

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

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

Andrew R. Parker

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK (*andrew.parker@zoo.ox.ac.uk*)

This study reports a previously undescribed and unique sensillum. Some species of *Lowrya* Parker 1998 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 ante 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 ante (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 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 cara-
pace. The ca sensilla are here termed coelotrichs, and are each centred within an almost spherical cavity in the cara-
pace. The cavity forms at the base of a depression, and the depression in turn lies within a sunken
channel on the e pace. 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 wide 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, a 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, s 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 visco 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

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

1. INTRODUCTION

1. **INTRODUCTION**
The carapace of Ostracoda often bears numerous sensory
setze. These extend from the valve surface through pore setae. 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 nonsetae. These extend from the valve surface through pore canals, and are serviced by dendrites within the nonsetae. 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 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 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 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) pore canals are distributed over the entire carapace
surface. Simple pore canals, including their innervating
setae, are prevalent in both Myodocopina (Myodocopa)
and Podocopa surface. Simple 1
setae, are preval
and Podocopa.
Ostracods gen ae, are prevalent in both Myodocopina (Myodocopa)
d Podocopa.
Ostracods generally operate at low Reynolds numbers
loben 1989) Therefore, there is a thick layer of viscous

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 & Ostracods generally operate at low Reynolds numbers me

(Cohen 1989). Therefore, there is a thick layer of viscous tic

water that surrounds ostracods in motion (see Emlet & extending a surrounds of the Strathman 1985) (Cohen 1989). Therefore, there is a thick layer of viscous water that surrounds ostracods in motion (see Emlet & Strathman 1985). tter that surrounds ostracods in motion (see Emlet &
cathman 1985).
Cypridinid ostracods probably spend most of their lives
ried a few millimetres into the sand substrate of their

Strathman 1985).
Cypridinid ostracods probably spend most of their lives
buried a few millimetres into the sand substrate of their
babitat (Vannier & Abe 1993). Species of Lawrya Parker 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 a 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 appa-
ratus typical of other scavenging cypridinids (Par 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 98, bear feeding appendages and putative sensory appatus typical of other scavenging cypridinids (Parker 1998).
One unique feature of some species of *Lowrya* is an usual structure composed of sensillae arranged in a

ratus 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 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 caranace 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 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 illustrate 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 taxovalves (figure 1). This appears as a row of circles at $\times 100$ bu
magnification (e.g. figure 1), as illustrated in the taxo-
nomic publication of *Lowrya taiti* (Parker 1998). The aim eth
of this study was to determine th 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. Fro nomic 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 envi 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 environ-
mental fluctuations is analysed. not the nervous innervation, of
information the response of the
mental fluctuations is analysed.
The structure under examina Formation the response of the structure to environ-

ental fluctuations is analysed.

The structure under examination is here termed the

relatrich' (from the Greek meaning cavity of hair)

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 collec-Specimens of *L*. *taiti* Parker 1998 were obtained from collections at the Australian Museum (AM P45077). They had been
sought in a baited tran set suggestive outside of Bate Bay. Now Specimens of *L. tatti* 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 Walse, Australia (24°44'S, 150°20 caught in a baited trap set overnight outside of Bate Bay, New South Wales, Australia $(34°44' S, 150°39' E)$, at $25 m$ depth, and 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.
The appairance of uth Wales, Australia (34°44′S, 150°39′E), at 25 m depth, and
bsequently fixed in 5% formalin and preserved in 70% ethanol.
Ten specimens of *L. taiti* were dissected and their carapaces
sunted in glucaral and avamined unde

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 micro-
scope. One specimen was embedded in pa The specimens of *L. tath* were dissected and their carapaces
mounted in glycerol and examined under a compound micro-
scope. One specimen was embedded in paraffin wax and long-
indingly acational at *Aum*. Sections were t scope. One specimen was embedded in paraffin wax and long-
itudinally sectioned at $4 \mu m$. Sections were treated with a scope. One specimen was embedded in paraffin wax and long-
itudinally sectioned at 4 µm. Sections were treated with a
modified Mallory solution (F. Crandle, personal communica-
tion) a multisemponent stein suitable for the itudinally sectioned at 4 µm. Sections were treated with a
modified Mallory solution (F. Crandle, personal communica-
tion), a multicomponent stain suitable for the study of crusta-
cean sensory structures and again the co tion), a multicomponent stain suitable for the study of crusta-
cean sensory structures, and again the coelotrichs were observed
under a compound microscope. cean sensory structures, and again the coelotrichs were observed an sensory structures, and again the coelotrichs were observed
der a compound microscope.
One specimen was cut into 0.2 mm thick sections using a
sex blode. These sections, together with a complete carenage.

