

# Ctenophora of Australia

**Lisa-ann GERSHWIN**

South Australian Museum, North Terrace, Adelaide, South Australia 5000 (Honorary).  
Email: lisa.gershwin@stingeradvisor.com

**Wolfgang ZEIDLER**

South Australian Museum, North Terrace, Adelaide, South Australia 5000.  
Email: Wolfgang.Zeidler@samuseum.sa.gov.au

**Peter J.F. DAVIE**

Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101

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## ABSTRACT

An overview of the Ctenophora of Australia is presented based on limited collecting efforts, together with the description of seven species new to science. *Euplokamis evansae* sp. nov. (Cydippida: Euplokamididae), has only been found in Tasmanian waters; it is distinguished from its congeners in the comb rows being about 4/5 of the body length, the tentacle bulbs being long and close to the stomach, and having extremely long polar plates. *Pukia falcata* gen. nov., sp. nov. (Cydippida: Pukiidae fam. nov.), is found across the tropical and subtropical north of Australia from Port Hedland, Western Australia, to the Moreton Bay region of southeastern Queensland; it has beehive-coiled tentilla, similar to those of the Euplokamididae, but differs from all other cydippids in having crescentic-shaped tentacle bulbs. *Bolinopsis ashleyi* sp. nov. (Lobata: Bolinopsidae), from Moreton Bay, differs from its large-lobed congeners in its striking pattern of broad red streaks along the ctene rows. *Leucothea filmersankeyi* sp. nov. (Lobata: Leucotheidae), from northwestern Tasmania, differs from other species in its genus in having narrow, blind tentacular pits; long slender papillae; and a pale orange tint to the body core. *Ocyropsis vance* sp. nov. (Lobata: Ocyropsidae), from southeastern Tasmania, is distinguished from other ocyropsids with a deeply-indented hourglass-shaped stomach in lacking tentacle bulbs and spots. Finally, three new forms of benthic ctenophores are reported from the Great Barrier Reef: *Coeloplana mellosa* sp. nov. (Platyctenida: Coeloplanidae) is found on the soft coral *Sarcophyton* sp., and differs from its congeners in a unique combination of pigmentation pattern, papillae number and distribution, and statocyst palp morphology; *Coeloplana reichelti* sp. nov., a larger form found on algae and seagrasses, differs from others in the number and form of papillae, colour pattern, and distribution; the last, a minute form found on the Crown-of-thorns starfish, *Acanthaster planci*, must await additional material for proper description. The distribution of *Neis cordigera* is broadened to include South Australia and Western Australia, and a redescription of the species is provided. The potential fisheries impacts by a form of *Bolinopsis* in Spencer Gulf, South Australia, are discussed. An annotated classification and a key for the ctenophores of Australia are given. □ *Ctenophora*, *Ctenophores*, *comb jellyfish*, *Cydippida*, *Platyctenida*, *Lobata*, *Cestida*, *Beroida*, *new family*, *new genus*, *new species*, *new records*.

Gelatinous zooplankton species are not typically well known, and this is especially true for members of the Ctenophora. Though well repre-

sented in nearly all marine pelagic zones, they are often difficult to capture and impossible (or nearly so) to preserve. Furthermore, their taxon-

omy is poorly resolved, making identification often difficult and inconclusive.

Australian ctenophores are no exception and are, in fact, even more poorly known than those of many other regions. Ironically, von Lendenfeld (1885a) stated that the Australian ctenophores 'really appear to be rare.' And while few species are reported, most are certainly not rare! In our experience, a small cydippid that is described as new herein and placed into a new family, is one of the commonest members of the Australian coastal gelatinous zooplankton community, and may be found throughout the year in just about any tropical and subtropical region. Furthermore, an unidentified species of *Bolinopsis* blooms in such plague proportions in the South Australian gulfs in the summertime that one must wonder what effect this might have on the larvae and food sources of other species in the gulfs.

The first mention of a ctenophore in Australian waters was by Quoy & Gaimard (1824: 575), who noted a *Beroë* from Port Jackson. Since that time, at least 24 additional species of ctenophores have been reported from Australian coastal waters, with another ten newly reported herein, including seven new to science.

During the course of the Thirteenth International Marine Biological Workshop, in Moreton Bay, Queensland, numerous collections were made of ctenophores. As we were identifying this material, we realised that it would be very useful to attempt to compile the first synopsis of Australian ctenophores, and thus provide a foundation for productive future work. To do this it was necessary to document not only the historical literature, but also specimens in museum collections, and our own samples gathered over the last ten years. This has resulted in numerous new distribution records, and the descriptions of the seven new species presented here. It is highly likely that many more species will prove to be present than so far recognised, and our knowledge of the distributional ranges of many will no doubt increase significantly with further targeted collecting.

#### MATERIALS AND METHODS

The collections of ctenophores held in all Australian museums were examined; in most

cases comparative type material was non-existent. Field-collected specimens were either captured individually in plastic bags or glass jars while snorkeling, dipped individually from jetties with a 500 µm mesh, 0.5 m-wide plankton net, or else 'trawled' with the net from a fixed location relying on existing current for flow.

Difficulties in preservation and inherent problems with shrinkage are a fundamental problem in ctenophore taxonomy. Thus, whenever possible, live specimens were observed, photographed, and morphological and behavioural characters noted prior to preservation attempts. Tissue samples were also collected for future study when tissues from congeners become available.

Extensive efforts were made to relax and fix live material, often without success. For cydippids and beroids, room temperature asphyxiation was the only effective method of relaxation, but was extremely labour intensive; preservation in about 2% formalin produced moderately good specimens. For lobates, no method of relaxation could be obtained, and efforts to preserve specimens universally resulted in total tissue disintegration, leaving only scattered ctenes; the only exception was *Ocyropsis vance* sp. nov., which preserved quite perfectly in 1-2% formalin.

Measurements were made on preserved material with Max-Cal digital calipers, to the nearest 0.01 mm. Every effort was made to obtain true dimensions across the widest points; however, some specimens were too brittle to be spread out, in which case absolute measurements were taken across the two farthest available points. Body length (BL) was measured from the aboral pole to the tip of the mouth for all specimens. In lobate ctenophores, lobe length (LL) was measured from the inner corner where the lobe attaches to the body to the distal tip; total length (TL) includes the lobes.

Morphological examinations were made under a variety of dissecting scopes, depending on what was available at the institution where the specimens were studied. Microscopic and macroscopic digital images were made of all observable structures with Fujifilm MX-700 and MX-2700 cameras, Nikon CoolPix 995, and Sony DVD-201e in JPG format. While it was not possible to publish all photographs made of each taxon, we have compiled a library of images of

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**Table 1.** An annotated checklist of ctenophores recorded from Australian waters, including all previous records from Moreton Bay. Nomenclatural notes are given in parentheses, where appropriate. Abbreviations used: Queensland (QLD), New South Wales (NSW), Victoria (Vic), Tasmania (Tas), South Australia (SA), Western Australia (WA), Northern Territory (NT), Great Barrier Reef (GBR), Australia 'Unspecified' (AU), Southern Australia (SO), Northern Australia (NO); Species names highlighted in **bold** are dealt with in more detail in the present work.

Family	Species	Moreton Bay Records	Endemic/Australian Distribution
Phylum CTENOPHORA Eschscholtz, 1829			
Class TENTACULATA Eschscholtz, 1825			
Order CYDIPPIDA Lesson, 1843			
<b>Euplokamididae</b> Mills, 1987	<b><i>Euplokamis evansae</i> sp. nov.</b>		Endemic: TAS.
<b>Pleurobrachiidae</b> Chun, 1880	<b><i>Pleurobrachia pileus</i></b> (O. F. Müller, 1776)	Moreton Bay (Greenwood 1980; Gorman 1988); incorrect ID; referable to <i>Pukia falcata</i> , gen. nov., sp. nov.	
	<i>Pleurobrachia</i> spp.		NSW (Dakin & Colefax 1940); QLD (Hamond 1971; Greenwood 1980). [All previous records probably referable to <i>Pukia falcata</i> gen. nov., sp. nov.]. New records for SA, WA, and TAS.
	Pleurobrachiidae indet.		Southern Australia (Gowlet-Holmes 2008).
<b>Pukiidae</b> fam. nov.	'Sea Gooseberry'	Moreton Bay (Davie 1998).	
	<b><i>Pukia falcata</i> gen. nov., sp. nov.</b>	Moreton Bay [herein]	Endemic tropical Australia: QLD, NT, WA.
Order PLATYCTENIDA Bourne 1900			
<b>Coeloplanidae</b> Willey, 1896	<i>Coeloplana meteoris</i> Thiel, 1968		QLD (Arnold 1993).
	<i>Coeloplana scaberiae</i> Matsumoto & Gowlett-Holmes, 1996		Endemic: SA.
	<i>Coeloplana thomsoni</i> Matsumoto, 1999		Endemic: WA.
	<i>Coeloplana willeyi</i> Abbott, 1907		VIC (Smith & Plant 1976).
	<i>Coeloplana</i> spp.		QLD (Stephenson <i>et al.</i> 1931). Southern Australia (Edgar 1997, 2000).
	<b><i>Coeloplana mellosa</i> sp. nov.</b>		Endemic: Great Barrier Reef on <i>Sarcophyton</i> sp.
	<b><i>Coeloplana reichelti</i> sp. nov.</b>		Endemic: Great Barrier Reef on algae and seagrass.

continued ...



Table 1 (continued) ...

Family	Species	Moreton Bay Records	Endemic/Australian Distribution
	<i>Coeloplana</i> sp. A		Great Barrier Reef on <i>Acanthaster planci</i> .
<b>Ctenoplanidae</b> Willey, 1896	<i>Ctenoplana</i> sp.		Off Townsville, planktonic (Hamner, in Matsumoto 1999).
Order LOBATA Eschscholtz, 1825			
<b>Bolinopsidae</b> Bigelow, 1912	<i>Bolinopsis duuni</i> (von Lendenfeld, 1885a)		Endemic: NSW (Whitelegge 1889; Dakin & Colefax 1933).
	<i>Bolinopsis</i> spp.		NSW (Dakin & Colefax 1940; Dakin & Bennett 1987; Edgar 1997, 2000); SA (Gershwin & Zeidler 2003; Gowlett-Holmes 2008). New records for QLD, TAS, NT, and WA.
	<i>Bolinopsis ashleyi</i> sp. nov.	Moreton Bay [herein]	So far only known from Moreton Bay.
	<i>Bolinopsis</i> sp.		SA (clear body with magenta canals).
	<i>Mueniopsis</i> sp.	Moreton Bay (Greenwood, 1980)	Probably erroneous ID.
<b>Leucotheidae</b> Lesson, 1843	<i>Leucothea filmersankeyi</i> sp. nov.		Endemic: TAS, SA.
	<i>Leucothea</i> spp.	Moreton Bay	QLD (Harbison & Miller 1986); VIC-TAS-NSW (Edgar 1997, 2000); QLD (Gershwin & Zeidler 2003)
<b>Ocyropsidae</b> Krumbach, 1925	<i>Ocyropsis crystallina crystallina</i> Harbison & Miller, 1986		QLD
	<i>Ocyropsis macnlata immaculata</i> Harbison & Miller, 1986		QLD
	<i>Ocyropsis maculata maculata</i> Harbison & Miller, 1986		QLD
	<i>Ocyropsis vance</i> sp. nov.		Endemic: TAS.
	<i>Ocyropsis</i> spp.		New records for QLD, NT, and WA.
Order CESTIDA Gegenbaur, 1856			
<b>Cestidae</b> Gegenbaur, 1856	<i>Velamen parallelum</i> (Fol, 1869)		Australia-wide (Gowlett-Holmes 2008). New records for TAS and QLD.

continued ...



