

Algal-dwelling Eophliantidae (Amphipoda): description of a new species and key to the world species, with notes on their biogeography

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Eophliantidae are poorly studied marine algal-dwelling amphipods with a wide distribution. A new species was found to excavate burrows across the main stem of *Carpophyllum maschalocarpum* (Turner) Grev. in the New Zealand subtidal, and a detailed morphological description of this amphipod is given. *Bircenna macayai* sp. nov. can be distinguished from other *Bircenna* species by a combination of the following characters: bilobed coxa 1, merus and carpus of pereopods 5–7 strongly extended posteriorly, crenulate basis of pereopod 7 and smooth posterior margin of epimeron 3, pereopod 7 basis longer than wide. A key to the fourteen world species of *Eophliantidae* is provided. Taxonomy, evolutionary sequences, functional morphology and biogeography of the *Eophliantidae* are briefly discussed. New Zealand and Australian shallow waters show the highest species diversity of *Eophliantidae*, containing both species bearing plesiomorphic and highly derived characters, suggesting that Australasia is an evolutionary centre for this amphipod family.

Keywords: Amphipoda, Eophliantidae, *Bircenna macayai*, new species, *Carpophyllum maschalocarpum*, functional morphology, algal-dwelling, biogeography, New Zealand, Australasia, evolutionary centre

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INTRODUCTION

According to Barnard (1972) the New Zealand intertidal zone can be considered to be a distinct gammaridean biogeographical province, since more than 50 per cent of its species are endemic. More than 100 species of gammaridean amphipods are known to live amongst algae in New Zealand, but few are considered to be obligate algal dwellers or tunnellers. The family Eophliantidae, however, are one such group.

The Eophliantidae contain 14 species belonging to six genera. The main distribution is in the southern hemisphere, with the exception of *Ceinina japonica* Stephensen, 1933 found in Japan and *Wandelia orghidani* Ortiz & Lalana, 1997 from Indonesia, just north of the equator. *Lignophliantis pyrifer* J.L. Barnard, 1969 is described from California, but the placement of this species in the Eophliantidae is uncertain. Its taxonomic position is briefly discussed below. Information regarding species of the Eophliantidae is scattered throughout the literature, and to facilitate identification we have also included a key to the world species. Finally, a new species was found burrowing in the algae *Carpophyllum maschalocarpum* (Turner) Grev. off New Zealand and is described in detail below.

All eophliantids are assumed to be algal dwellers, although no record of algae association is found for *Cylindrylloides*

kaikoura Barnard, 1972 or for *Wandelia orghidani* Ortiz & Lalana, 1997. Several species from the family Eophliantidae live in positively buoyant macroalgae, such as *Macrocystis pyrifer* (L.) C. Agardh, *Durvillaea antarctica* (Cham.) Har. or *C. maschalocarpum*. These algae are commonly found floating in coastal waters of New Zealand (Kingsford, 1992) and in the Southern Ocean (Helmuth *et al.*, 1994). Several recent studies indicate that the biota (including Eophliantidae) associated with these floating macroalgae might be dispersed via algal rafting (e.g. Donald *et al.*, 2005). This will also influence the phylogeography of these organisms. We propose that algal rafting might have contributed to the evolutionary radiation of the Eophliantidae, originating in Australasia.

MATERIALS AND METHODS

Field collecting

The alga *Carpophyllum maschalocarpum* was collected by snorkelling in about 2 m depth at Kau Bay, Wellington Peninsula, New Zealand, in May 2009. The brown alga *Carpophyllum maschalocarpum* is common in coastal regions of New Zealand (including the Wellington area), where it grows in shallow subtidal waters. *Carpophyllum* is a common habitat for several groups of peracarids (e.g. Taylor & Cole, 1994; Taylor, 1998) and a food source for herbivorous labroid fish (Choat & Clements, 1993). It has a distinct main stem with alternating lateral blades, and its texture is

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characterized as leathery and tough (Adams, 1997). Several pieces were kept in seawater before examination under a stereomicroscope. Photographs were taken of live amphipods in their holes in the algae stem. Amphipods were removed from small holes in the algae by forceps and fixed in either buffered formalin or in 90% ethanol.

Morphological description

Specimens were examined and dissected under a Leica MZ9.5 stereomicroscope and drawn using a camera lucida. One of the selected paratypes was completely dissected and mounted on one slide in Faure's solution. The holotype was temporarily mounted in glycerol. These specimens were examined and drawn using a Nikon compound microscope fitted with a camera lucida. The body lengths of specimens examined were measured by tracing individual's mid-trunk lengths (tip of the rostrum to end of telson) using a camera lucida. All illustrations were digitally 'inked' following Coleman (2003). Setal terminology follows Watling (1989).

Type material is held in the National Institute of Water and Atmospheric Research Invertebrate Collection, Wellington, New Zealand (NIWA). Comparative material of *Wandelia dronga* (Myers, 1985) was borrowed from the Australian Museum, Sydney.

Functional morphology

An extensive literature search was conducted for all species of Eophliantidae. Morphometric measurements were taken from published descriptions (e.g. length of coxae related to length of pereonites).