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,

range onitial point dried, goated with gold and aromined in a razor blade. These sections, together with a complete carapace, were critical-point dried, coated with gold and examined in 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
sutamal views and internal approach were critical-point dried, coated with gold
scanning electron microscope. Coelotrichs
external views and internal cross-sections.

external views and internal cross-sections.
Two specimens were prepared for transmission electron external views and internal cross-sections.
Two specimens were prepared for transmission electron
microscopy by (i) treating with 2.5% glutaraldehyde in 0.1M
phosphata buffar for the transmit temperature (ii) ringing with Two specimens were prepared for transmission electron
microscopy by (i) treating with 2.5% glutaraldehyde in 0.1M
phosphate buffer for 1h at room temperature, (ii) rinsing with
0.1M buffan (iii) treating with 1% camium ta phosphate buffer for 1h at room temperature, (ii) rinsing with 0.1 M buffer, (iii) treating with 1% osmium tetroxide in 0.1 M buffer for 1h at room temperature, (iv) dehydrating through an $0.1 M$ buffer, (iii) treating with 1% osmium tetroxide in $0.1 M$ ethanol series, and (v) infiltrating with Epon resin via a resinbuffer for I 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
natatan) Sections (60 nm 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 transmis-
sign electron minoscopes rotator). Sections (60 nm thick) were examined in a transmission electron microscope.

Because ostracods are surrounded by a viscous boundary sion 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 solvulated. After modelling a 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
solatiish from the results of the share am 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 coelotrichs as small circles (setae not visible at this
magnification). Note that the number of coelotrichs varies in showing coelotrichs as small circles (setae not visible at this magnification). Note that the number of coelotrichs varies in different species of *Lowrya* (often less numerous than in the magnification). Note that the number of coelotrichs varies is
different species of $Lowrya$ (often less numerous than in the
species illustrated, although always more closely spaced
anteriorly than nosteriorly) different species of *Lowrya* (oft
species illustrated, although al
anteriorly than posteriorly).

effect of fluctuations in the external environment on the coeffect of fluctuations i:
elotrich was assessed.

3. RESULTS

(a) *Microscopic analyses*

The results of the microscopy are summarized in the (a) *Microscopic analyses*
The results of the microscopy are summarized in the
three-dimensional representation of a coelotrich shown in
figure 2. Coelotrichs are structures based within almost The results of the microscopy are summarized in the
three-dimensional representation of a coelotrich shown in
figure 2. Coelotrichs are structures based within almost
spherical (or volumes equivalent to two overlanning three-dimensional representation of a coelotrich shown in
figure 2. Coelotrichs are structures based within almost
spherical (or volumes equivalent to two overlapping
spheres) invaginations of the caranace enjoyticle formi figure 2. Coelotrichs are structures based within almost spherical (or volumes equivalent to two overlapping spheres) invaginations of the carapace epicuticle, forming spherical (or volumes equivalent to two overlapping
spheres) invaginations of the carapace epicuticle, forming
cavities about 10 µm deep, but not reaching beyond the
boundary of the endocuticle. Each cavity lies within its spheres) invaginations of the carapace epicuticle, forming
cavities about $10 \mu m$ deep, but not reaching beyond the
boundary of the endocuticle. Each cavity lies within its
own circular depression, or pit in the external cavities about 10 μ 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 caranace. At the cavity entrance there is a 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 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 bole, through which a s 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 great (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 coelectr 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 coelotrich seta lies raised from, but almost parallel to, the carapace than, or equal to, that of the setal base. The coelotrich
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 type 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. 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 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 coelotrich setae that lie perpendicular to the carapace surface and
do not usually emerge from recessed areas. The coelotrich
seta arises from inside the cavity, near the plug, and joins
with the cavity wall. A chitinized tube in the do not usually emerge from recessed areas. The coelotrich
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 t 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 um), fine and st 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 $20 \,\mu m$), fine and stiff distally, leads from this part of the cavity wall to the epithelium.
The seta is long (about $20 \mu m$), fine and stiff distally,
bifurcating near its base, just external to the plug (about
 $2 \mu m$ from the plug). The long distal part 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 sligh bifurcating near its base, just external to the plug (about 2 µm from the plug). The long, distal part of the seta lies
almost parallel (usually slightly angled) with the external
caranace surface, about 2 µm from this sur 2 µm from the plug). The long, distal part of the seta lies
almost parallel (usually slightly angled) with the external
carapace surface, about 2 µm from this surface. There are
no pores in the seta Internally, the seta bo almost parallel (usually slightly angled) with the external
carapace surface, about 2 µm from this surface. There are
no pores in the seta. Internally, the seta houses two
cylindrical cavities of different cross-sectional carapace surface, about $2 \mu m$ 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 different cross-sectional diameters
for at least some of its length. The tip of the seta may
reach as far as the adjacent coelotrich cavity, but never
overlaps or touches the seta of the adjacent coelot for at least some of its length. The tip of the seta may
reach as far as the adjacent coelotrich cavity, but never
overlaps or touches the seta of the adjacent coelotrich.
The setae of a row of coelotrichs are all orientat reach as far as the adjacent coelotrich cavity, but never
overlaps or touches the seta of the adjacent coelotrich.
The setae of a row of coelotrichs are all orientated simi-
larly: they lie parallel to the valve margin and overlaps or touches the seta of the adjacent coelotrich.
The setae of a row of coelotrichs are all orientated similarly; they lie parallel to the valve margin and point in a
wentral or posterior direction depending on thei The setae of a row of coelotrichs 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 caranace larly; they lie para
ventral or posterio
on the carapace. *Phil. Trans. R. Soc. Lond.* B (2000)