Table 1 (continued) ...

Family	Species	Moreton Bay Records	Endemic/Australian Distribution
Class NUDA Chun 1879			
Order BEROIDA Eschscholtz, 1825			
Beroidae Eschscholtz, 1825	<i>Beroe cucumis</i> Fabricius, 1780		NSW (Stiasny 1931); southern Australia (Edgar 1997, 2000).
	<i>Beroe macrostomus</i> Péron, 1807		QLD (Lesson 1829).
	<i>Beroe ovale</i> Bosc, 1802		NSW (Quoy & Gaimard 1824).
	<i>Beroe ovata</i> Bruguière, 1792	Moreton Bay (Greenwood 1980)	WA (Goy 1990); QLD (Steene 1990).
	<i>Beroe</i> spp.	Moreton Bay (Hamond 1971)	WA (Péron 1807); NSW (Dakin & Colefax 1933, 1940); VIC (Zeidler & Gowlett-Holmes 1998); SA (Gowlett-Holmes 2008). New records for NT and TAS.
	<i>Neis cordigera</i> Lesson, 1829		Endemic: Australia. NSW (von Lendenfeld 1885b, 1885c; Whitelegge 1889; Stiasny 1931). New records for QLD, WA and SA.

Australian ctenophore specimens; images from this library are available upon request.

Abbreviations used: Australian states are abbreviated as follows: South Australia (SA), Western Australia (WA), Northern Territory (NT), Tasmania (Tas), Queensland (Qld), Victoria (VIC), and New South Wales (NSW). The Great Barrier Reef is abbreviated 'GBR'. Other institutional abbreviations used: the Australian Museum, Sydney, NSW (AM); the Museum and Art Gallery of the Northern Territory, Darwin, NT (NTM); the Museum of Tropical Queensland, Townsville, Qld (MTQ); the Museum of Victoria, Melbourne, VIC (MV); the Queensland Museum, Brisbane, Qld (QM); the Queen Victoria Museum and Art Gallery, Launceston, Tas. (QVMAG); the Tasmanian Museum and Art Gallery, Hobart, Tas. (TMAG); and the Western Australian Museum, Perth, WA (WAM). Copies of colour slides of specimens photographed by Karen Gowlett-Holmes are kept in the SAM photo-index collection (prefix 'PH'), with copyright retained by KGH; digital images of specimens photographed by LG are archived

in the SAM collection. The prefix 'GZ', refers to field collection numbers that correspond to field notes and digital photos (archived in SAM); in some instances where material was unpreservable (e.g. species of *Pleurobrachia*, *Leucothea* and *Bolinopsis*) these notes and photos are the only remaining evidence of the material examined. Lots consist of single specimens, unless otherwise noted.

Latin and Greek names were derived using Brown (1956). German and French texts were translated with Globalink Power Translator v. 6.02 for Windows. Taxonomic classification is modified from Mills (2007).

#### SYSTEMATIC ACCOUNT

PHYLUM CTENOPHORA Eschscholtz, 1829  
CLASS TENTACULATA Eschscholtz, 1825  
ORDER CYDIPPIDA Gegenbaur, 1856

Family Euplokamididae Mills, 1987

*Euplokamis* Chun, 1880

*Euplokamis evansae* sp. nov.

(Fig. 1A, B)

**Material examined.** HOLOTYPE: SAM-H1557 (PH 0248), Shag Rock Bay, Tasman Peninsula, Tas., 0–2 m, K. Gowlett-Holmes, 24.05.1995; 13.32 mm BL, 5.07 mm tentacular width, 5.8 mm stomodaeal width.

**Diagnosis.** *Euplokamis* with a nearly spherical body; long ctene rows, nearly  $4/5$  the body length; long tentacle bulbs, parallel to one another and closer to the stomach than to the body wall; with extremely long polar plates; lacking pigment.

**Description.** Preserved body elongated, cylindrical with rounded ends (Fig. 1A; somewhat more spherical in life: Fig. 1B), of a very soft gelatinous consistency; with mouth protruding both in life and preserved.

Comb rows 8, equally spaced around body, extending from aboral end to about  $4/5$  body length toward oral end, leaving oral region

free. Comb plates about 25–30 per comb row, spaced approximately 2–3 comb row-widths apart in the live animal, about  $2/3$  to 1 comb row-widths apart in the preserved animal.

Tentacles 2, with distantly-spaced, coiled, robust tentilla in life (Fig. 1B); could not be completely studied in preserved retracted state without damaging the delicate specimen. Tentacle bulbs elongate, arranged closer to stomodaeum than to outer body wall; sub-parallel to each other; about  $1/4$  total body length; located just forward of midline on oral-aboral axis. Tentacle sheaths long, slender, opening very close to aboral end; with very small ostia.

Infundibulum very narrow, straight, transparent, difficult to discern; short, less than  $1/3$  body length.

Stomodaeum broad, flat, about  $2/3$  body length; narrowed somewhat behind mouth at

**Table 2.** Comparison of diagnostic characters of the species of *Euplokamis* as considered valid by Mills (1987). Data derived from original descriptions, plus Chun (1880), and Mills (1987). Abbreviations: Body length (BL), Substomodaeal (SS), Subtentacular (ST), Comb row (CR).

	Body	Comb rows	Tentacle bulbs	Other features
<i>E. crinita</i> (Moser, 1909)	4 mm BL; elongate, slightly compressed	Whole BL	Very small; between the stomach and body wall	Extraordinarily long ctenes covering most of the body; Seychelles
<i>E. dunlapae</i> Mills, 1987	20 mm BL; elongate, slightly compressed	$2/3$ – $3/4$ BL	Parallel to stomodaeum; midway between stomodaeum and outer body surface	Red patches along comb rows, tentilla, and tentacle bases; Puget Sound
<i>E. helicoides</i> (Ralph & Kaberry, 1950)	11 mm BL; cylindrical	Nearly whole BL	Parallel to stomodaeum; midway between stomodaeum and outer body surface	Very broad paragastric canals; faint pink colour under comb rows; New Zealand
<i>E. octoptera</i> (Mertens, 1833)	'Pea-sized body'; pear-shaped	$2/3$ – $3/4$ BL, along crest of raised wing-like structures	Leaf-shaped, parallel to stomodaeum; midway between stomodaeum and outer body surface	Canals faintly pink; tentilla red; central coast of Chile and Bay of St Lawrence in the Bering Strait
<i>E. stationis</i> Chun, 1879	25 mm BL; cylindrical	Full length of the body	Small, oblique; midway between stomach and body wall	Transparent and unpigmented; Gulf of Naples
<i>E. evansae</i> sp. nov.	13 mm BL; nearly spherical live, cylindrical preserved; not compressed	$4/5$ BL	Long, parallel; closer to stomach than body wall	Colourless; combs distantly spaced; polar plates extremely long; Tasmania

about the level of ctene termination; mouth with straight sides. Stomodaeum bears a sharp, aborally-orientated out-pocketing along one edge, believed to be an artifact.

Meridional canals round in cross section; smooth-edged; smaller diameter than ctene rows they underlie, and thus obscured by them. Internal canals could not be discerned in preserved specimen without dissection, or in photograph of live specimen.

Statocyst in shallow, broad, nipple-shaped indentation, less than body length deep. Polar plates extremely long.

Polar plates extremely long, extending orally up onto sides of body wall for a distance of about 7 comb rows.

**Etymology.** The specific name, *evansae*, is named after Jill Evans, librarian at the South Australian Museum, in recognition of the heroic service, often unsung, that librarians perform in the pursuit of scientific knowledge.

**Remarks.** The morphological characters of this species are inconsistent with known cydippid genera, but most similar to the genus *Euplokamis*. However, the specimen was unfortunately too delicate to be dissected in order to prove the existence of striated muscle in the tentilla, considered a defining character for the genus by Mills (1987). Nonetheless, we conservatively place this species in the genus *Euplokamis*, rather than destroying the type specimen or erecting a new genus, pending collection and examination of more material.

*Euplokamis* was reviewed by Mills (1987) who regarded five species as valid (Table 2). Of those, *E. evansae* is most similar to *E. dunlapae* Mills (1987) and *E. helicoides* (Ralph & Kaberry, 1950) in general size of the body and shape of the tentacle bulbs, but differs from both in colouration and position of the tentacle bulbs, and the body is more spherical in the living specimens, and not compressed. It is also similar to *E. stationis* Chun (1879) in colouration, i.e., both are transparent and unpigmented; however, the two would be unlikely to be confused, with *E. stationis* having obliquely-orientated tentacular bulbs. *Euplokamis evansae* bears less resemblance to the other species in the genus, with *E. crinita* (Moser, 1909) having very long ctenes covering most of the body, and

*E. octoptera* (Mertens, 1833) having red tentilla and the ctene rows set upon raised gelatinous wing-like structures.

#### Family Pleurobrachiidae Chun, 1880

##### *Pleurobrachia* Fleming, 1822

The following *Pleurobrachia* species have been previously reported from Australia:

*Pleurobrachia pileus* (O. F. Müller, 1776) – Greenwood, 1980: 91 (Moreton Bay, Qld); Gorman, 1988: 17 and throughout, pl. 12; (Moreton Bay, Qld) [incorrect identification = *Pukia falcata* sp. nov.].

*Pleurobrachia* spp. – Dakin & Colefax, 1940: 211 (NSW); Hamond, 1971: 27 (Moreton Bay); Greenwood, 1980: 88, 91 (Moreton Bay, Qld) [All probably erroneous identifications.]

Pleurobrachiidae indet. – Gowlett-Holmes, 2008: 54 (southern Australia).

**Material examined (mostly unpreservable).** SA: Kangaroo I., L. Gershwin, 5.05.1999, with short tentacle bulbs orientated parallel to stomodaeum in aboral half of body. Robe, W. Zeidler & L. Gershwin, 9.02.2002 (GZ0232); very spherical body with short parallel tentacle bulbs; found in large numbers; many specimens had either ?parasitic worms, or bright yellow eggs (believed to be from the worms), or both, in the infundibulum and tentacle bulbs (GZ0234). Robe, W. Zeidler & L. Gershwin, 21-22.01.2002 (GZ0103, GZ0108); with short parallel tentacle bulbs but with distinctively teardrop-shaped body; found in very large numbers; some infested with the hyperiid amphipod *Hyperoche mediterranea*. WA: Derby Jetty, W. Zeidler & L. Gershwin, 22.11.2000; several small specimens. Port of Broome, W. Zeidler & L. Gershwin, 25.11.2000; 5 mm juvenile. TAS: Triabunna, W. Zeidler & L. Gershwin, 26.01.2002 (GZ0146). Constitution Dock, Hobart, W. Zeidler & L. Gershwin, 29.01.2002 (GZ0170). CSIRO wharf, Hobart, W. Zeidler & L. Gershwin, 1-2.02.2002.

**Field identification.** Body spherical in life, cylindrical preserved; colourless and transparent, about 1 cm. Tentacle bulbs short, parallel, and closer to stomach than to body wall.