RESULTS

SYSTEMATICS

Order AMPHIPODA Latreille, 1816

Suborder GAMMARIDEA Latreille, 1803

Superfamily TALITROIDEA Rafinesque, 1815

Family EOPHLIANTIDAE Sheard, 1936

DIAGNOSIS (AFTER BARNARD & KARAMAN, 1991)

Body cylindroid (vermiform), coxae small, often discontinuous. Head spheroid. Cuticle smooth. Eyes bilateral. Antennae short, sparsely articulate, accessory flagellum absent. Mandibular palp vestigial or absent; molar nontritritative, often absent or spinose, rakers sparse to absent. Palp of maxilla 1 vestigial or absent. Gnathopods thin, feeble, parachelate, or minutely subchelate. Pereopods short, article 2 of pereopods 5–7 expanded. Uropod 3 vestigial, ramus absent. Telson usually deeply cleft or fully bilobate, with exception of *Lignophliantis* bearing an entire telson. The telson lobes usually forming tent and slightly fleshy. Urosomites 2–3 occasionally coalesced.

Genus *Bircenna* Chilton, 1884

DIAGNOSIS (AFTER BARNARD & KARAMAN, 1991)

Pereonite 1 with ventral cradle for support of head.

Flagella of antennae 1–2 with four or more articles. Coxae 2–4 or 4–5 discontinuous. Posterior lobe on articles 4–5 of

pereopods 5–7 with 2–3 medium size setae. Pleopods biramous, peduncles expanded. Telson almost fully cleft.

REMARKS

Examination of the type material of *Bircenna dronga* Myers, 1985 revealed that this species lacks a cradle on pereonite 1 and its coxae are contiguous. Based on this we herewith remove this species from *Bircenna* to the genus *Wandelia* Chevreux, 1906.

Bircenna macayai sp. nov.

(Figures 1–4)

TYPE MATERIAL

Holotype: adult male 1.52 mm, in ethanol; New Zealand, Kau Bay, Wellington Peninsula, 174°49'48"E–41°17'16"S, subtidal water depth 2 m, NIWA 49241. Collected by snorkelling 5 May 2009.

Paratype: adult female 2.6 mm, (bearing 4 spherical eggs, 0.2 mm in diameter each) NIWA 49242 collection details as for holotype, in ethanol.

Specimen of undetermined sex, 1.4 mm, NIWA 49243, fully dissected on one slide.

COMPARATIVE MATERIAL EXAMINED

Bircenna dronga Myers, 1985, holotype AMP35194 and paratype AMP35195 from the Australian Museum, Sydney. Fiji, Makuluva Isaland, Viti Levu, collected 13 August 1979 from mixed red algae, by A. Myers.

Bircenna fulva Chilton, 1884 from the NIWA Invertebrate Collection, NIWA7188, NIWA 7181. New Zealand, 174°49'60"E–41°20'05"S, collected November 1968 by J. Barnard, 0 m depth.

ETYMOLOGY

The species is named for Erasmo Macaya Horta, in acknowledgement of his hospitality, participation in collection of algae, and taking photographs of specimens during the visit of M. Thiel to Wellington.

DESCRIPTION OF *BIRCENNA MACAYAI* SP. NOV.

Body shape cylindrical, head rounded with hemispherical incision anteroventrally. Eyes round. Coxae 1–5 small and discontinuous. Pereopods 5–7 increasing in length, pereopod 7 twice the length of pereonite 7. Urosomites two and three are fused (Figure 1A).

Antennae 1 and 2 subequal in length (Figure 1B, C). Antenna 1 flagellum with four articles. Upper lip rounded and slightly setose apically (Figure 1D). Mandible lacking palp, incisor dentate, bearing 4 to 5 teeth (Figure 2A, B); lacinia mobilis not apparent, potentially modified to resemble spine in spine row. Maxilla 1 lacking palp; inner plate slender, bearing 1 stout seta; outer plate with 7 setal teeth (Figure 1F). Lower lip slender lobe, apically setose (Figure 1E). Maxilliped palp four articulate; article four blunt; inner plate long, reaching fourth article of palp; inner plate bearing three apical robust setae; outer plate shorter than inner plate (Figure 2C).

Gnathopod 1 coxa bilobed, twice as wide as long; ischium two-thirds of basis length; carpus and merus subequal in length; propodus posterodistally produced into triangular parachela; dactylus unguiform (Figure 2D). Gnathopod 2 coxa small, rectangular; basis to dactylus similar to gnathopod 1 (Figure 2E). Pereopods 3 and 4 very similar; merus