Figure 2. Generalized diagrams of a coelotrich of *L. taiti*.

(*a*) Longitudinal section through centre of cavity; X represents

the direction of water flow parallel to the groove in which a Figure 2. Generalized diagrams of a coelotrich 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 coelotrichs lies. (*h*) (*a*) Longitudinal section through centre of cavity; X represents
the direction of water flow parallel to the groove in which a
row of coelotrichs lies. (*b*) Three-dimensional model; cavity is
sectioned transversely and the direction of water flow parallel to the groove in which a
row of coelotrichs lies. (*b*) Three-dimensional model; cavity is
sectioned transversely and off-centre (near edge of plug); X, Y
and Z represent different dire sectioned transversely and off-centre (near edge of plug); X , Y and Z represent different directions of water flow over the 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) and Z represent differents that
seta; B1 represents that
(of viscous water).

A row of coelotrich pits always occurs in regions of the A row of coelotrich pits always occurs in regions of the carapace exhibiting some further type of recess. Along the rostrum and lower incisure margin, the coelotrich A row of coelotrich pits always occurs in regions of the
carapace exhibiting some further type of recess. Along
the rostrum and lower incisure margin, the coelotrich
row is at the most sunken part of a depressed area or carapace exhibiting some further type of recess. Along
the rostrum and lower incisure margin, the coelotrich
row is at the most sunken part of a depressed area or

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trough in the carapace. Along the anteroventral, ventral,
and posterior carapace margins they lie at the base of a trough in the carapace. Along the anteroventral, ventral,
and posterior carapace margins they lie at the base of a
ridge or lin of the carapace margin, which extends about 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 um laterally. These recessed areas form channels 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 ridge or lip of the carapace margin, which
5 µm laterally. These recessed areas form
which the coelotrich pits and setae all lie.
Nerves were not evident in the specime Im laterally. These recessed areas form channels, in
ich the coelotrich pits and setae all lie.
Nerves were not evident in the specimens examined;
known specimens of *Lowrya* have been treated with

solutions unsuitable for the preservation of nervous tissue. 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 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. For example, the internal spaces of
and tube leading from the cavity w
contain nerve fibres, yet are hollow.
Coelotrichs always occur near the d tube leading from the cavity would be expected to
ntain nerve fibres, yet are hollow.
Coelotrichs always occur near the anterior, ventral and
sterior margins of the caranace: never near the dorsal

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 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 adult 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 invenile stages margins, or far from any margin. They oc
described above in both males and fema
and at least the final two juvenile stages.