**Remarks.** No morphological comments or figures were given by most of the authors that have reported on Australian material, so it is impossible to determine which species they found. While it is clear to us from our own collections that *Pleurobrachia* does exist in Australia, it is uncommon relative to *Pukia falcata* gen. nov., sp. nov. Thus, it seems likely



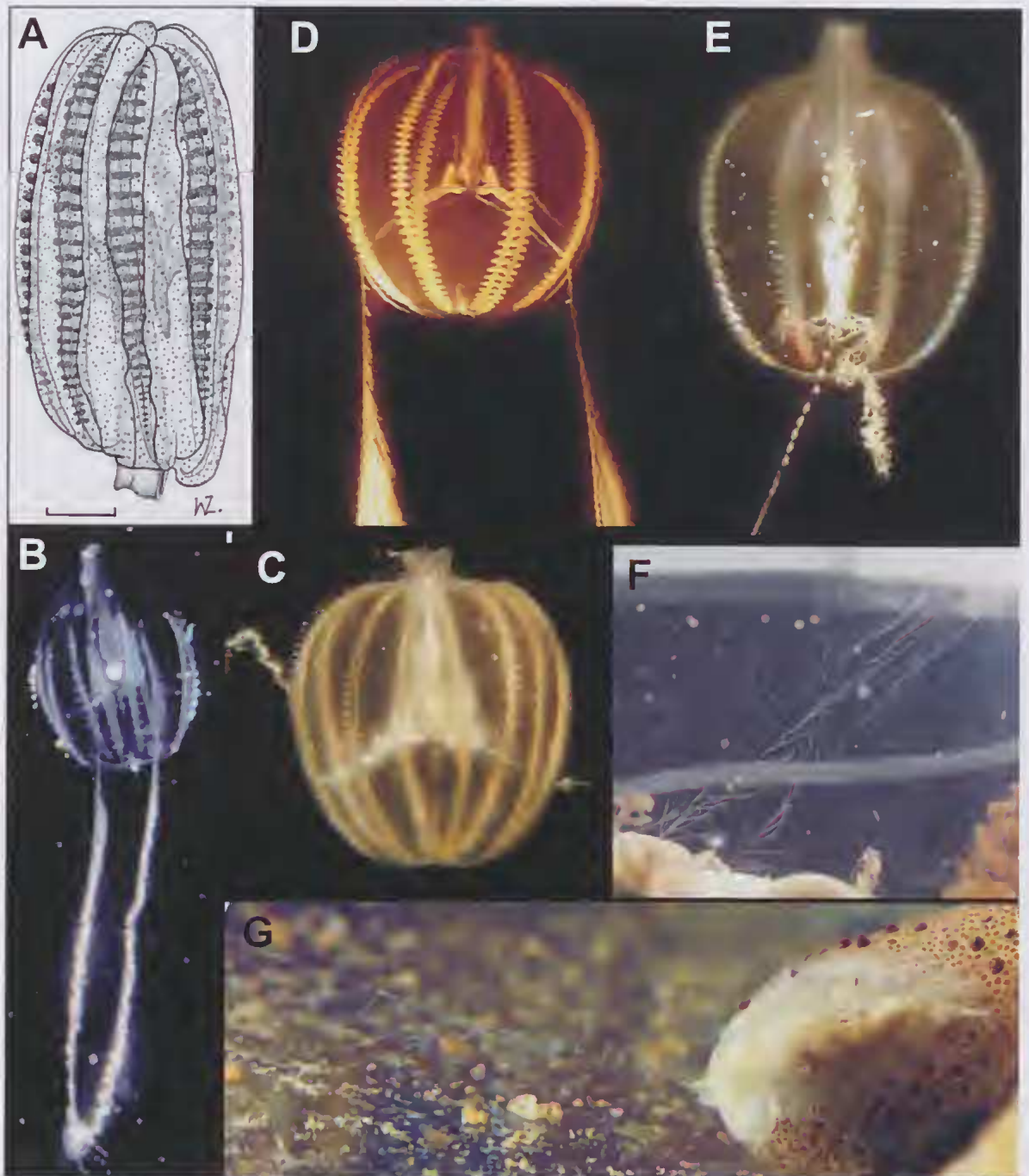


FIG. 1. A-B, *Euplokamis evansae* sp. nov., holotype (Tasmania). A. Preserved. B. Live, in situ; scale bar = 2 mm; photograph by Karen Gowlett-Holmes, used with permission. C-E, *Pukia falcata*, gen. et sp. nov. C. Holotype (Moreton Bay), in life. D. Sagittal view. E. Tentacular view. Note in C and D crescentic tentacle bulbs that wrap around base of stomodaeum rather than running parallel to it. Note in D and E coiled tentilla near proximal ends of tentacles. Note also permanently protruding mouth. Yellowish colouration under comb rows in C & D are due to recent consumption of brine shrimp nauplii in captivity. F-G, *Coeloplana mellosa* sp. nov., living specimens on *Sarcophyton* soft coral (Great Barrier Reef). Note tentacle branching pattern in F, and tentacle streaming off to left near mid-height of G. Photographs F & G by Bette Willis (James Cook University); used with permission.

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**Table 3.** Comparison of diagnostic characters of ctenophore genera within the order Cydippida. Data derived from original literature, plus Bigelow (1912), Mayer (1912), Mills (1987), Harbison (1996), Wrobel & Mills (1998).

	Tentacle bulbs	Tentilla	Other features
<b>Pleurobrachiidae</b>			
<i>Cerocteuia</i> Carré & Carré, 1991	Wide, subcylindrical, red, opening aborally	Filiform	Body pear-shaped with two large aboral digitiform papillae
<i>Horuiphora</i> L. Agassiz, 1860	Long, running parallel to stomodaeum	Two or more kinds of side branches	Body oval or egg-shaped
<i>Minictena</i> Carré and Carré, 1993b	Large, globular sheaths	Filiform with 5 types of colloblasts	Body small with two unequal pairs of aboral papillae; comb rows 2/3 body length
<i>Moseria</i> Ghigi, 1909	Very long, reaching the oral collar, parallel to stomodaeum	Not described	Body cylindrical; comb rows broad, full body length, ending before the mouth
<i>Pleurobrachia</i> Fleming, 1822	Short, parallel to stomodaeum	Numerous, filiform	Body more or less spherical; comb rows about 2/3 body length; mouth non-extensile
<i>Sabaudia</i> Ghigi, 1909	Long, voluminous, running parallel to stomodaeum	Numerous, simple, yellow	Cylindrical, boxy body
<i>Tiuerfe</i> Chun, 1898	Long tentacle bases	Filamentous	Body elongate; two kidney-shaped gelatinous apical protuberances
<b>Euplokamididae</b>			
<i>Euplokaniis</i> Chun, 1880 ( <i>sensu</i> Mills, 1987)	Orientated midway between stomodaeum and outer body wall, opening aborally	Sparsely arranged, coiled, with smooth muscle	Body elongate; comb rows extend at least 2/3 of body length
<b>Haeckeliidae</b>			
<i>Aulacoctena</i> Mortensen, 1932	With lateral processes	Lacking; tentacles with large terminal knob	Body ovate, distinctly compressed in sagittal axis, with deep lateral furrow and apical prolongation
<i>Haeckelia</i> Carus, 1863	Long, narrow, opening toward oral pole	Lacking	Body ellipsoidal; tentacles with kleptocnidae; comb rows about 1/2 body length
<b>Ctenellidae</b>			
<i>Cteuella</i> Carré & Carré, 1993a	Teardrop-shaped, in oral third of body, opening medially	Tentacles lacking tentilla and colloblasts	Comb rows arranged in pairs; kleptocnidae in gastrovascular wall; suckers on lips
<b>Bathyctenidae</b>			
<i>Bathyctena</i> Mortensen, 1912	Crescentic at base of stomodaeum, opening close to mouth	Present	Body spherical, firm, darkly pigmented; canals with numerous blind side branches

Table 3 (continued) ...

	Tentacle bulbs	Tentilla	Other features
<b>Lampeidae</b>			
<i>Lampea</i> Stechow, 1921	Short, at midpoint of body, parallel to stomodaeum	Numerous, long, filamentous	Long, cylindrical body, with highly eversible pharynx
<b>Cryptocodidae</b>			
<i>Cryptocoda</i> Leloup, 1938	About half the body length, parallel to pharynx	Present	Fusiform body, with large combs running nearly full length
<b>Mertensiidae</b>			
<i>Callianira</i> Péron & Lesueur, 1810	Short, oblique, pointing oral-abaxially	Numerous, long, filamentous	Body strongly compressed, with two very long aboral processes
<i>Charistephane</i> Chun, 1880	Small and angled obliquely, at the midline of the body very near the outer body wall	Short, widely spaced	Strongly compressed body, lacking aboral 'keels'
<i>Mertensia</i> Lesson, 1836	Large, crescentic against pharynx; opening aborally	Filiform, long, red	Strongly compressed body, with two short aboral 'keels'
<b>Dryodoridae</b>			
<i>Dryodora</i> L. Agassiz, 1860	Small, globular, near the midline of the body very near the outer body wall	Tentacles fine, unbranched	Oral opening is actually margin of a large medusa-like chamber where food is captured; mouth is deep inside.
<b>Pukiidae fam. nov.</b>			
<i>Pukia</i> gen. nov.	Crescentic, curled around base of stomodaeum, opening aborally	Numerous, short, alternately filiform and coiled	Apple-shaped body; extensile mouth; no aboral papillae

that most or all earlier reports are probably *P. falcata* gen. nov., sp. nov., which is present in abundance throughout most of the year in the areas they studied. Gorman (1988) is the only author who provided figures, and the species she studied was unquestionably *Pukia falcata* gen. nov., sp. nov.

However, while the new form is common throughout the tropics and sub-tropics of Australia, we have found *Pleurobrachia* spp. occasionally in temperate waters of Tasmania and South Australia, as well as twice in tropical Western Australia. We identify those cydippid ctenophores with spherical or globular bodies; short, parallel tentacle bulbs; and with 'normal' cydippid tentilla (i.e., without the *Euplokamis*

'beehive' form), as *Pleurobrachia*. As suggested by Mortensen (1912) and Bigelow (1912), and echoed by Ralph (1950), 'great variability in shape, size, and the position of various body structures is found ... observations on a large number of living specimens are necessary in order to decide whether these differences occur in the living animal' (Ralph 1950: 79). We agree with these authors that *Pleurobrachia* is a problematic genus, and because we have not had sufficient comparative material available, we hesitate to identify any of these forms to species. The genus is in need of revision.

This is the first report of *Pleurobrachia* in the waters of Tasmania, South Australia, and Western Australia.



## Pukiidae new family

**Diagnosis.** Cydippida with tentacle bases crescentic, curling around aboral end of stomodaeum; tentacles with numerous fine coiling tentilla; with very long polar plate; with apple-shaped body, with protruding mouth.

**Type genus.** *Pukia* gen. nov.

**Remarks.** *Pukia* shares some characters with various members of different families throughout the Cydippida (a comparison of generic characters of cydippids is given in Table 3). While we hesitate to erect another monotypic family, the conspicuous crescentic tentacle bulbs and the combination of other characters preclude it from existing families.

*Pukia* gen. nov.

**Diagnosis.** As for family.

**Type species.** *P. falcata* sp. nov.

**Etymology.** The generic name *Pukia* (pronounced 'pook-ee-uh') is to honor Puk Scivyer (nee Petersen), who while at Underwater World on the Sunshine Coast, Queensland, gathered these and other interesting gelatinous animals for public display and research, and generously allowed us to study and keep many specimens. Her name has Danish origins and is also the name of Shakespeare's merry trickster in *A Midsummer Night's Dream*.

