Ten specimens of *L. taiti* were dissected and their carapaces mounted in glycerol and examined under a compound microscope. One specimen was embedded in paraffin wax and longitudinally sectioned at $4 \mu\text{m}$. Sections were treated with a modified Mallory solution (F. Crandle, personal communication), a multicomponent stain suitable for the study of crustacean sensory structures, and again the coelotrichs were observed under a compound microscope.

One specimen was cut into 0.2 mm thick sections using a razor blade. These sections, together with a complete carapace, were critical-point dried, coated with gold and examined in a scanning electron microscope. Coelotrichs were observed from external views and internal cross-sections.

Two specimens were prepared for transmission electron microscopy by (i) treating with 2.5% glutaraldehyde in 0.1 M phosphate buffer for 1 h at room temperature, (ii) rinsing with 0.1 M buffer, (iii) treating with 1% osmium tetroxide in 0.1 M buffer for 1 h at room temperature, (iv) dehydrating through an ethanol series, and (v) infiltrating with Epon resin via a resin-ethanol series (each dilution treatment took place overnight on a rotator). Sections (60 nm thick) were examined in a transmission electron microscope.

Because ostracods are surrounded by a viscous boundary layer (Cohen 1989), to which coelotrichs are directly exposed, the thickness of this layer was calculated. After modelling a coelotrich from the results of the above experimentation, the

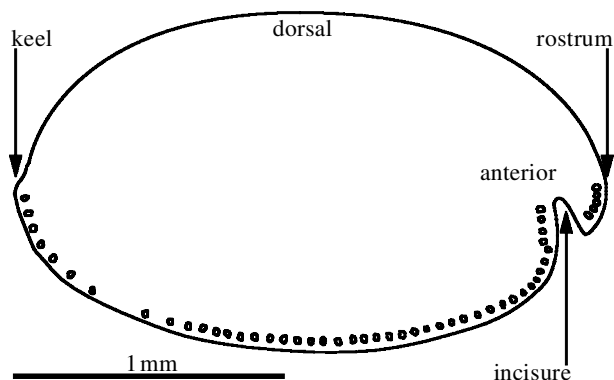


Figure 1. Right valve of *L. taiti*, adult female, lateral view, showing coelotrachs as small circles (setae not visible at this magnification). Note that the number of coelotrachs varies in different species of *Lowrya* (often less numerous than in the species illustrated, although always more closely spaced anteriorly than posteriorly).

effect of fluctuations in the external environment on the coelotrach was assessed.

3. RESULTS

(a) *Microscopic analyses*

The results of the microscopy are summarized in the three-dimensional representation of a coelotrach shown in figure 2. Coelotrachs are structures based within almost spherical (or volumes equivalent to two overlapping spheres) invaginations of the carapace epicuticle, forming cavities about $10\ \mu\text{m}$ deep, but not reaching beyond the boundary of the endocuticle. Each cavity lies within its own circular depression, or pit in the external surface of the carapace. At the cavity entrance there is a 'plug' of material (stains red in modified Mallory solution) with a composition very different from the rest of the cuticle (which stains blue, indicating chitin). This plug is a circular plate with a central hole, through which a seta passes. The central hole has a diameter slightly greater than, or equal to, that of the setal base. The coelotrach 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 that lie perpendicular to the carapace surface and do not usually emerge from recessed areas. The coelotrach seta arises from inside the cavity, near the plug, and joins with the cavity wall. A chitinized tube in the endocuticle leads from this part of the cavity wall to the epithelium. The seta is long (about $20\ \mu\text{m}$), fine and stiff distally, bifurcating near its base, just external to the plug (about $2\ \mu\text{m}$ from the plug). The long, distal part of the seta lies almost parallel (usually slightly angled) with the external carapace surface, about $2\ \mu\text{m}$ from this surface. There are no pores in the seta. Internally, the seta houses two cylindrical cavities of different cross-sectional diameters for at least some of its length. The tip of the seta may reach as far as the adjacent coelotrach cavity, but never overlaps or touches the seta of the adjacent coelotrach. The setae of a row of coelotrachs are all orientated similarly; they lie parallel to the valve margin and point in a ventral or posterior direction, depending on their position on the carapace.