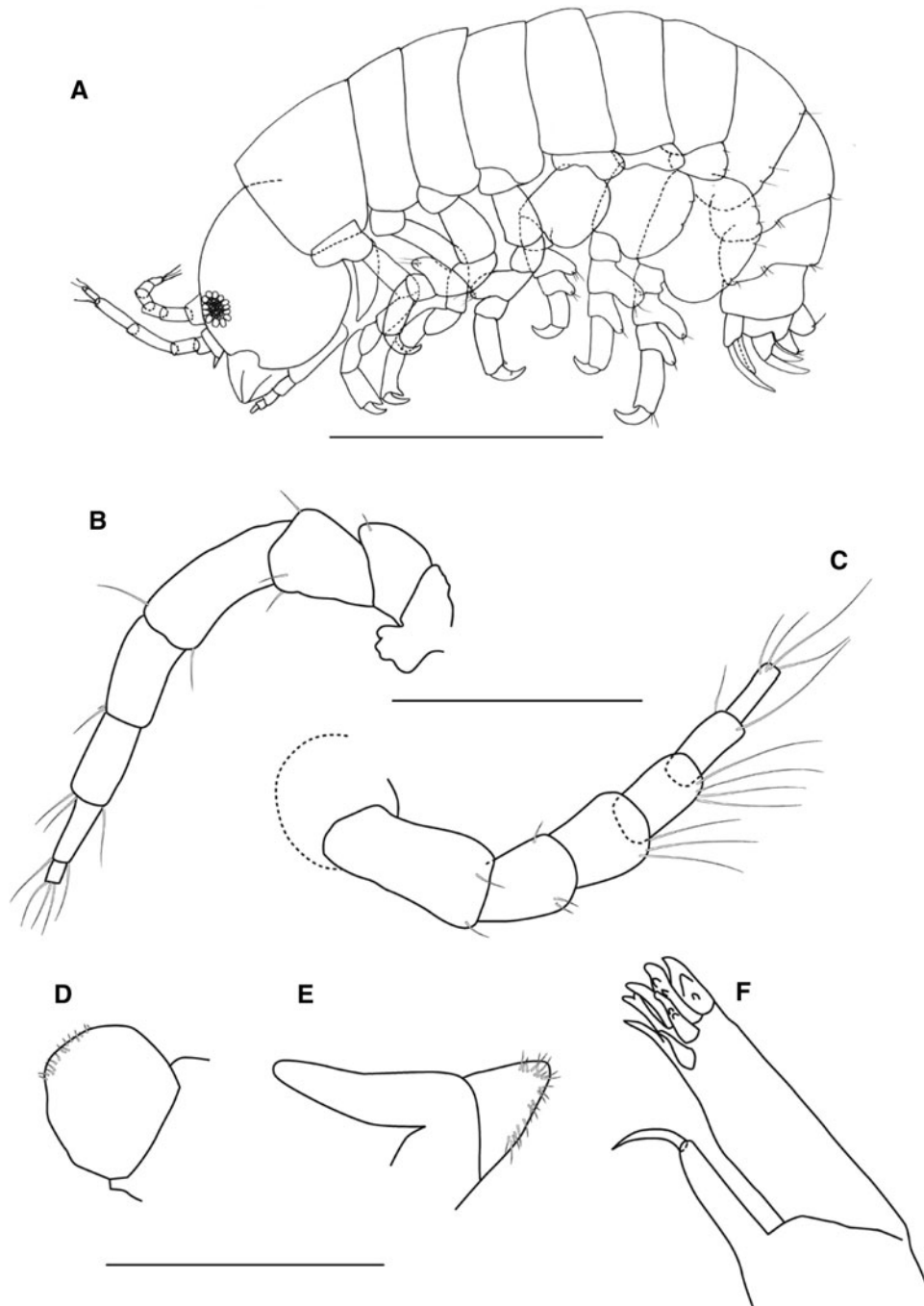


Fig. 1. *Bircenna macayai* sp. nov. (A) Holotype: adult male 1.52 mm, NIWA 49241; (B–F) paratype undetermined sex, 1.4 mm, NIWA 49243. (A) Habitus; (B) antenna 1; (C) antenna 2; (D) labrum; (E) hypopharynx (lower lip); (F) maxilla 1. Scale bars: A: 0.4 mm, B–F: 0.1 mm.

expanded anterodistally (Figure 2F). Pereopod 5 basis subrectangular, merus and carpus anterodistally produced; rounded protrusion of merus bearing five long setae, protrusion of carpus bearing one seta; dactylus unguiform (Figure 3A). Pereopod 6 basis as wide as long; merus and carpus anterodistally produced; rounded protrusion of merus bearing eight long setae, protrusion of carpus bearing three seta; dactylus unguiform (Figure 3B). Pereopod 7 basis rounded posteriorly and crenulated; merus and carpus anterodistally produced; protrusion of merus bearing two long setae, protrusion of carpus bearing one seta; dactylus unguiform (Figure 3C).

Pleopods 1–3 peduncle broad; pleopods 1–3 biramous (not drawn). Urosomite 1 more than double the length of fused urosomites 2 and 3; uropod 1 peduncle shorter than outer ramus; outer ramus about two-thirds the length of inner ramus (Figure 3D). Uropod 2 peduncle shorter than outer ramus; outer ramus about 75% of inner ramus (Figure 3D). Uropod 3 very small, unarticulate, two apical slender setae. Telson fleshy, bilobed, deeply cleft; each lobe with 1 apical slender seta (Figure 3D).

DISTRIBUTION

On *Carpophyllum maschalocarpum* in Kau Bay and Breaker's Bay, Wellington, New Zealand, subtidal.