**Remarks.** The crescentic tentacle bulbs are the most obvious and diagnostic character for *Pukia falcata* gen. nov., sp. nov. They are readily visible in all specimens with even casual examination; they are prominently curled around the aboral end of the pharynx. In most cydippids, the tentacle bulbs are more or less cylindrical and run parallel to the pharynx; generic distinctions are often based on relative length of the bulbs (e.g., *Pleurobrachia*, *Hormiphora*, see Wrobel & Mills (1998)). In a few other forms the bulbs are globular, as in *Minictena* (Carré & Carré, 1993b) and *Dryodora* (Agassiz, 1860), or teardrop-shaped, as in *Ctenella* (Carré & Carré, 1993a), while those of *Aulacoctena* have lateral processes (Mortensen 1932). Two other forms have crescentic tentacle bulbs like *Pukia*, but are wholly unlike *Pukia* in all other respects, namely *Bathychtena* and *Mertensia*. In *Bathychtena*, the tentacle bulbs open orally, whereas in *Mertensia* and *Pukia* they

open aborally. It may then be said that, at least when it comes to the tentacle bulbs, *Pukia* is most similar to *Mertensia*; however *Mertensia* has a strongly compressed body with two short aboral 'keels'.

*Pukia falcata* sp. nov.

(Fig. 1C-E)

*Pleurobrachia piteus* – Gorman, 1988: 17, pl. 12, and throughout (Moreton Bay, Qld); ? Greenwood, 1980: 91 (Moreton Bay, Qld).

? *Pleurobrachia* sp. – Dakin & Colefax, 1940: 211 (NSW); Hamond, 1971: 27 (Moreton Bay, Qld); Greenwood, 1980: 88, 91 (Moreton Bay, Qld).

Sea Gooseberry – Davie, 1998: 240 (Moreton Bay, Qld).

**Material examined.** HOLOTYPE: QM-G315861, 200 m offshore of Bribie I., in Moreton Bay, Queensland, surface to 2 m, water temp 24°C, 0700 hours, Puk Petersen for display at Underwater World (Sunshine Coast), 25.11.1999. 16.2 mm total length, 14.37 mm widest diameter, measured live. PARATYPES: Qld: QM-G315862, same data as holotype, 34 spec.; 2 spec. also distributed from this series each to AM, SAM, NTM, MTQ, and WAM. QM-G322302, Dunwich fishing jetty, North Stradbroke I., L. Gershwin, 10.02.2005; 4 spec. QM-G322303, same loc. as G322302, 23.02.2005; 1 juv. spec. QM-G329015, same loc. as G322302, 18.02.2005; 2 spec. QM-G329019, same loc. as G322302, 10.02.2005; 1 spec. QM-G329029, same loc. as G322302, 12.02.2005; 2 spec. NT: NTM unreg., Stokes Hill Wharf, Darwin Harbour, Darwin, L. Gershwin, 17.08.1998; 2 spec., A) 16.92 mm BL, 10.92 mm BW; B) 11.5 mm BL, 7.86 mm BW. SAM unreg. (= GZ0005), Mandorah Jetty, 12.11.2000; numerous spec. in dilute formalin plus 3 in liquid nitrogen. WA: SAM-XH00427 (= GZ 0034 and 0041), Port Hedland main jetty, 20°18.679'S, 118°34.438'E, 27–28.11.2000, W. Zeidler and L. Gershwin; many spec. of various sizes; preserved in dilute formalin, EtOH, and frozen.

**Non-type material.** Qld: SAM-H1586, Palm Cove, Cairns, L. Gershwin, 16.12.1999; 4 juv. spec., c. 1 mm. Palm Cove, Dec 1999 to Feb 2000; hundreds of spec. captured during routine sampling and examined and kept to various stages. Breakwater Marina, Townsville, 24.09.2003; numerous, examined in field and released. Weipa, Evans Landing, 12°39'52.6"S, 141°50'51.4"E, 10.01.2004; numerous, examined in field and released. NT: SAM-H970 (= XH0174), Stokes Hill Wharf, Darwin Harbour, L. Gershwin, 17.08.1998; preserved in EtOH. WA: 19°13.021'S, 121°15.399'E, off Eighty Mile Beach, L. Gershwin, 16.04.2004; numerous small, pointy, with rows half body length.

**Description.** Body apple-shaped (Fig. 1C), with the oral end broader and flatter than the indented aboral end; octagonal to circular in cross-section;

of fairly rigid gelatinous consistency. Mouth typically protruding (Fig. 1C-E).

Comb rows 8, of equal length, nearly reaching mouth, extending aborally to halfway point of each wing of polar plate. Combs 30-35 per row.

Tentacles reaching over 175 mm when relaxed, with numerous tentilla, spaced approximately 1mm apart at equal intervals. Tentilla filamentous, all alike, held coiled much of the time in life (Fig. 1D-E). When tentacles are fully retracted into bulbs, portions of tentacle extend part way into sheath. Tentacle sheaths running obliquely from mid-line to body wall, opening closer to the midline than to the aboral pole; with short projection toward oral end, giving the overall appearance of a triangle with the shortest side braced along the stomodaeum, the longest being the oral side of the sheath to the body wall, and the middle length being the aboral side of the sheath. Tentacle bulbs crescentic, curled around aboral end of stomodaeum (Fig. 1C-D).

Stomodaeum broad, extending halfway to aboral pole. Infundibulum long, narrow, slightly conical, tapering toward statocyst.

Statocyst deeply embedded within the aboral indentation of the body.

Meridional canals broad, with bilateral diverticula beneath each comb plate. Interradial canals short, with adradial canals branched close to the infundibulum, as in Fig. 6.2b of Harbison (1985); perradial canals lacking.

Polar plate very elongated, with two opposing narrow, straight-sided wings, each extending approximately 5 mm in length beyond statocyst, nearly reaching the curvature of the body.

Body colourless and extremely transparent in life, though radial canals may retain pigment from food for many hours; in preservative, transparent with whitish or yellow-orange tentacles.

**Etymology.** The specific name is derived from the Latin adjective *falcatus* (= sickle-shaped, feminine *falcata*), in reference to the shape of the tentacular bulbs (Brown 1956: 314).

**Behaviour in life.** The tentilla are uncoiled in the relaxed state. The tentacles continuously pull in and out of the sheaths, with the tentilla along the proximal half coiling into beehive-like beads as they retract.

The mouth is generally held in the extended state. When disturbed, the animal might partially retract the mouth briefly, but will soon resume the extended state.

Captive specimens were maintained for months in pseudo-kreisels and modified box-kreisels, on a twice-daily feeding of newly-hatched *Artemia* nauplii enriched with Super Selco. As in the other forms with aborally-directed tentacle sheaths, *P. falcata* whirls to ingest its captured prey.

**Bioluminescence.** Numerous attempts to stimulate light responses under different conditions have been unsuccessful; it seems fairly convincing that this species is not bioluminescent. Haddock & Case (1995) noted that while most ctenophores are capable of producing light, 'several species from the family Pleurobrachiidae produced no evidence of bioluminescence capability'; thus, it is possible that as more species in the Pukiidae become known, this may also prove to contain other non-luminous forms.

**Distribution.** In Moreton Bay, Queensland, *Pukia falcata* was found in large numbers near the surface throughout September-December, 1999. Individuals ranged in size from about 5 to 15 mm, though smaller specimens were lost through the outflow mesh. This species is the most abundant ctenophore from at least Moreton Bay, Queensland, up around the coast to Darwin, Northern Territory. It was also found in large numbers through much of the summer (1999-2008) in the Cairns area, especially during northerly winds, in Darwin Harbour in August 1998, and along much of the coastline of Western Australia in spring 2000 and autumn 2004. Gorman (1988: 21) reported that this species (as *Pleurobrachia pilens*) was 'found in large numbers', and that it was among the three most common species in four of six sampling trips. It may also be the species reported as *Pleurobrachia* by Dakin & Colefax (1940: 211), and said to be 'so numerous as to block up not only plankton nets but even the dredge and fishing nets such as the seine used from the shore...', but this is not certain.

**Field identification.** Body apple-shaped in life, cylindrical preserved; colourless and transparent, about 1.5 cm. Ctenes rows almost entire



body length. Tentacle bulbs crescentic, curving around aboral end of stomach.

**Remarks.** The spherical apple shape of the body bears some discussion. Most cydippids have an oval or cylindrical body, while some are pear-shaped. However, the body of *Pukia* is distinctly apple-shaped, i.e., largest near the oral end, slightly smaller toward the aboral end. This is most similar to that of *Pleurobractia*, which is more spherical.

The mouth is somewhat different, too. In *Pukia*, the mouth is typically held rigidly in the extended position, whereas in some cydippids it is highly extensile, while in others it is just a slit.

*Pukia* often coils its tentilla; the coiled tentilla are a key character of the Euplokamididae (Mills, 1987). While we were unable to determine the type of muscle present in the tentilla of *P. falcata*, the overall description does not match that given by Mills (1987) for *Euplokamius*. Specifically, she indicates that the side branches of euplokamids are widely spaced, and normally held coiled when relaxed and not in use, but stretching out at high velocity when triggered by contact with prey. She further refers to 'the natural tendency for all ctenophore tentilla to coil to some extent'. In *P. falcata*, the tentilla are sometimes coiled and sometimes filamentous, frequently switching between the two states, but are most often filamentous when at rest; furthermore, the tentilla are numerous and closely spaced.

#### ORDER PLATYCTENIDA Bourne 1900

**Remarks.** Benthic ctenophores were first identified in Australian waters by Stephenson *et al.* (1931), but he gave no morphological details to allow a species determination. Subsequent records have indicated fairly high rates of endemism, suggesting that the biodiversity of this peculiar group is potentially much greater in Australia than currently known.

The Australian benthic ctenophores have been well studied in comparison to their pelagic cousins. They appear to be relatively common in the temperate waters of southern Australia, with two endemic species described by Matsumoto & Gowlett-Holmes (1996) and Matsumoto (1999). However, Arnold (1993) and Hamner

(in Matsumoto (1999)) reported tropical forms, as we do below.

#### Family Coeloplanaidae Willey, 1896

##### *Coeloplana* Kowalevsky, 1880

The following *Coeloplana* species have been previously reported from Australia:

*Coeloplana ueteoris* Thiel, 1968 — Arnold, 1993: 16 (Pioneer Bay, Orpheus I., Qld, free-living in muddy sand).

*Coeloplana scaberiae* Matsumoto & Gowlett-Holmes, 1996: 33–40, figs 1–4 (on both sides of the Yorke Peninsula, SA, on the brown alga *Scaberia agardhii*).

*Coeloplana thousouii* Matsumoto, 1999: 385–393, figs. 2, 3 (Thomson Bay, Rottneest I., WA, on the coralline alga *Jania* sp.).

*Coeloplana willeyi* Abbott, 1902 — Smith & Plant, 1976: 43–46 (near Portsea, Port Philip Bay, VIC, on the green alga *Caulerpa* sp. and on red algae).

*Coeloplana* spp. — Stephenson *et al.*, 1931: 72 (Low Is., Qld, on an alcyonarian); Edgar, 1997: 149 (southern Australia); Edgar, 2000: 149 (southern Australia).

**Remarks.** We describe below two new tropical species of *Coeloplana*. One additional tropical form has been identified, but is presently awaiting additional material, and is thus beyond the scope of this paper. It is a minute form with a more or less transparent body, observed in abundance on the Crown-of-thorns starfish *Acaulthaster planci*, collected off Townsville 2003–2007.

##### *Coeloplana mellosa* sp. nov.

(Figs 1F–G, 2 A, B)

**Material examined.** HOLOTYPE: QM-G329570, off Townsville, Qld, Bette Willis, Jun 2005, commensal on *Sarcophyton* sp. (Octocorallia, Alcyoniidae); c. 2.5 cm long (live). PARATYPES: SAM-H1596, same coll. data as holotype; 1 spec., c. 2 cm long (live). SAM-XH00437, same data as holotype; 2 spec. in EtOH, c. 1–2 cm long (live).