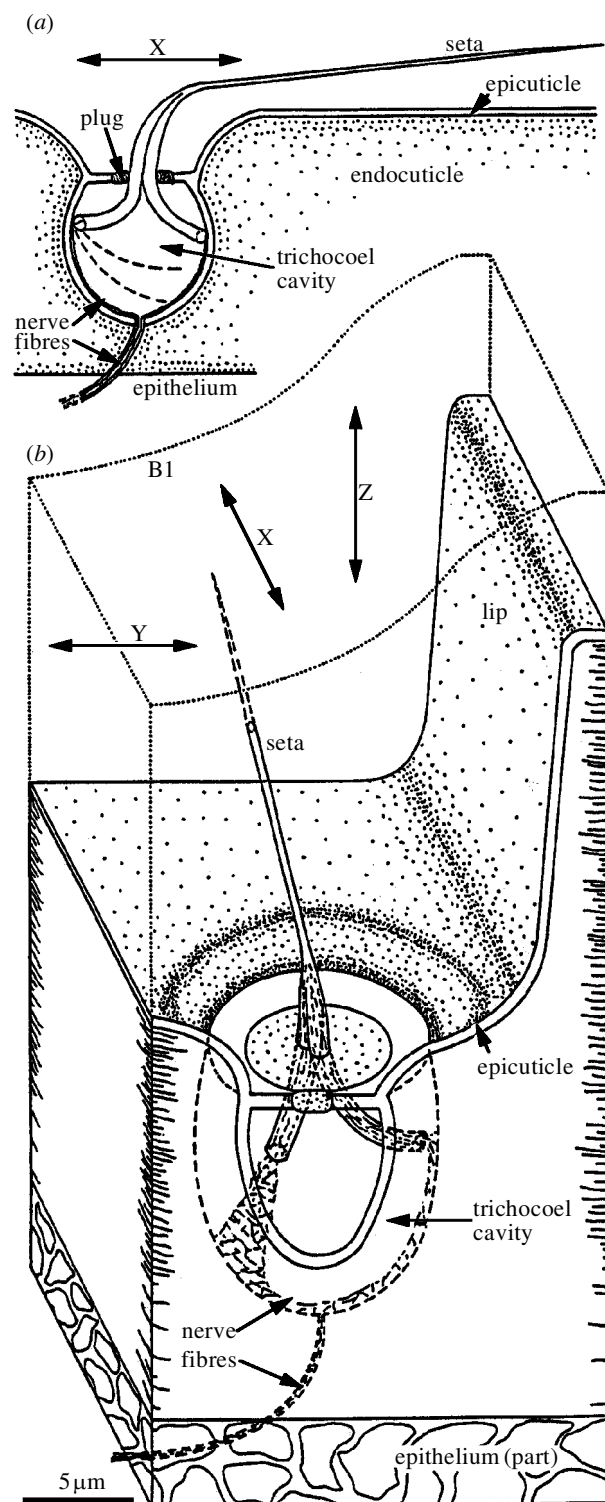


Figure 2. Generalized diagrams of a coelotrach of *L. taiti*. (a) Longitudinal section through centre of cavity; X represents the direction of water flow parallel to the groove in which a row of coelotrachs lies. (b) Three-dimensional model; cavity is sectioned transversely and off-centre (near edge of plug); X, Y and Z represent different directions of water flow over the seta; B1 represents the proximal part of the boundary layer (of viscous water).

A row of coelotrach pits always occurs in regions of the carapace exhibiting some further type of recess. Along the rostrum and lower incisure margin, the coelotrach 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 5 μm laterally. These recessed areas form channels, in which the coelotrich pits and setae all lie.