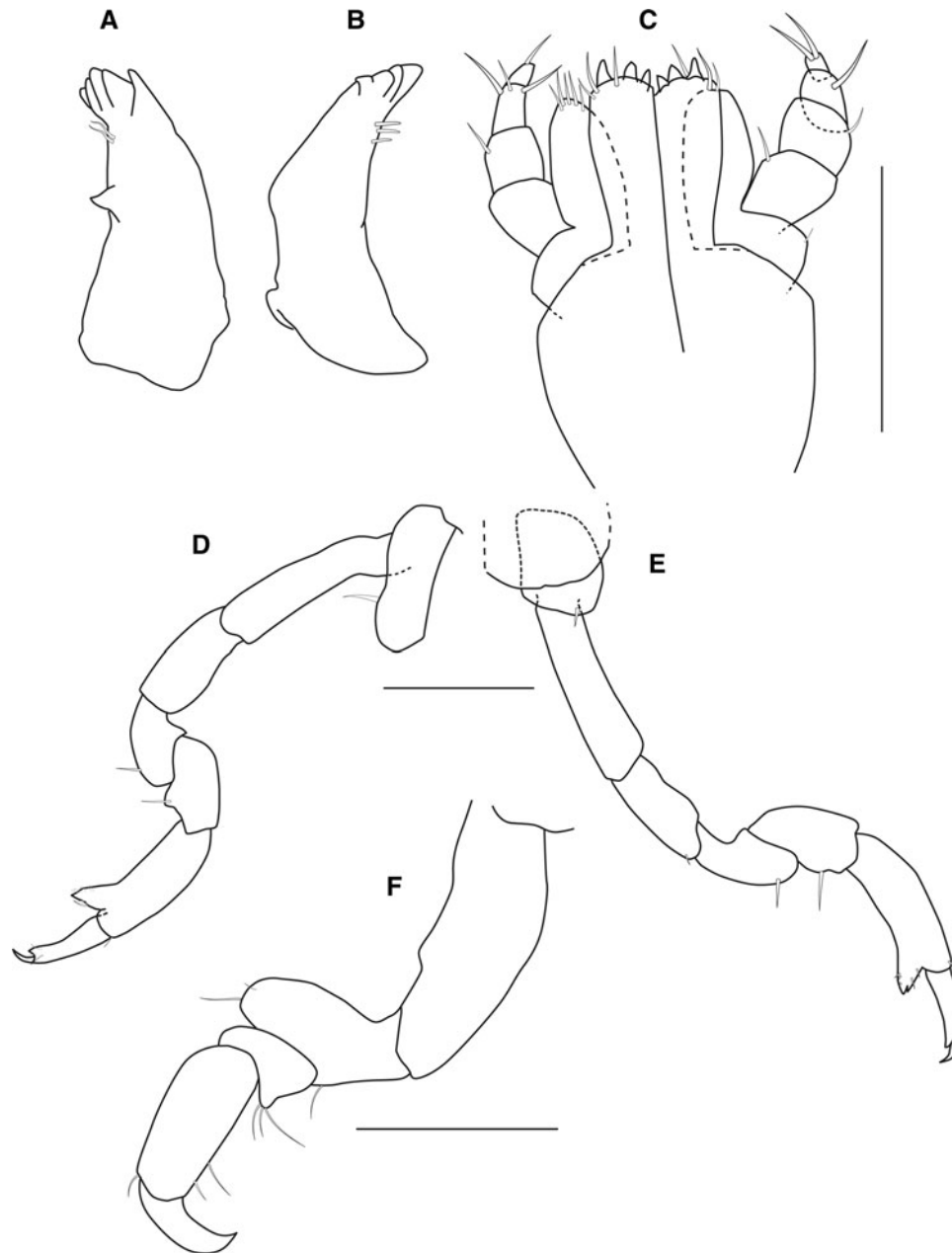


Fig. 2. *Bircenna macayai* sp. nov. (A–E) Paratype undetermined sex, 1.4 mm, NIWA 49243; (F) holotype: adult male 1.52 mm, NIWA 49241 (A, B) mandible; (C) maxilliped; (D) gnathopod 1; (E) gnathopod 2; (F) pereopod 4. Scale bars: 0.1 mm.

NOTES ON THE BIOLOGY OF *BIRCENNA MACAYAI*
SP. NOV.

Bircenna macayai sp. nov. excavate burrows across the main stem of *Carpophyllum maschalocarpum* (Figure 4A–C). Burrows of large individuals have two openings on either side of the stem, but burrows of smaller individuals may have only a single opening. Around the openings of the burrows, circular holes of brownish-yellowish colour indicate the presence of active amphipod burrows (Figure 4A, B). These holes are produced by the grazing activity of the amphipods, which removes the dark brownish meristoderm layer on the blade-like stems of the thallus. Living amphipods can frequently be seen consuming algal tissues within their burrows (Figure 4C). Occasionally they ventilate their burrows with repeated pleopod beats. They

can easily turn around in their burrows. Specimens of *Bircenna macayai* sp. nov. appear quite reluctant to abandon their burrows: only cutting away of surrounding tissues and slight squeezing of the remaining burrow walls induces amphipods to leave. They can then be seen walking around on the blade stems. Eophliantids are also relatively agile swimmers.

Several burrows are often found together on individual thallus stems of *C. maschalocarpum*. Other grazers (e.g. snails) appear to be attracted to burrows of *Bircenna macayai* sp. nov. where they can be seen feeding in the burrow holes. In combination with a high prevalence of amphipod burrows, the combined grazing activity of different grazer species causes weakening and subsequent breakage of the stems.

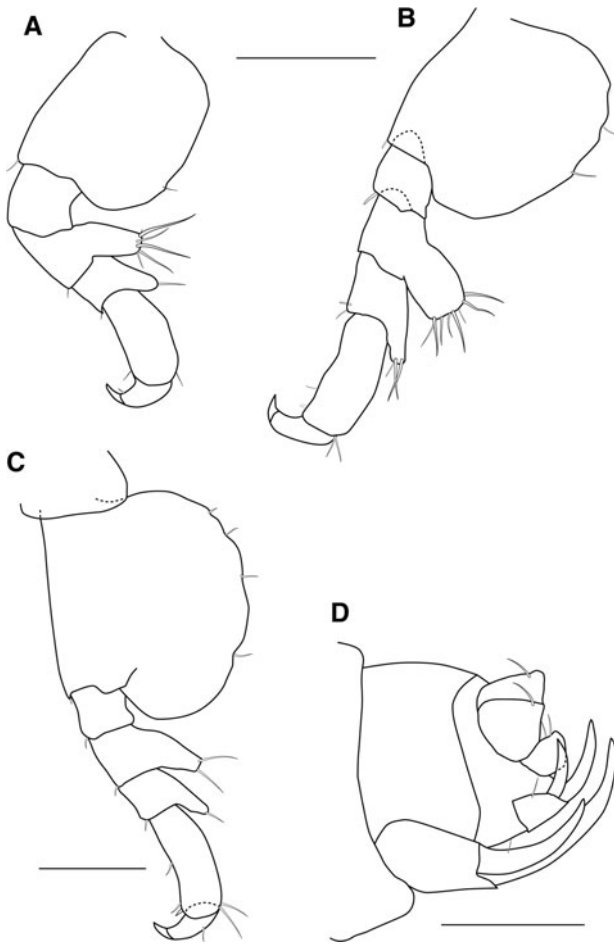


Fig. 3. *Bircenna macayai* sp. nov. (A–C) Holotype, adult male 1.52 mm, NIWA 49241; (D) paratype undetermined sex, 1.4 mm, NIWA 49243. (A) pereopod 5; (B) pereopod 6; (C) pereopod 7; (D) urosome including uropods and telson. Scale bars 0.1 mm.