**Diagnosis.** *Coeloplana* on *Sarcophyton* host; with brown translucent body with whitish ectodermal fine meshwork pattern, appearing to the unaided eye as a whitish body with hundreds of tiny brown dots; in live animals,



papillae about 20, cylindrical, in longitudinal X-pattern through the statocyst; or in preserved specimens over 100, in 16 rows, in three sizes, of two types; with four-lobed statocyst palps.

**Description of living specimens** [primarily based on holotype]. Body extremely flattened, filmy, modified for creeping, resembling a platyhelminth flatworm; approx. 1.5 times as long as wide, more or less oval in shape with undulating margin, with outline constantly changing in amoeboid manner. Dorsal surface with deep groove down centre of body longitudinally, defined along both sides by ridges bearing ephemeral papillae; longitudinal ridges divided at statocyst by latitudinal groove.

About 20 papillae, extensile, with different ones appearing and disappearing with movement, and in response to stimuli; circular in outline, with straight sides and an evenly rounded top; mostly of same size, but occasionally one or two appearing about half again as broad. Arranged loosely in an X-pattern, converging at statocyst. When papillae are not extended, their position cannot be distinguished.

Tentacles 2, highly extensile and retractable into sheaths inside the body; emitting through two 'chimneys' (Fig. 1G), at opposite ends of the body. Main shaft cylindrical, bearing numerous filiform, pointed tentilla, more or less evenly and sparsely spaced along length of tentacle; the tentilla branch from main shaft dichotomously rather than laterally (Fig. 1F-G). Tentacle bulb shape was uninterpretable due to opacity of the body; placing the ctenophores over or near a light resulted in their balling up rapidly and tightly for over 30 minutes.

Statocyst placed dorsally near midpoint of body; appearing as tiny white granule, deeply embedded in niche between pair of permanently raised, opposing, crescentic, four-lobed, palmate palps, resembling fleshy, scalloped lips (compare with Dawydoff 1938: fig. II).

Gonads were not observed, but at least one specimen was brooding live cydippid embryos on ventral side of body, which began streaming out in mucus strands when disturbed.

Radial canals were not observed due to avoidance of light by ctenophores and partial opacity of their pigmentation.

**Colouration:** To unaided eye, uniformly whitish crowded with numerous tiny brown pin-point dots (Fig. 1F); under microscopic examination, body translucent brown, with cream-coloured ectodermal reticulations, giving an overall impression of honeycomb. Papillae resemble colourless bubbles, and are very difficult to observe at length due to their absolute transparency; when viewed dorsally, they act as windows through to the underside of the ctenophore's body. Tentacles are coloured with alternating whitish and clear bands. Crescentic statocyst-palp structures are opaque off-white.

**Notes on preserved holotype.** The specimen preserved extremely well, and a thorough study of its morphology could be made. Curiously, however, several features evident in the live specimen differed markedly in the preserved specimen. Most noticeably different were the number and arrangement of papillae, and the transparency of the animal.

The live colour pattern and opacity was such that the internal morphology, particularly the tentacle bulbs, gonads, and radial canals, could not be interpreted; however, while preservation typically makes most coelenterates more opaque, *C. mellosa* actually became considerably more transparent (Fig. 2A-B). The tentacle bulbs are large but without particular shape (e.g., anchor, cross-bar). The radial canals form an anastomosing network along the periphery of the animal. The gonads are arranged in eight distinct rows: four forming a double-turret-shaped figure-8 through the statocyst, orientated along the short axis of the animal; the other four, form loosely S-shaped structures along both sides of each of the two tentacle bulbs and sheaths. Sex or maturity of the gonads was not investigated; however, they appear from external examination to be well developed.

The papillae were difficult to study in the live specimens, due to their total transparency and ephemeral nature. Over about six hours of study of four specimens, it was concluded that they typically had about 20 papillae arranged in an X-pattern centred on the statocyst, running along the tentacular axis, i.e., opening toward the tentacles. However, a considerably more complex arrangement was revealed in the preserved holotype (Fig. 2A-B), where these

papillae have taken on an opaque pointed form, protruding neatly from the body wall, and are readily visible. A total of well over 100 papillae are present, of two different types and three different sizes, in 16 distinct rows. The four primary papillae rows, i.e., crossing the statocyst, each contain about 20 small, cylindrical papillae, arranged in two opposing double-turret-shaped configurations along the short axis, arising along the abaxial edge of the gonad rows. Four rows of secondary papillae each contain about five papillae of the same size as in the primary rows; these papillae are arranged in a crescentic row, overlying the abaxial edge of the proximal portions of the lateral gonads, which run alongside the tentacle bases. Distal to this row of papillae and along the same gonad rows, lies the tertiary set of papillae, considerably smaller than the primaries and secondaries but of the same form; each of the four rows has about 15–20, crowded papillae, arranged along the adaxial side of the gonads. In addition, eight broad papillae, about ten times the size of the tertiary papillae, are arranged two on each side of each tentacle sheath near the opening, abaxial to, but not overlying, the corresponding gonad rows, and are of a different form, i.e., more like diverticula in the body wall rather than the more numerous opaque, pointy, cylindrical papillae.

**Etymology.** The specific name, *mellosa*, is from the Latin *mellosus* (= honey-coloured; feminine), in triple reference: A) to the honeycomb-colour pattern of this species, B) to the overall honey colour, and C) to the sticky viscosity of honey in a slow trickle, for this benthic, creeping form.

**Type locality.** Reefs off Townsville, North Queensland, on *Sarcophyton* sp. The exact locality is unknown, as the ctenophores were first observed in the laboratory on corals that had been collected from a variety of places for the zoology classes at James Cook University.

**Behaviour.** In addition to the morphological behaviour noted above in the description, *Coeloplana mellosa* displays a marked sensitivity to light, actively and rapidly moving away from lighted areas, or balling up tightly or sinking into crevices if light is shone directly on the animal. If left to its own will in darkness, it would be found anywhere on the coral or the

sides of the study bowl; in dim light it would quickly seek branch-axil crevices or the underside of coral branches. Examined on a black-back petri dish, it readily spread out, but balled up again with direct light (e.g., for photography).

**Preservation technique.** Good formalin preserved specimens were obtained using the following technique. A specimen was placed into a small petri dish (55 mm diameter) nearly full of the seawater that the specimen had been living in. It was put in the dark and allowed to relax and adhere. If it hid in a corner, it would be gently prodded to get it moving, until it finally settled and relaxed on the flat bottom. It was then put into the refrigerator to immobilise it. After about one hour, the petri dish containing the relaxed ctenophore was very gently lowered with forceps into a 250 ml container of chilled seawater, so as to create as little water current as possible. Once settled on the bottom, a single drop of concentrated formalin was added along one side of the jar, and allowed to diffuse over 30 minutes, then another to a different side, and so on, until about 8–10 drops of formalin had been added and the specimen began to look dead (i.e., slightly crinkled and with muddled colour), at which time a little more formalin was added to bring the concentration to about 1–2%, and the jar was left at room temperature.

**Field identification.** Benthic ctenophores, with an extremely flattened body modified for creeping, often mistaken for flatworms, until the tentacles are observed. Tentacles of the typical ctenophore form (i.e., with tentilla), emitting from two ephemeral 'chimneys' near the farthest opposing ends upon the dorsal surface. Comb rows lacking in adults. Colour usually camouflaged with host, which may be algae, soft coral, echinoderm, or other. Characters specific to *Coeloplana mellosa* include its host, *Sarcophyton* sp. from the Great Barrier Reef, the brownish body with whitish reticulations, the 20 or so papillae in an X-arrangement in the live animal or over 100 in 16 rows in the preserved specimens, and the four-lobed form of the statocyst-palps.

**Remarks.** *Coeloplana mellosa* differs from all other species mainly in the number and



Table 4. Characters used to distinguish species of *Coeloplana*. Species are those considered valid by Matsumoto (1999). Data derived from original descriptions plus Dawydoff (1938) and Matsumoto (1999).

	Host	Colour	Papillae	Locality
<i>C. agniae</i> Dawydoff, 1930b	Cnidarian: Alcyonacean: <i>Simularia</i>	Clear, milky white, or violet brown	4 distinct rows of 8-12 simple papillae each in an X-pattern through the statocyst, plus 3-4 each in 4 more rows, 2 flanking each tentacle bulb	Vietnam
<i>C. astericola</i> Mortensen, 1927	Echinoderm: Asteroid: <i>Echinaster</i> <i>luzonicus</i>	Deep red or claret with large, irregular spots of creamy-yellow, or the inverse	4 crescentic rows of 4 simple papillae, emanating from the statocyst in a figure-8 pattern	Amboina; Kei Is.
<i>C. banmwarthi</i> Krumbach, 1933	Echinoderm: Echinoid: <i>Diadema</i>	Dark purple	[Not described]	Red Sea
<i>C. bocki</i> Komai, 1920	Cnidarian: Alcyonacean: <i>Stereonephthya</i>	Dark vermilion, dark red, brick red, pink, orange, or grey stripes branching and anastomosing	[Not described]	Misaki, Japan
<i>C. duboscqui</i> Dawydoff, 1930c	Cnidarian: Pennatulid: <i>Pteroeides</i>	Intense orange or vermillion to orange; tentacles colourless	Papillae not observed	Vietnam, Hawaii
<i>C. echinicola</i> Tanaka, 1932	Echinoderm: Echinoid: <i>Toxopneustes</i> <i>pileolus</i>	Yellow brown with wide pale green margin	32 simple papillae: 8 larger, 24 smaller	Japan
<i>C. gonoctena</i> Krempf, 1920	Cnidarian: Alcyonacean: <i>Alcyonium</i>	Milky white or grey with brown spots	5 simple papillae in each of 4 rows forming an X-shape or figure-8, with the distal-most in each row larger	Vietnam
<i>C. kouai</i> Utinomi, 1963	Cnidarian: Alcyonacean: <i>Alcyonium</i>	Uniformly milky white or seashell pink, with yellow tentacle bases	4-6 pairs of simple papillae	Sagami Bay, Japan
<i>C. krusadiensis</i> Devanesan & Varadarajan, 1942	Echinoderm: Asteroid: <i>'Pentaceros</i> <i>hedemaniai'</i>	Red	6-20 simple papillae	India
<i>C. lineolata</i> Fricke, 1970	Cnidarian: Alcyonacean: <i>Sarcophyton</i>	Milky white or greenish with pale yellow or yellow-green spots	60-70 simple papillae	Madagascar
<i>C. mesnili</i> Dawydoff, 1938	Planktonic	Transparent pale green, with bright orange statocyst and papillae	32 simple orange papillae arranged in 8 short rows	Vietnam
				Continued ...



Table 4 (continued) ...