Nerves were not evident in the specimens examined; all known specimens of *Lowrya* have been treated with solutions unsuitable for the preservation of nervous tissue. For example, the internal spaces of the coelotrich seta and tube leading from the cavity would be expected to contain nerve fibres, yet are hollow.

Coelotrichs 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 at least the final two juvenile stages.

(b) *Calculations and modelling of a coelotrich and its microenvironment*

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

$$\sqrt{[\nu/(2\pi f)]}, \quad (1)$$

where ν is the kinematic viscosity of the fluid (ν is approximately $1.0 \times 10^{-6} \text{m}^2 \text{s}^{-1}$ for water) and f is the frequency involved.

This is about 40 μm at 100 Hz (a possible frequency encountered in the marine environment). Within the boundary layer fluid velocity increases nearly linearly with distance from the stationary surface of the animal.

The sediment in which cypridinids are buried for most of their lives (Vannier & Abe 1993) 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 ostracods' 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 (see Fletcher 1992, p.89). The amplitude of this motion depends upon the difference in density, but is comparable with 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.

There are three possible directions of water flow past one of the coelotrich setae relative to the ostracod's carapace (figure 2). 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 coelotrich 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. The coelotrich seta is therefore only affected by flow in this direction.

Flow in the X-direction is essentially parallel to the distal part of the coelotrich seta and pulls 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 sometimes to a lateral displacement, both of which would stimulate the coelotrich's sensory cells.

When the coelotrich seta is bent by an external vibration, the force required to return the seta to its original position (as adapted from Fletcher 1992) is $-F_c$:

$$F_c = -ES\kappa^2 \frac{d^4 z}{dx^4}, \quad (2)$$

where $\kappa = a/2$ (a is the radius of the cross-section of the distal setal section), $S = \pi a^2$, E is the Young's modulus of the material of the seta, and dz/dx is the angular deflection.

The plug is simply compliant, i.e. it does not clamp the seta. Therefore the angular deflection is proportional to the bending moment

$$\frac{dz}{dx} = \mu ES_2 \frac{d^2 z}{dx^2}, \quad (3)$$

where μ represents the angular compliance of the plug.

Additionally,

$$\mu s = ES\kappa^2, \quad (4)$$

where μs is the angular compliance of the seta and l represents the length of the seta.

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

$$\mu/\mu s = \mu ES\kappa^2/l. \quad (5)$$

Each coelotrich seta will have a figure-of-eight sensitivity pattern along the direction of the channel in which it lies. In a body of water that is large compared with the boundary layer thickness, the deflection of a coelotrich seta will be inversely proportional to the boundary layer thickness.

4. DISCUSSION

(a) *Functional morphology of a coelotrich*

The coelotrich is not tactile (i.e. a touch receptor) because its seta does not reach beyond the adjacent raised area (lip) of the carapace. The possibility that a coelotrich is an acceleration detector can also be dismissed because the seta is without a dense mass on its free end (see Fletcher 1992, p.64). The absence of pores combined with the long, fine but stiff nature of the seta means that the coelotrich is not chemosensory but rather a mechanoreceptor. The specific distributional pattern of the coelotrichs over the carapace surface excludes the function of carapace stress reception. The evidence suggests that coelotrichs are velocity detectors, acted upon by the viscous drag of the surrounding fluid.

At 100 Hz, the boundary layer is large compared with the size of the coelotrich seta. This means that, considering the increase in fluid velocity within the boundary

layer, for an acoustic disturbance the angular amplitude of motion of the coelotrich seta is independent of its length. The deflecting torque, however, is proportional to the cube of the setal length. In the coelotrich, since the seta is protected by the plug, its base (inside the cavity) can be very flexible, giving a considerable response without requiring a large torque.

The setae of a row of coelotrichs are arranged so that adjacent setae almost touch (i.e. with minimal gaps between setae), therefore the probability of detecting any vibrations is extremely high. The figure-of-eight sensitivity pattern of each seta means that the ostracod can judge the direction from which the signal is coming, with an uncertainty of 180°. Therefore the semicircular arrangement of coelotrichs around the carapace margins is sufficient to detect signals from any direction.