KEY TO THE WORLD SPECIES OF EOPHLIANTIDAE,
14 SPECIES IN TOTAL

1. Telson uncleft and fused to urosomites 2–3, flagella of antennae 1–2 with one article only ... (*Lignophliantis*, 1 species) ... *Lignophliantis pyrifer* J.L. Barnard, 1969
 - Telson cleft, distinct from urosome, flagella of antennae 1–2 with more than 1 article 2
2. Pleopods with 1 ramus 3 (*Cylindrylloides*, 2 species)
 - Pleopods with 2 rami 4
3. Uropod 3 with heavy apical jewel spine; telson rounded, bilobed; upper lip evenly rounded *Cylindrylloides kaikoura* Barnard, 1972
 - Uropod 3 lacking apical jewel spine; telson pointed, deeply cleft, upper lip bilobed. *Cylindrylloides mawsoni* Nicholls, 1938
4. All coxae contiguous 5 (*Wandelia*, 4 species)
 - Some or all coxa discontinuous 8
5. Slightly bilobed coxa 1, posterior lobe longer than anterior lobe, not overlapping coxa 2; upper lip rounded and setulose; telson lobes triangular shaped *Wandelia crassipes* Chevreux, 1906
 - Coxa 1 not bilobed, telson lobes rectangular shaped 6
6. Broad coxa 1, overlapping coxa 2; upper lip quadrate and asetulose; distinct incision of head for reception of antenna 2; antenna 1 flagellum 2 articulate. ... *Wandelia wairarapa* Barnard, 1972
 - Head not incised; flagellum of antenna 1 more than 2 articles 7
7. Uropod 1 outer ramus distinctly shorter than inner ramus; epimeral plate 3 posterior margin smooth, ... *Wandelia orghidani* Ortiz & Lalana, 1997
 - Uropod 1 outer ramus about subequal to inner ramus; crenulate posterior margin of epimeral plate 3 *Wandelia dronga* (Myers, 1985)
8. Pereonite 1 with ventral cradle 9 (*Bircenna*, 4 species)
 - Pereonite 1 lacking ventral cradle 12

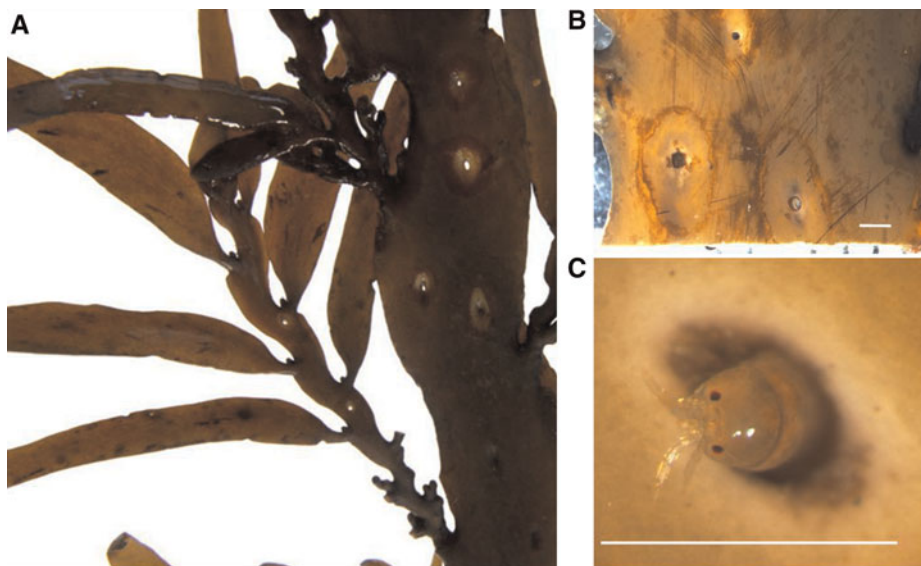


Fig. 4. (A) *Carpophyllum maschalocarpum*; (B) thallus detail of *Carpophyllum maschalocarpum* with holes burrowed by *Bircenna macayai* sp. nov. (C) *Bircenna macayai* sp. nov. within its hole. Scale bars: 1 mm.