	Host	Colour	Papillae	Locality
<i>C. meteoris</i> Thiel, 1968	Free-living on soft sediments	Clear with yellow-white reticulations covering body, and red pigmentation around canals, tentacle sheaths and papillae	4 rows of simple papillae, 3–4 per row	Somalia; North Queensland, Australia
<i>C. metschnikowii</i> Kowalevsky, 1880	Seagrass <i>Zostera</i>	Dorsal grey, ventral white	[Not described]	Red Sea
<i>C. mitsukurii</i> Abbott, 1902	Algae: red <i>Melobesia</i> sp., or brown <i>Sargassum</i> sp.	Pigmentless to chocolate brown, with yellow white cells around margin and two bands of yellow around statocyst	4 curved rows of 6–8 papillae per row with 2–5 digitate processes, radiating around the sense organ in a figure-8	Japan
<i>C. perrieri</i> Dawydoff, 1930a	Seagrass <i>Posidonia</i>	Deep olive green with sepia spots, with narrow yellow orange margin; tentacles yellow-brown	Lacking papillae (? , but see Dawydoff, 1938)	Vietnam
<i>C. punctata</i> Fricke, 1970	Cnidarian: Alcyonacean: <i>Sarcophyton</i>	Transparent with brown or grey lines parallel to the tentacle axis	70–100 simple papillae	Madagascar
<i>C. scaberiae</i> Matsumoto & Gowlett-Holmes, 1996	Algae: <i>Scaberia agardhii</i>	Solid dark orange or vivid red, without spots of any kind	Four rows of simple papillae in a figure-8 pattern, and also along the margin	Yorke Peninsula, South Australia
<i>C. sophiae</i> Dawydoff, 1938	Cnidarian: Gorgonian: <i>Solenocaulon</i>	Brick red with milky white spots	4 rows of 3–5 simple papillae	Vietnam
<i>C. tattersalli</i> Devanesan & Varadarajan, 1942	Planktonic	Transparent green	8 simple papillae; sometimes with secondary papillae, which may appear branched	India
<i>C. thomsoni</i> Matsumoto, 1999	Algae: <i>Jania</i>	Pale green or white with yellow white cells scattered over dorsal surface	Green morph has 16 papillae (8 rows of 2), four branched, others simple; white morph with 4 large permanent papillae and 12 small ephemeral papillae	Rottneest I., Western Australia
<i>C. weilli</i> Dawydoff, 1938	Echinoderm: Echinoid: <i>Heterocentrotus mammillatus</i>	Uniform brownish red	Lacking papillae	Gulf of Thailand

Continued ...

Table 4 (continued) ...

	Host	Colour	Papillae	Locality
<i>C. willeyi</i> Abbott, 1902	Not specific: seagrasses, all colours of algae, echinoderms	Deep purple, red or orange fading to pink, with white spots along margin and yellow blotches at base of papillae	20–30 cylindrical or club-shaped papillae	Japan; Hawaii
<i>C. wuennenbergi</i> Fricke, 1970	Cnidarian: Alcyonacean: <i>Sarcophyton</i>	Whitish to grey, with dark red/violet spots	40 simple papillae	Madagascar
<i>C. mellosa</i> sp. nov.	Cnidarian: Alcyonacean: <i>Sarcophyton</i>	Overall impression whitish with hundreds of tiny brown dots; close-up, body brownish with cream-coloured ectodermal reticulations	20 simple papillae arranged in a X-shape in life; preserved: over 100 papillae in 16 rows, 3 sizes, and two types	Great Barrier Reef off Townsville, Queensland
<i>C. reichelti</i> sp. nov.	Botanical: variety of red and green algae and seagrass	Transparent pale yellowish body with hundreds of ectodermal and endodermal green specks, with 'frosty' white cells on papillae and margin	8–20 large, branched, permanent papillae, plus 8 smaller, cylindrical, ephemeral papillae midway to margin	Great Barrier Reef off Townsville, Queensland

arrangement of papillae (Table 4), although this character becomes clearer upon preservation. In the preserved condition, it is the only species with 16 rows of papillae. Some species do have complex papillae patterns, e.g., *C. agniae* Dawydoff, 1930(c), and *C. mesuili* Dawydoff, 1938, with eight rows, *C. gonoctena* Krempf, 1920, with the distal-most in each of four rows larger than the others, *C. scaberiae* Matsumoto & Gowlett-Holmes, 1996, with papillae along the margin as well as in the primary figure-8, and *C. thomsoni* Matsumoto, 1999, with two different types of papillae in both colour morphs. Similarly, *C. lineolata* Fricke, 1970, and *C. punctata* Fricke, 1970, are both characterised by having a very large number of papillae, 60–70 in the former and 70–100 in the latter. However, in all these cases, the hosts and colour patterns serve to readily differentiate *C. mellosa* from each, and even though there are generalities such as 'a large number of papillae' or 'multiple rows or types of papillae', they are nonetheless dissimilar in actual number and arrangement.

The colour of live specimens of *C. mellosa* is most similar to *C. gonoctena* with a milky white body with brown spots; however, in *C. gonoctena* the brown spots are quite large, whereas in *C. mellosa* they are minute.

*Coeloplana reichelti* sp. nov.  
(Fig. 2C–F)

**Material examined.** HOLOTYPE: QM-G329571, off Townsville, Qld, 14.05.2008 from Reef HQ Aquarium, living on broad-leafy green algae; c. 1.0 cm body length (live). PARATYPES: QM-G329572, same coll. data as holotype; 1 spec., c. 0.4 cm BL (live); living on seagrass overgrown with dark red algae. QM-G329573, same coll. data as holotype; 1 spec., c. 0.5 cm BL when stretched out (live); living on green algae. SAM-H1629, same coll. data as holotype; 2 specs, c. 0.5 cm BL (live); living on green algae.

**Diagnosis.** *Coeloplana* on various green and red algal and seagrass hosts; with yellowish translucent body with numerous tiny ectodermal green specks, with whitish cells on branches of papillae and around margin, giving frosted appearance; in live animals, 20 permanent

irregularly branched, primary papillae, arranged in figure-8 pattern, plus 8 ephemeral secondary papillae, 4 each in two rows, cylindrical, unbranched; with smoothly rounded statocyst palps.

**Description.** (Based on notes from laboratory examination of live specimens, primarily the holotype (Fig. 2C)).

Body extremely flattened, filmy, modified for creeping, resembling a platyhelminth flatworm; approximately 2–3 times as long as wide, more or less oval-shaped to lemon-shaped with an undulating margin, with outline constantly changing in an amoeboid manner. During study period, specimens changed shape several times from a primarily 'short, broad form' to a primarily 'long, narrow form' and back again, with respect to the direction of movement (perpendicular to the tentacular axis). Dorsal surface lacking a deep groove down centre; ventral surface with deep groove down centre of body in tentacular axis.

Papillae 28, of two types, arranged as follows in holotype: permanent papillae 20, irregularly digitate, arranged in a figure-8 pattern through statocyst (Fig. 2C); two other rows of smaller, unbranched, ephemeral cylindrical secondary papillae, 4 in each row, arranged about midway between primary rows and margin. In paratypes, which are smaller in body size, permanent papillae are arranged in 2 rows of 4, close to, but either side of, midline (Fig. 2E).

Tentacles 2, highly extensile and retractable into sheaths inside body, at opposite ends of body; 'chimneys' not apparent; instead, tentacles emitted from an opening just proximal to 'edge' of body margin. Main shaft of tentacles cylindrical, bearing numerous filiform, pointed tentilla, more or less evenly and sparsely spaced along length of tentacle; tentilla branch from main shaft laterally rather than dichotomously. Tentacle bulbs in shape of angular 'C' or half a hexagon, with tentacle emitting from 'outside' or 'back' of central bar.

Statocyst dorsal, conspicuous, located at centre of body, midway between four central-most branched papillae; appearing as a tiny pale orange granule, deeply embedded in a niche between a pair of permanently raised, opposing, crescentic, simple, smoothly rounded, unscaloped palps, resembling fleshy lips.

Gonads were not observed.

Radial canals numerous, throughout body region peripheral to tentacle bulbs and papillae; not anastomosing; repeatedly branching toward margin into progressively finer canals (Fig. 2E–F). Gastrovascular origin of some canals not apparent.

**Colouration:** uniform transparent pale green to the unaided eye; under microscopic examination, the body is transparent and colourless, with hundreds of bright green ectodermal and endodermal specks, particularly over the vital region between tentacle bulbs and in a ring around just proximal to the periphery, and with frost-like whitish granules haphazardly arranged around the margin. Branched papillae transparent, with conspicuously 'frosted' appearance on some surfaces of tips and branches (Fig. 2C–D). Cylindrical papillae completely transparent and colourless, resembling bubbles, and remarkably difficult to see; microscopic examination through these windows into the inside of the animal revealed presence of numerous particles whirling around in a random motion, contained within papillae. Tentacles slightly translucent whitish. Crescentic statocyst-palp structures are opaque pale orange coloured, with granular appearance, resembling sand.

**Etymology.** The specific name, *reichelti*, is given to honour Dr Russell Reichelt, Chairman of the Great Barrier Reef Marine Park Authority which owns the Reef HQ Aquarium where this species was discovered; also because Dr. Reichelt has been extremely supportive of scientific projects relating to jellyfish and marine-stinger safety; and more personally because Russell has been an inspiring mentor to the senior author.

**Type locality.** Algal and seagrass beds off Townsville, north Queensland. The exact locality is unknown as they were first discovered at the Reef HQ Aquarium flourishing on algae and seagrasses that had been collected from a variety of locations nearby.

**Behaviour.** *Coeloplana reichelti* showed a marked propensity toward the air/water interface, and had to be repeatedly drawn off it during examination. Whether this is due to some feature of the study conditions, or is perhaps a natural dispersal mechanism, is unknown. In its undisturbed condition, *C. reichelti* spends