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

(b) *Calculations and modelling of a coelotrich*

and its microenvironment

The viscous boundary layer adjacent to the surface of
 ϵ caranace has a thickness of and its microent
The viscous boundary layer a
the carapace has a thickness of

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

where ν is the kinematic viscosity of the fluid (ν is where ν is the kinematic viscosity of the fluid (ν is approximately 1.0×10^{-6} m²s⁻¹ for water) and *f* is the frequency involved where ν is the kine
approximately 1.0×1
frequency involved.
This is about 40 proximately 1.0×10^{-6} m² s⁻¹ for water) and f is the
quency involved.
This is about 40 µm at 100 Hz (a possible frequency
countered in the marine environment). Within the

frequency involved.
This is about $40 \mu m$ at 100 Hz (a possible frequency encountered in the marine environment). Within the This is about $40 \mu m$ 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 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 with distance from the stationary surface of the animal.
The sediment in which cypridinids are buried for most

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 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 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 vibrat 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 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' cara-
pace. The second case is less obvious. It can be s In the first case, the water clearly moves relative to the sand grains of the sediment and to the ostracods' cara-
pace. The second case is less obvious. It can be shown
that when a sound wave propagates through a composit sand grains of the sediment and to the ostracods' cara-
pace. 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 pace. 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 the 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 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 parti-
cles (see Eletcher 1992, p.89). The app solid particles is different from that of the liquid, there is
an acoustic motion of the liquid relative to the solid partian 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 cles (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
caranace of the ostraced behaves like the solid particles of 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 comparable with the overall acoustic amplitude. The (a) Functional morphology of a coelotrich
carapace of the ostracod behaves like the solid particles of The coelotrich is not tactile (i.e. a touch receptor)
the sedimen 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 velo-
city over the caranace the sediment because it
water. Therefore, in eacl
city over the carapace.
There are three possi water. Therefore, in each case, there is a fluid flow velocity over the carapace.
There are three possible directions of water flow past

city over the carapace.
There are three possible directions of water flow past
one of the coelotrich setae relative to the ostracod's cara-
pace (figure 2) For flow in the Z-direction, normal to the There are three possible directions of water flow past
one of the coelotrich setae relative to the ostracod's cara-
pace (figure 2). For flow in the Z-direction, normal to the
caranace, the seta is ideally orientated to be one of the coelotrich setae relative to the ostracod's cara-
pace (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, h pace (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. 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 para possible 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 caranace, the groove orientation protects 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 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 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 evert viscous direction, parallel to the groove, the flowing water can come in contact with the seta and exert viscous drag

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forces upon it. The coelotrich seta is therefore only forces upon it. The coelotrich s
affected by flow in this direction.
Flow in the X-direction is esse rces upon it. The coelotrich seta is therefore only
fected by flow in this direction.
Flow in the X-direction is essentially parallel to the
stal part of the coelotrich seta and pulls it in the flow

which the coelotrich pits and setae all lie. direction by the action of viscous forces. Because of the Nerves were not evident in the specimens examined; bend near the base of the seta, this drag force is all known specime 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 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 direction by the action of viscous forces. Because of the converted to an angular deflection, as well as sometimes 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 converted to an angular defle
to a lateral displacement, both
the coelotrich's sensory cells.
When the coelotrich seta is a lateral displacement, both of which would stimulate
e coelotrich's sensory cells.
When the coelotrich seta is bent by an external vibra-
on the force required to return the seta to its original

the coelotrich's sensory cells.
When the coelotrich seta is bent by an external vibra-
tion, the force required to return the seta to its original
position (as adapted from Eletcher 1992) is $-F$. When the coelotrich seta is bent by an externation, the force required to return the seta to its oposition (as adapted from Fletcher 1992) is $-F_e$:

$$
F_{\rm e} = -ES_{\kappa}^2 \frac{\mathrm{d}^4 z}{\mathrm{d} x^4},\tag{2}
$$

 $F_e = -ES_\kappa^2 \frac{d^2}{dx^4}$, (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 for 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 for the material of the seta and dz/dx is the angular deflec- 2 F 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 for the material of the seta, and d*z*/d*x* is the angular deflection tion. the material of the seta, and dz/dx is the angular deflection.
The plug is simply compliant, i.e. it does not clamp the

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

$$
\frac{\mathrm{d}z}{\mathrm{d}x} = \mu ES_2 \frac{\mathrm{d}^2 z}{\mathrm{d}x^2},\tag{3}
$$

where μ represents the angular compliance of the plug.