9. Outer rami of uropods 1–2 reaching less than 75 per cent along inner rami, locking spine on pereopods 1–5 very small, parachela of gnathopods strong. . . . *Bircenna fulva* Chilton, 1884
 — Outer rami of uropods 1–2 reaching more than 75 per cent along inner rami, locking spine on pereopods 1–5 large, parachela of gnathopods weak. 10
10. Parachela of gnathopods quadrate, pereopod 7 length about equal to height of pereonite 7, antenna slender. *Bircenna nicholli* Sheard, 1936
 — Parachela of gnathopods triangular, pereopod 7 length about twice height of pereonite 7, bilobed coxa 1. 11
11. Posterior margin of epimeron 3 and of pereopod 7 basis smooth, merus and carpus of pereopods 5–7 weakly extended posteriorly, pereopod 7 basis subequal in length and width *Bircenna ignea* Nicholls, 1939
 — Merus and carpus of pereopods 5–7 strongly extended posteriorly, crenulate basis of pereopod 7 and smooth posterior margin of epimeron 3; pereopod 7 basis longer than wide. *Bircenna macayai* sp. nov.
12. Posterior lobe on articles 4–5 of pereopods 5–7 with 0–1 vestigial seta 13 (*Ceinina*, 2 species)
 — Posterior lobe on articles 4–5 of pereopods 5–7 densely setose, setae elongate (*Eophliantis*, 1 species) *Eophliantis tindalei* Sheard, 1936
13. Basis of pereopods 6 and 7 posteroventral corner enlarged, carpus of pereopods 6 and 7 posteriorly produced *Ceinina japonica* Stephensen, 1933
 — Basis of pereopods 6 and 7 inflated, carpus of pereopods 6 and 7 not produced. *Ceinina latipes* Ledoyer, 1978

DISCUSSION

Taxonomy

We assume the Eophliantidae (excluding *Lignophliantis*) are a monophyletic line. Discussing evolutionary patterns in gammaridean amphipods, Barnard (1974) noted that the cylindroid Eophliantidae may be a monophyletic line based on a neotenous phliantid. Hatched juveniles of phliantids resemble eophliantids, but phliantids have special cuticular craters found also in ceinids and rudimentarily in hyalids, whereas eophliantids have apparently lost these structures. The eophliantid uropod 3 is slightly more complex than that of phliantids, the juveniles recapitulating their phylogeny. Two genera have been removed from the Eophliantidae by Barnard (1972): *Amphitholina* Ruffo 1953 (to the Ampithoidae) based on its biramous ampithoid uropod 3 and *Biancolina* Della Valle 1893 (to the Biancolinidae) based on the shape of the uropod 3 and the maxillipedal plates.

Lignophliantis is a monotypic genus bearing characters, which distinguish it clearly from other species of eophliantids: an uncleft telson, a very short first antenna with only one article, and a maxilliped outer plate that is much larger than the inner plate. Therefore, *Lignophliantis* should probably be removed from the family Eophliantidae, and as such, a phylogenetic analysis of the family Eophliantidae is needed to clarify

the position of this genus. We have thus excluded the genus *Lignophliantis* in the following discussion regarding evolutionary trends in the Eophliantidae.

Barnard (1972) noted a general trend within eophliantid genera towards reduction of coxae in the sequence of *Wandelia*–*Bircenna*–*Eophliantis*–*Ceinina*–*Cylindrylloides*. Based on the body shape, after measuring the coxa height in relation to height of the corresponding pereonite we suggest that *Wandelia wairarapa* and *Wandelia dronga* are primitive species, whereas *Cylindrylloides kaikoura* and *Bircenna macayai* sp. nov. are highly developed species. While we therefore in general agree with Barnard's (1972) observations regarding evolutionary trends, based on the description of new species and additional data since 1972, we regard our new species of *Bircenna* as highly derived. Barnard (1972) also noted an evolutionary trend within eophliantid genera towards a loss or reduction of lacinia mobilis in the sequence of *Wandelia* to *Ceinina*, incision of head from *Bircenna* to *Ceinina*, loss of inner lobes on lower lip from *Wandelia* to the others.

Functional morphology

We agree with Barnard's (1972) suggestion that the evolutionary trend of the eophliantids is characterized by morphological adaptations for life in an algal habitat. The species benefit from three main morphological characters: (a) narrow, cylindrical body shape; (b) mouthparts combined with a strongly rotating head suitable for shaving algal tissue; and (c) reduced pleopods.

A cylindrical body shape confers distinct advantages to algae-boring arthropods, streamlining the body to enable the animal to fit neatly into and move easily within its tunnel. As such, this trait has also evolved convergently in other algal-dwelling taxa such as the amphipod *Biancolina* (previously considered to be an eophliantid until removed to its own family by Barnard, 1972), and in the wood- and kelp-boring limnoriid isopods (Kreibohm de Paternoster & Escofet, 1976).

The loss or reduction of the lacinia mobilis would seem to be a disadvantage to a burrowing organism, as the lacinia mobilis should double the rasping ability of the mandible; however, the strongly rotating head coupled with the flattening of the incisor may together be better for boring soft living tissues of algae (Barnard, 1972). Barnard (1972) noted that living plant tissues may actually have to be shaved rather than rasped and the buccal mass of *Wandelia wairarapa* (from New Zealand) appears well suited to that task; the mandibles project in such a way as to suggest a blade in a razor. Our preliminary examination of the mouthparts of the Eophliantidae revealed this to be true for all fourteen species.

The reduction of pleopodal peduncles from *Wandelia* to *Bircenna* and *Ceinina* with an aberrancy in *Cylindrylloides* suggests that the prototypical eophliantid may have had expanded peduncles and that narrowing those is the evolutionary trend (Barnard, 1972). Our initial morphological examination of the eophliantids agrees with Barnard's (1972) theory and supports the hypothesis of *Wandelia* being the most primitive genus. The strong peduncular paddles on the pleopods may be a substitute for decreased ramal lengths, necessarily advantageous because of confinement of the organism in a tunnel, but the reduction of the adaptation in *Cylindrylloides* can, according to Barnard (1972) only suggest that this genus has a habitat distinct

from its congeners. However, since *C. mawsoni* is found on *Macrocystis* sp. (Table 1) and *B. fulva* is also found on *Macrocystis* sp., we assume that the genus *Cylindrylloides* does not have an algal habitat different from other members of Eophliantidae.