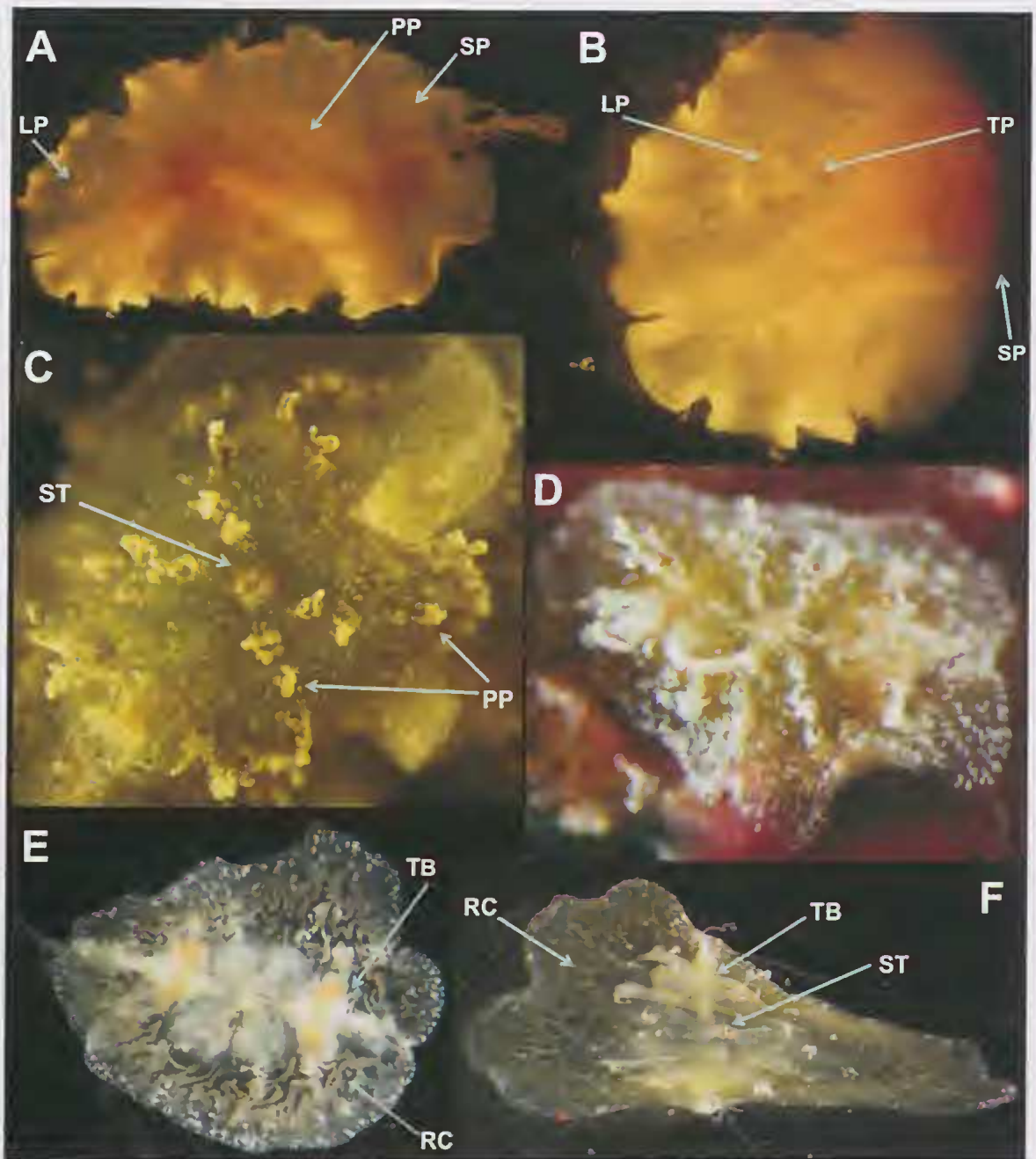


FIG. 2. A–B, *Coeloplana mellosa* sp. nov., holotype, preserved. A. Whole animal; note one tentacle extending beyond right edge of image, the other tentacle retracted into bulb left of centre; note also arrangement of papillae. B. Close up of left side of A. Note three different sized papillae: Primary papillae (PP) forming double-turret-shaped figure-8 in centre of A; secondary papillae (SP) along lateral gonads in A & B; tertiary papillae (TP) along adaxial side of lateral gonads in B; and large papillae (LP) along abaxial side of lateral gonads in A & B. C–F, *Coeloplana reichelti* sp. nov. C. Holotype, dorsal view, note figure-8 arrangement of permanent papillae. D. Paratype QM-G329572, in life, dorsal view, direction of movement is to lower right. E. Paratype QM-G329573, in life, ventral view. F. Dorsal view of E; note branching nature and arrangement of papillae in two rows. Abbreviations in C–F: radial canals (RC), tentacle bulb (TB), statocyst (ST), permanent papillae (PP).

most of its time near the tips of algae and seagrass, with the tentacles streamed out, up to about 20 cm, both day and night.

**Field identification.** *C. reichelti* is highly cryptic but appears to prefer tropical algal and plant hosts. Diagnostic characters are: yellowish body with green flecks and whitish frost-like cells on papillae and margin; conspicuous, irregularly branched permanent papillae, plus simple, ephemeral papillae; and the smoothly rounded form of the statocyst-palps.

**Remarks.** *Coeloplana reichelti* appears to be most similar in general form to *C. mitsukurii* from Japan. Both have branched papillae, and both have white cells around the margin and are found on various species of algae. However, *C. mitsukurii* has 24–32 branched papillae and no mention of secondary, simple papillae, whereas there are only 8–20 branched papillae in *C. reichelti*, plus eight simple, ephemeral papillae. Interestingly, Abbott (1902) described the papillae of *C. mitsukurii* as being 'entire or digitate and fringed'; this raises the possibility of further difference between the two in the actual form of the papillae, as one would not describe the papillae of *C. reichelti* as digitate and fringed, but possibly more as 'jaggedly branched, or haphazardly dendritic'. Without seeing fresh material of *C. mitsukurii*, it is difficult to compare the papillae branching forms between the two species. The two species further differ in colour, with *C. mitsukurii* being pigmentless to chocolate brown, but *C. reichelti* being whitish to yellowish with many bright green flecks. Furthermore, whereas *C. mitsukurii* is found in temperate northern hemisphere, *C. reichelti* is found in the tropical southern hemisphere. *C. reichelti* is also found on seagrass, but this does not appear to have been recorded for *C. mitsukurii*. Whilst the ephemeral papillae and seagrass host could have been overlooked, the number of primary papillae, the colour differences, and the great geographical separation, would seem to differentiate the two quite readily.

Two other species of *Coeloplana* also have branched papillae. In *C. tattersalli* Devanesan & Varadarajan, 1942, the secondary papillae are said to sometimes appear branched, but in *C. reichelti* the primary papillae are permanently

and conspicuously branched, and greatly outnumber those in *C. tattersalli*. *C. tattersalli* is also planktonic, whereas *C. reichelti* is benthic.

*C. thomsoni* Matsumoto, 1999, has four large, branched, permanent papillae, plus 12 smaller, simple ephemeral papillae, whereas *C. reichelti* has 20 and 8, respectively; furthermore, *C. thomsoni* is found only on a single algal host, whereas *C. reichelti* is less discerning. As already described *C. reichelti* has a distinctive colour pattern within the genus. A comparison of primary diagnostic characters for species of *Coeloplana* is presented in Table 4.

Family Ctenoplanidae Willey, 1896

*Ctenoplana* Korotneff, 1886

*Ctenoplana* sp.

Only one unidentified *Ctenoplana* species has been previously reported from Australia:

*Ctenoplana* sp. — Hamner, in Matsumoto, 1999: 386 (off Townsville, Qld; planktonic).

**Field identification.** Essentially a planktonic version of a benthic ctenophore.

**Remarks.** The above report by Hamner noted only that the specimen was transparent and planktonic, and found off Townsville, but gave no further details. It will be interesting to see what species is/are present in Australian waters, when found again.

ORDER LOBATA Eschscholtz, 1825

Family Bolinopsidae Bigelow, 1912

*Bolinopsis* L. Agassiz, 1860  
(*sensu* Mayer, 1912)

*Bolinopsis* species  
(Fig. 3A–B)

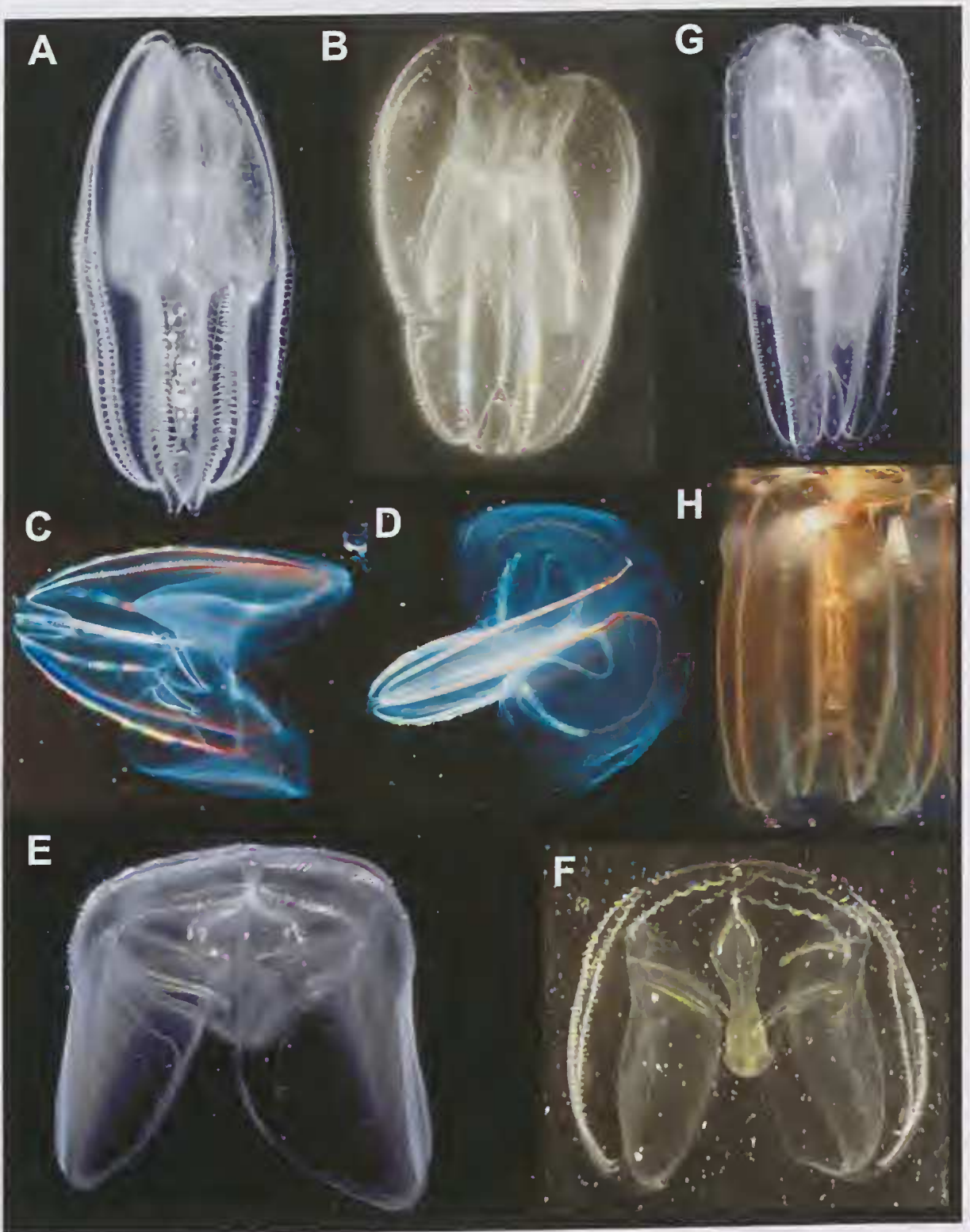
The following *Bolinopsis* species have been previously reported from Australia:

*Bolina chuni* von Lendenfeld, 1885a: 929–931, pl. 44–45 (Port Jackson, NSW); Whitelegge, 1889: 197 (Port Jackson); Dakin & Colefax, 1933: 198 (NSW).

*Bolina* sp. — Dakin & Colefax, 1940: 211 (NSW).

Comb jellies — Dakin & Bennett, 1987: 179 (NSW).







*Bolinopsis* spp. — Edgar, 1997: 150 (NSW); Edgar, 2000: 150 (NSW); Gershwin & Zeidler, 2003: 237 (Great Australian Bight); Gowlett-Holmes, 2008: 54 (SA).

**Material examined (mostly unpreservable).** Wholly transparent forms: Qld: Palm Cove, Dec 1999 to Feb 2000; hundreds of specimens captured during routine sampling and examined to various stages; to about 7 cm long (Fig. 3B). SAM-XH436, Palm Cove, 10.12.1999; 1 spec. in EtOH. Palm Cove, 19.02.2000; transparent with 2 red dots on each side. Palm Cove, 22.02.2000; 1 spec. with 2 red dots on each side, 2 cm BL. Quarter-deck Marina, Townsville, 5.11.2003; 1 small, examined in the field and released. NT: Stokes Hill Wharf, Darwin Harbour, 6.08.1998; numerous specs. Mandorah Jetty, 12.11.2000; 2 specs in liquid nitrogen and EtOH. Dundee Beach, Fog Bay, 15.11.2000; numerous. WA: Cockburn Groin, Cockburn Sound, 7.03.1999; numerous specs examined. Derby Jetty, 22.11.2000; several small to medium, purplish clear. Port of Broome, 25.11.2000; 4 specs, 1–2 cm; 5 frozen (GZ0024). Port Hedland Jetty, 27–28 Nov 2000; numerous. Hearson Cove, near Dampier, 30.11.2000; 1 spec. 19°13.021S, 121°15.399E, off Eighty Mile Beach, 16.04.2004; numerous. 19°07'56.3S, 121°18'26.3E, off Eighty Mile Beach, 10.05.2004; numerous. 19°02'09.0S, 121°21'44.1E, off Eighty Mile Beach, 11.05.2004; numerous. SA: Whyalla Marina, 12.05.1999; in plague proportions up to about 4cm long, typically orientating in water column with aboral end up; highly bioluminescent. Murat Bay Jetty, Ceduna, 19–20.02.2002; large numbers; 6 frozen in liquid nitrogen (GZ0528). NSW: Bare Rock, Botany Bay, 20.12.1998; numerous examined. Tas.: Photograph by Karen Gowlett-Holmes, Waterfall Bay (Fig. 3A); specimen not preserved. Transparent body with magenta canals: SA: Whyalla Marina, 18.02.1999; thousands of specimens 3–8cm, casually examined in the field; numerous growth stages examined in detail. Kingscote Jetty, Kangaroo I., 1.05.1999; numerous, to 12 cm long; very highly bioluminescent; preyed upon in large numbers by *Cyanea* (Scyphozoa). Streaky Bay and Smoky Bay jetties, 19.02.2002; numerous. St Francis and Dog Is., Nuyts Arch., Great Australian Bight, 21–25.02.2002;

numerous. WA: 19°07'56.3S, 121°18'26.3E, off Eighty Mile Beach, 10.05.2004; several with thick comb rows.