Additionally,

$$
\mu s = ES_{\kappa}^2,\tag{4}
$$

 $\mu s = ES_{\kappa}^2$, (4)
where μs is the angular compliance of the seta and *l*
represents the length of the seta where μ_s is the angular complistive represents the length of the seta.
Therefore, the behaviour of the 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:

$$
\mu/\mu s = \mu E S \kappa^2 / l. \tag{5}
$$

Each coelotrich seta will have a figure-of-eight sensi-Each coelotrich seta will have a figure-of-eight sensi-
tivity pattern along the direction of the channel in which
it lies. In a body of water that is large compared with the Each coelotrich seta will have a figure-of-eight sensi-
tivity pattern along the direction of the channel in which
it lies. In a body of water that is large compared with the
houndary layer thickness the deflection of a co tivity 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 bou 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 thickness.

4. DISCUSSION

(a) *Functional morphology of a coelotrich*

(a) **Functional morphology of a coelotrich**
The coelotrich is not tactile (i.e. a touch receptor)
cause its seta does not reach beyond the adjacent rajed (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 (lin) of the caranace. The possibility that a coelo-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 coelo-
trich is an acceleration detector can also be dismi because its seta does not reach beyond the adjacent raised
area (lip) of the carapace. The possibility that a coelo-
trich is an acceleration detector can also be dismissed because the seta is without a dense mass on its free end trich 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 mea 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 coelectrich is not chemosensory but rather a (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 mechano-
receptor. The specific distributional pattern o with the long, fine but stiff nature of the seta means that
the coelotrich is not chemosensory but rather a mechano-
receptor. The specific distributional pattern of the coelothe coelotrich is not chemosensory but rather a mechano-
receptor. The specific distributional pattern of the coelo-
trichs over the carapace surface excludes the function of
carapace stress reception. The evidence suggest receptor. The specific distributional pattern of the coelo-
trichs over the carapace surface excludes the function of
carapace stress reception. The evidence suggests that
coelotrichs are velocity detectors, acted upon by trichs 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 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 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 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 sin 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 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 r 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 seta is protected by the plug, its b
can be very flexible, giving a
without requiring a large torque.
The setae of a row of coelotrich In the very flexible, giving a considerable response
thout requiring a large torque.
The setae of a row of coelotrichs are arranged so that
iacent setae almost touch (i.e. with minimal gans

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 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 sensiadjacent setae almost touch (i.e. with minimal gaps
between setae), therefore the probability of detecting any
vibrations is extremely high. The figure-of-eight sensi-
tivity pattern of each seta means that the ostracod ca between setae), therefore the probability of detecting any
vibrations is extremely high. The figure-of-eight sensi-
tivity pattern of each seta means that the ostracod can
sediment surface, most animals burrow below these judge the direction from which the signal is coming, with cods. Therefore the can uncertainty of 180°. Therefore the semicircular detect such movement. tivity 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 caranace margins 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 an uncertainty of 180°. Therefore the sem
arrangement of coelotrichs around the carapace
is sufficient to detect signals from any direction.
If the seta is acting as a lever when the tip of 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

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 Simi-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. Simi-
larly when the tip of the seta moves away from the moves towards the carapace the 'upper' basal section
becomes stressed and the 'lower' section is relaxed. Simi-
larly, when the tip of the seta moves away from the cara-
pace, the lower basal section becomes stressed and t 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 unner section is relaxed. Such states of stress could larly, when the tip of the seta moves away from the cara-
pace, 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 sh pace, 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 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 flexi 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 o stiff enough to prevent the seta ever undergoing too la
an angular displacement. The greater the flexibility of
plug, the smaller the resonance frequency of the seta.
The function of the coelotrich cavity (or rather angular displacement. The greater the flexibility of the
ug, the smaller the resonance frequency of the seta.
The function of the coelotrich cavity (or rather the
vity wall) formed by an invagination of the enjoyticle