Ceinina is reported to penetrate the stem of the brown alga *Undaria pinnatifida* (Harv.) Suringar and the pleopodal paddles seem very solid, although the peduncle is not as expanded as in other eophliantids. *Ceinina* does retain a strong, sharply serrate lacinia mobili, has the thinnest body of eophliantids, and generally the shortest legs and antennae, and is therefore well adapted as a tunneller. Perhaps the other species bore into more tender species of algae (Barnard, 1972). Unfortunately, most authors describing species of eophliantids do not name the species of the associated algae (Table 1). Nevertheless two species bearing very differently shaped pleopods (*Lignophliantis pyrifera* and *Bircenna fulva*) are reported from the same species of algae: *Macrocystis pyrifera*. *Cylindrylloides mawsoni*, bearing very

narrow pleopodal peduncles, also lives on *M. pyrifera* (in the original publication this alga was reported as *M. laevis*).

Biogeography

Currently our knowledge about the biogeography of the eophliantids is so speculative, that it is only briefly discussed in the following. A more substantial biogeography of the Eophliantidae will follow a detailed phylogenetic analysis which is presently in preparation.

All species of Eophliantidae are found in shallow waters, from 0–4 m (see Table 1), except *Bircenna fulva* (0–25 m) and *Wandelia crassipes* (1–126 m). Since the reported depth below 10 m often refers to stations sampled by dredges (e.g. Chevreux, 1906; De Broyer *et al.*, 2007) and this gear has no closing mechanism, thus also sampling the water column, it is very likely that the eophliantids were taken on pieces of algae close to the surface. All eophliantids are algal dwellers,

Table 1. Record of distribution and host algae of the Eophliantidae.

Species	Author	Type locality	Other known areas	Host algae	Water depth
<i>Lignophliantis pyrifera</i>	J.L. Barnard, 1969	Goleta, California		Wash of rhizomes of <i>Macrocystis pyrifera</i>	3 m
<i>Cylindrylloides kaikoura</i>	Barnard, 1972	Morgan's Pool, Kaikoura, New Zealand		Not given	0–2 m
<i>Cylindrylloides mawsoni</i>	Nicholls, 1938	Macquarie Island	Kerguelen, Îles Crozet, Marion Island	<i>Macrocystis</i> sp., <i>Durvillia antarctica</i> , <i>Desmarestia rossi</i> , <i>Durvillaea</i> sp.	0–2 m
<i>Wandelia crassipes</i>	Chevreux, 1906	Wilhelm Archipelago, Antarctic peninsula	Palmer Archipelago, South Orkney Islands, South Shetland Islands, Tristan de Cunha	'avec des eponges, dragage'	1–126 m
<i>Wandelia wairarapa</i>	Barnard, 1972	Wellington, New Zealand		'intertidal wash of algae'	0–4 m
<i>Wandelia orghidani</i>	Ortiz & Lalana, 1997	Bunaken Island, Indonesia		Not given	2–2.5 m
<i>Wandelia dronga</i>	(Myers, 1985)	Makuluva Island, Fiji		'mixed red algae from leeward side of reef flat'	0–3 m
<i>Bircenna fulva</i>	Chilton, 1884	Lytelton Harbour, New Zealand	Australia, Argentina (Chubut and the Magellan area, Southern Tierra del Fuego), Chile	<i>Macrocystis pyrifera</i>	0–25 m
<i>Bircenna nicholli</i>	Sheard, 1936	Gulf St Vincent, South Australia		'among algae growing on the film of sand covering rocks below low tide mark'	~2 m
<i>Bircenna ignea</i>	Nicholls, 1939	Shelly Beach, south-western Australia		'among fine seaweed and sand'	0 m?
<i>Bircenna macayai</i> sp. nov.	Lörz, Kilgallen & Thiel (this publication)	Kau Bay, Wellington, New Zealand		<i>Carpophyllum maschalocarpum</i>	2 m
<i>Eophliantis tindalei</i>	Sheard, 1936	Port Wynyard, Tasmania		'in fine sand and algae, on tidal rocks, periodically flooded with river water'	0 m
<i>Ceinina japonica</i>	Stephensen, 1933	Yoichi, Hokkaido, Japan		Stem of <i>Undaria pinnatifida</i>	0 m?
<i>Ceinina latipes</i>	Ledoyer, 1978	Recif de Balaclava, Mauritius		Zone of <i>Melobesia</i> (Corallines)	0–5 m

even though not all authors mention the associated algae (Table 1).

There are currently two main mechanisms hypothesized for long-range biotic distributions in the southern hemisphere; vicariance due to continental drift and rafting dispersal via the West Wind Drift (Waters, 2008). Numerous studies have remarked on biogeographical connections among biota from regions linked by the West Wind Drift (Thiel & Haye, 2006). For example, recent molecular studies have identified biogeographical links between South Africa, Tasmania and New Zealand (e.g. Waters & Roy, 2004). An extensive literature search has revealed five algae identified to species level that are associated with eophliantids (Table 1). *Ceinina japonica* is described from the stem of *Undaria pinnatifida* in Yoichi, Hokkaido (Stephensen, 1933). *Cylindrylloides mawsoni* has been found on Macquarie Island, Kerguelen, Crozet Island and Marion Island on *Macrocystis pyrifera* (reported as *M. laevis*) and *Durvillaea antarctica* (e.g. Beckley & Branch, 1992). *Macrocystis pyrifera* is also the habitat of *Lignophliantis pyrifera* from California (Barnard, 1972), while *Bircenna fulva* is known from *M. pyrifera* off Argentina (Kreibohm de Paternoster & Escofet, 1976; Alonso, 1980), off Chile (Martin Thiel, personal observation), and off New Zealand (Chilton, 1884). Thus, due to the algal-dwelling habitat of these animals, we assume that they are ideal candidates for dispersal via rafting.