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. Similarly, when the tip of the seta moves away from the carapace, the lower basal section becomes stressed and the upper section is relaxed. Such states of stress could be interpreted by innervating nerve fibres. The plug 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.

The function of the coelotrich cavity (or rather the cavity wall), 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 flexible carapace wall. The layer of epicuticle which surrounds the cavity is also more highly sclerotized than the endocuticle, adding further strength to the cavity wall. If one function of the cavity wall is to dampen vibrations transmitting through the carapace, 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 coelotrich detects external vibrations, by excluding confusing vibrations from within the carapace wall caused by movements of the ostracod itself.

(b) *Source of the stimuli detected by a coelotrich*

Coelotrichs must detect either steady fluid drainage motion or acoustic motion in the surrounding liquid, while the ostracod is buried in the sediment.

All known species of *Lowrya* scavenge (A. R. Parker, unpublished data). The rapid sinking of an animal carcass and its impact on the bottom generates rapid and wide-spreading vibrations through the water (Dahl 1979), and top layers of sediment. Such vibrations would cause movement in coelotrich setae of buried specimens. *Vargula hilgendorffii* (Müller, 1890), a cypridinid with a similar morphology to species of *Lowrya*, buries at an angle of 45–60° between the longitudinal axis of the carapace and the surface of the substratum, anterior end first (Vannier & Abe 1993). In this position, the coelotrichs of *Lowrya*

species face away from the water column, which is not the ideal position to detect stimuli from the water column or sediment surface. For similar reasons, the detection of other sounds created in the water column (see Myrberg *et al.* 1965; Horch & Salmon 1969) or temperature variations (see Altner & Prillinger 1980) may not be the function of the strategically positioned coelotrichs.

A source of acoustic motion which would cause movement in the coelotrich setae is from predators which burrow through the sediment, such as deposit-feeding polychaetes. Because Cypridinidae only bury near the sediment surface, most animals burrow below these ostracods. Therefore the coelotrichs are well positioned to detect such movement.

Another explanation for the function of the coelotrichs is to detect drainage currents through the sand. From these currents the ostracod could determine which direction was towards the shallow water. For unidirectional signals such as this there is no ambiguity, and an array of sensory setae allows the ostracod to localize the direction with precision.

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REFERENCES

- Altner, A. & Prillinger, L. 1980 Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *Int. Rev. Cytol.* **67**, 69–134.
- Cohen, A. C. 1989 Comparison of myodocopid ostracodes in two zones of the Belize barrier reef near Carrie Bow Cay with changes in distribution 1978–1981. *Bull. Mar. Sci.* **45**, 316–337.
- Dahl, E. 1979 Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. *Oikos* **33**, 167–175.
- Emler, R. B. & Strathman R. 1985 Gravity, drag, and feeding currents of small zooplankton. *Science* **228**, 1016–1017.
- Fletcher, N. H. 1992 *Acoustic systems in biology*. New York: Oxford University Press.
- Horch, K. W. & Salmon, M. 1969 Production, perception and reception of acoustic stimuli by semiterrestrial crabs (genus *Ocypode* and *Uca*, family Ocypodidae). *Forma Functio* **1**, 1–25.
- Myrberg, A., Kramer, E. & Heinecke, P. 1965 Sound production by cichlid fishes. *Science* **149**, 555.
- Parker, A. R. 1998 A new genus and two new species of Cypridinidae (Crustacea: Ostracoda: Myodocopina) from Australia. *Rec. Aust. Mus.* **50**, 1–17.
- Tsukagoshi, A. 1990 Ontogenetic change of distributional patterns of pore systems in *Cythere* species and its phylogenetic significance. *Lethaia* **23**, 225–241.
- Vannier, J. & Abe, K. 1993 Functional morphology and behaviour of *Vargula hilgendorffii* (Ostracoda: Myodocopida) from Japan, and discussion of its crustacean ectoparasites: preliminary results from video recordings. *J. Crust. Biol.* **13**, 51–76.