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 annarent. It is spherical (or the result of two 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 over-
lanning spheres) in shane: this shane would prov 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 aga 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 caranace wall. The layer of enjoystrongest mechanical properties (protection against
collapsing) but also maximum dampening of vibrations
from within the flexible carapace wall. The layer of epicu-
ticle which surrounds the cavity is also more highly scle collapsing) but also maximum dampening of vibrations
from within the flexible carapace wall. The layer of epicu-
ticle which surrounds the cavity is also more highly scler-
otized than the endocuticle, adding further stren 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 ticle which surrounds the cavity is also more highly scler-
otized than the endocuticle, adding further strength to
the cavity wall. If one function of the cavity wall is to
damnen vibrations transmitting through the caran otized 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 almo 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 laver) woul 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 th 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 ex 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 caranace wa 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 entire coelotrich detects external vibrations,
confusing vibrations from within the ca
caused by movements of the ostracod itself.

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

(b) Source of the stimuli detected by a coelotrich
Coelotrichs must detect either steady fluid drainage
ption or acoustic motion in the surrounding liquid (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 ostraced is buried in the sediment Coelotrichs must detect either steady fluimotion or acoustic motion in the surround
while the ostracod is buried in the sediment.
All known species of *Lourna* scavenge (A 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,

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-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 (Dabl 1979) and 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 m 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 move-
ment in coeletrich setze of buried specimens. Varaula spreading vibrations through the water (Dahl 1979), and
top layers of sediment. Such vibrations would cause move-
ment in coelotrich setae of buried specimens. *Vargula*
hilaendorfii (Müller, 1890), a cypridinid with a s top layers of sediment. Such vibrations would cause movement in coelotrich setae of buried specimens. *Vargula hilgendorfii* (Müller, 1890), a cypridinid with a similar morphology to species of *Lowrya*, buries at an angle of hilgendorfii (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 (V morphology to species of *Lowrya*, buries at an angle of $45-60^{\circ}$ between the longitudinal axis of the carapace and the surface of the substratum, anterior end first (Vannier $\&$ Abe 1993). In this position, the coelo 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 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 ideal position to detect stimuli from the water column or sediment surface. For similar reasons, the detection of 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 var *alment 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 func al. 1965; Horch & Salmon 1969) or temperature variations (see Altner & Prillinger 1980) may not be the function of the strategically positioned coelotrichs. al. 1965; Horch & Salmon 1969) or temperat
tions (see Altner & Prillinger 1980) may not be
tion of the strategically positioned coelotrichs.
A source of acoustic motion which would ca In the source Alther & Prillinger 1980) may not be the function of the strategically positioned coelotrichs.
A source of acoustic motion which would cause move-
ent in the coelotrich setae is from predators which

tion of the strategically positioned coelotrichs.
A source of acoustic motion which would cause move-
ment in the coelotrich setae is from predators which
burrow through the sediment, such as denosit-feeding A source of acoustic motion which would cause move-
ment in the coelotrich setae is from predators which
burrow through the sediment, such as deposit-feeding
polychaetes. Because Cypridinidae only bury near the ment 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 ostraburrow through the sediment, such as deposit-feeding
polychaetes. Because Cypridinidae only bury near the
sediment surface, most animals burrow below these ostra-
cods. Therefore the coelotrichs are well positioned to 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 sediment surface, most a
cods. Therefore the co
detect such movement.
Another explanation f ds. Therefore the coelotrichs are well positioned to
tect such movement.
Another explanation for the function of the coelotrichs
to detect drainage currents through the sand From

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

Thanks are due to Neville Fletcher (Australian National

University) for advice on the interpretation of the results of this Thanks are due to Neville Fletcher (Australian National
University) for advice on the interpretation of the results of this
study I also thank Noel Tait (Macquarie University) Iim Thanks are due to Neville Fletcher (Australian National University) for advice on the interpretation of the results of this study. I also thank Noel Tait (Macquarie University), Jim Lowry (Australian Museum) Louis Kornicke University) for advice on the interpretation of the results of this
study. I also thank Noel Tait (Macquarie University), Jim
Lowry (Australian Museum), Louis Kornicker, Duane Hope,
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comments on the manuscript and help with microscopy and
histology This study was funded by The Australian Frank Crandle and Cathy Price (Smithsonian Institution) for
comments on the manuscript and help with microscopy and
histology. This study was funded by The Australian Museum
Trust and The Roval Society comments on the manuscript
histology. This study was fun
Trust and The Royal Society.

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