Biotic connections between New Zealand and South America (e.g. Donald *et al.*, 2005; Fraser *et al.*, 2009) are often discussed controversially (e.g. Heads, 2005). Studies on the alpha-diversity of peracarids from New

Zealand and Chile have reported several peracarid species that are apparently common to both regions (e.g. Barnard, 1972; Thiel, 2002; Gonzalez *et al.*, 2008). However, there is a high possibility that these 'bi-regional' species such as *Bircenna fulva* are mis-identifications and/or represent (several) cryptic species but at the generic level the connections may be significant. If algal rafting was the main explanation for the biogeography of the Eophliantidae family, the same species should be found in, e.g. Chile, Australia and New Zealand. The current generic level connectivity may support a vicariant biogeography because similarities at generic level indicate an archaic relationship.

The highest eophliantid species diversity, four of the 14 known species, occurs in New Zealand. These represent three of the six genera. Another species is found on Macquarie Island, south of New Zealand, and a further three species in southern Australia (including Tasmania) (Figure 5). At this point, we therefore speculate that Australasia is the evolutionary origin of this amphipod family, and species have radiated to Antarctica, Chile, Mauritius and Japan from here. Again, without a detailed phylogenetic analysis of the family, this biogeographical hypothesis cannot be confirmed.

Summary and outlook

Very little is known about the systematics and evolution of obligate algae dwelling amphipods. This initial study, focusing on the taxonomy, has highlighted that the family

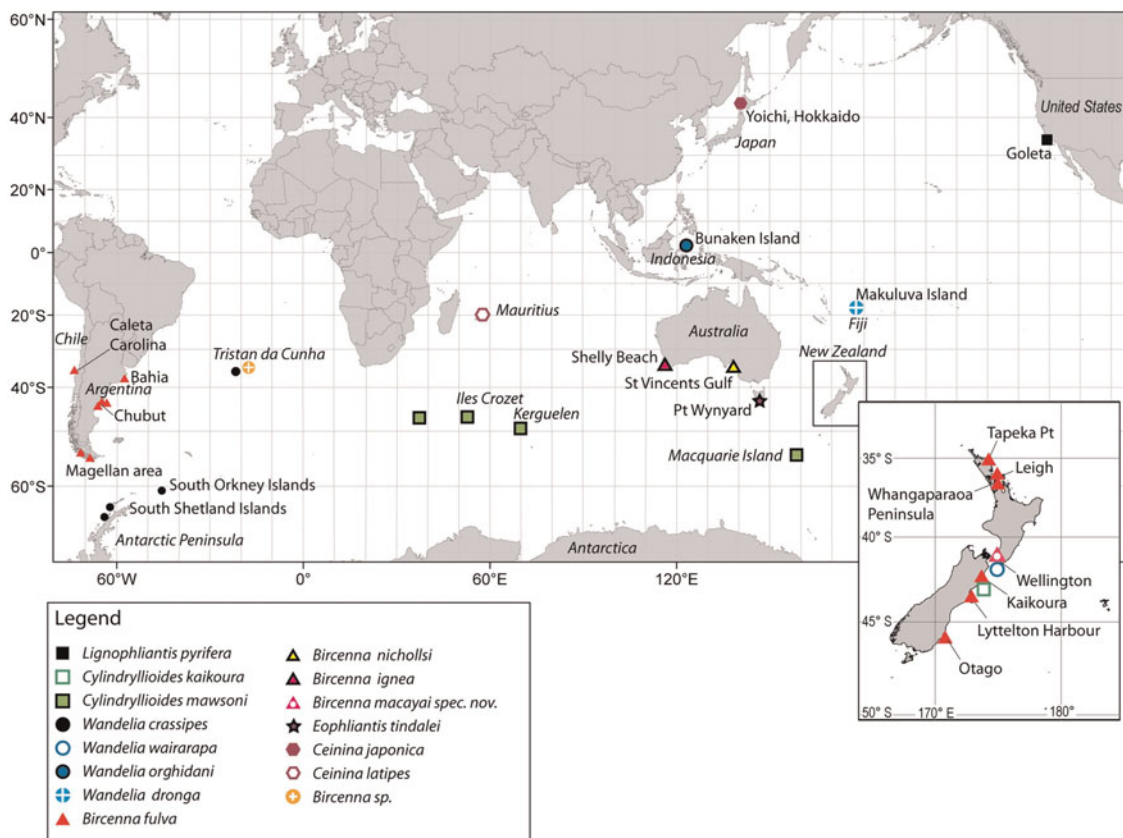


Fig. 5. Worldwide distribution of the species of Eophliantidae (Amphipoda).

Eophliantidae is a suitable model group to study the phylogeography of obligate algal dwellers.

We currently postulate Australasia as the evolutionary centre of the Eophliantidae, having four of the six currently known genera. Both species with putatively plesiomorphic and derived characters are found in Australasia. Based on the ecology of the algae dwelling Eophliantidae, their biogeographical distribution and that of their host algae, we believe rafting on macroalgae, e.g. on *Macrocystis* sp., is a viable distributional mechanism for this amphipod family. At present, the observed distributions could be consistent with vicariant or dispersalist mechanisms. A detailed phylogenetic analysis of the Eophliantidae will be conducted in a following paper to help clarify this issue.

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