**Field identification.** Body similar in outline to a chicken egg in size and shape, i.e., with one end somewhat larger and more rounded than the other; more or less colourless and transparent; to about 8 cm long. Two lobes at larger end, capable of expanding out somewhat like scoops, or often held curled in, giving the animal the egg-like shape. The body is extremely soft and breaks apart easily. Ctene rows extend along on the body, four extending out along the lobes, and the other four ending in rabbit-ear-like auricles between the lobes.

**Remarks.** Unidentified, unpreservable forms of the genus *Bolinopsis* were found in great abundance along much of coastal Qld, SA (especially upper Spencer Gulf and Kangaroo I.), along the south-west coast of WA, and in Darwin Harbour, NT. *Bolinopsis* has not been previously reported in the waters of these states. No species identification was made, though medium to small lobes and a transparent/colourless body were noted. Another transparent and colourless form from Tasmania is characterised by short, triangular aboral extensions (Fig. 3A); these have not been observed in other Australian forms. It is possible that one or more of these forms can be referred to *B. clunii* (von Lendenfeld, 1885a), the only *Bolinopsis* previously described from Australian waters, but von Lendenfeld's description of this NSW species is insufficient for confident determination.

A common form throughout Queensland is completely colourless and transparent (Fig. 3B), whereas another small Queensland form lacks lobes and has two small red granular dots along each side, and a common form in South

FIG. 3. A–B, *Bolinopsis* spp. A. *Bolinopsis* sp. A (Tasmania). B. *Bolinopsis* sp. B (North Queensland). Note aboral extensions in A, lacking in B; complexly winding radial canals in the lobes of A compared to B; and comparatively heavier, longer lobes in B than in A. Both specimens photographed live and orientated with oral end toward upper right. C–D, *Bolinopsis ashleyi* sp. nov., holotype (Moreton Bay) in life. C. Sagittal view. D. Tentacular view. E–F, *Ocyropsis* spp. E. *Ocyropsis vance*, gen. et sp. nov., holotype (Tasmania) in life, orientated oral end toward lower right. Note deeply indented hourglass-shaped stomach, indicating affinity with the *O. maculata* species group. F. *Ocyropsis* sp., in life (Cairns Harbour, Far North Queensland). Note ctene rows longer but with comb plates more sparsely arranged than *O. vance*. G–H, *Leucothea* spp. G. *Leucothea* sp. (southeastern Tasmania). H. *Leucothea* sp. (Moreton Bay). Both G and H are orientated with oral end toward the left. Photographs A, E, and G by Karen Gowlett-Holmes; used with permission. Photographs C, D by Ross Easton (UnderWater World, Sunshine Coast, Australia); used with permission. Photograph H by Puk Petersen (UnderWater World, Sunshine Coast, Australia); used with permission.

Australian waters has a fine but conspicuous bright magenta colouration to the canals. Attempts to preserve this third form ended in the animals writhing to the point of exploding and disintegrating. Experiments to relax the specimens prior to fixation included magnesium chloride, menthol, extremely dilute formalin, dilute ethanol, cooling, freezing, warming, tea tree oil, eucalyptus oil, oxygen deprivation, and seawater diluted 50% with tap water. All relaxing efforts proved unsuccessful; however, the dilute ethanol and the tap water dilution both produced a temporary specimen. Specimens killed in dilute ethanol lasted a few days but exploded with further preservation attempts; specimens killed with tap water dilution died quickly in a good form, but disintegrated quickly if left untreated, and also exploded in response to other treatments.

Another unidentified form was found once in abundance off Palm Cove, Cairns, Queensland, in about 1–2 m water. It had peculiar double round marks midway inside the body. It was found along with *Pukia falcata* sp. nov. (this paper), during a time of low medusa diversity.

The *Bolinopsis* species found in the gulfs of South Australia warrants further study. It appears that it may pose a nuisance in the semi-enclosed waters of Spencer Gulf where blooms in plague proportions have been observed (unpublished data, and correspondence with fishermen and researchers). While the trophic dynamics of *Bolinopsis* in Spencer Gulf are unknown, the predatory impact of this species is of concern, and should receive priority in sustainability studies of commercially important species that depend on the Spencer Gulf, and Gulf St. Vincent, as a nursery or feeding ground.

Coelenterates, and ctenophores in particular, are very successful competitors, preying on eggs and larvae of other animals, and also competing with them for food resources (Purcell 1990; Purcell 1991; Purcell & Arai 2001). A well documented example is *Mueniopsis*, which was accidentally introduced into the Black Sea in 1982, and by about 1990, was estimated to have a biomass over of a billion tons, and had led to the collapse of fisheries industries in the region (Shiganova 1998; Kideys 2002).

*Bolinopsis* and *Mueniopsis*, although separated based on the length of the lobes relative to

the body, have a similar functional biology and predation potential (Main 1928; Nagabhushanam 1959; Reeve *et al.* 1978; Kremer 1979; Schulze-Röbbecke 1984; Kasuya *et al.* 1994; Costello & Coverdale 1998). For example, *Bolinopsis vitrea* (Agassiz, 1860), which is similar to the Spencer Gulf *Bolinopsis* morphologically, was demonstrated by Kremer *et al.* (1986) to be a more efficient predator than *Mueniopsis*. Similarly, according to Mills (2001: 65), 'Uye & Kasuya (1999) suggest that numbers of indigenous ctenophores, especially *Bolinopsis mikado* (Moser, 1907), may be rising in some Japanese coastal waters; this situation bears following in coming years.' We assert, therefore, that *Bolinopsis* in Spencer Gulf could pose a similar ecological threat to that of *Mueniopsis* in the Black Sea.

*Bolinopsis ashleyi* sp. nov.

(Fig. 3C–D)

**Material examined.** HOLOTYPE: SAM-XH450, approx. 10 cm total live length, 1 km off Mooloolaba, Qld, coll. P. Petersen, M. Callaghan, and M. Rego, October, 1999. Preserved in 100% ethanol.

**Non-type material.** Video and photographs of several additional specimens (kept in the South Australian and Queensland Museums).

**Diagnosis.** *Bolinopsis* with large, hemispherical lobes; brilliant red pigmentation along most of the length of the ctene rows.

**Description.** Total length of specimens known to approximately 12 cm, slightly compressed in the tentacular plane. Aboral end of the body bluntly rounded, with mesogleal extensions slightly protruding past the aboral cleft. Lobes very broadly rounded, spanning approx. 4–5 times the body width in the sagittal plane.

Auricles narrow, ribbon-like, tapered distally, approximately 1/2 body length, reaching well beyond the mouth.

Ctene rows 8, wide, all with densely-packed comb plates. The four subtentacular comb rows, with about 60 comb plates, extend the entire distance from the apical pole to immediately short of the auricles; the four subsagittal rows, with well over 100 comb plates, almost touch where they begin slightly inward of the apical pole, and extend nearly to edges of the lobes, flaring a short distance along the path of the meridional canals before termination.



At approximately 4/5 of the distance to the outer edge of the lobe, the meridional canal continues from the distal end of each subsagittal ctene row, departs laterally, makes a broad wavy crescent following the contour of the lobe toward the central axis of the animal, then very near to the base of the lobe the canal loops back upon itself to the inside, once again following the contour of the lobe in a smaller, somewhat wavy crescent, back to the axis of the ctene row, then dips inward toward the mouth, then abruptly changes direction to unite with its mirror image in a finger-like, distal-pointing projection at the midline between the two ctene rows. The circumferential canal is not wavy, and closely mirrors the contour of the outer edge of the lobe along nearly its entire distance.

Statocyst situated within deep aboral cleft.

Stomodaeum reverse hourglass-shaped, widest immediately oral to the midpoint, tapered both aborally and orally, though wider in the oral half than the aboral half.

Body colourless and transparent, except for a brilliant red band of pigment beneath the distal 2/3 of the 4 subsagittal comb rows and out along most of the outer crescent of the lobe canals. This same colour-pattern and vibrancy has been observed in approximately 40 specimens of all sizes from 3 to 12 cm.

Type locality. About 1 km offshore, Mooloolaba, Sunshine Coast, Queensland.

**Etymology.** Named in honour of Ashley Scivyer, formerly of Underwater World on the Sunshine Coast. Ashley and his wife, Puk Petersen, have been extremely dedicated in discovering the medusa and ctenophore biodiversity of Queensland and other tropical regions of the world.

**Distribution.** Presently known from Mooloolaba, south to Moreton Bay. The material mentioned was all caught within 2 m of the surface, between October 1999 and about March 2000.

**Bioluminescence.** Could not be elicited with tapping on the tank, but direct stimulation was not attempted.

**Ecological notes.** Not observed during times of heavy salp blooms. Several specimens were captured with small (1–1.5 cm long) fish in the gut. In captivity they were fed a maintenance

diet of small fish, adult and newly hatched *Artemia*, and unidentified mysid shrimp. They were also offered dead fish, but did not take them. They survived approximately three months in captivity. Puk Petersen observed, 'We saw a definite reaction to light; as soon as we took the covers off for feeding they would locomote towards the surface. When feeding, the flaps would open wide like a feeding whale shark, we would gently touch them on the inside of the oral lobe with the fish and they would instantly close and grab it, the fish was immobilised very quickly. At 18° it took a 10 cm animal about 2 hours to digest a 1 cm fish (approximately) .... I don't think they intently hunted for a particular item of food as much as hunting in general with the oral lobes wider open than when they weren't feeding.'

**Field identification.** Like other *Bolinopsis* (see earlier), but with massive lobes, and red pigmentation along the ctene rows.

**Remarks.** Although we have designated a holotype, as mandated by Article 72.3 of the I.C.Z.N. (1999), we must acknowledge that this specimen will of limited use for morphologically discriminating this new species. Unfortunately it is impossible to adequately preserve many types of ctenophore, including *Bolinopsis ashleyi*. Others have also attempted to deal with this problem including: Harbison & Miller (1986), who deposited specimens of which only gonads and comb row fragments remained; Robillard & Dayton (1972), who embedded their specimens in wax; and Matsumoto & Robison (1992), who preserved their specimens in 4% buffered gluteraldehyde. However, scattered ctenes and wax-embedded specimens are unsuitable for study, and gluteraldehyde is problematical and only a temporary solution; ultimately, these species are based on photographic evidence. While no method has so far been found to preserve these delicate taxa, in fact, Matsumoto & Robison (1992: 20), have stated that morphological information obtained from *in situ* observations, photographs and video, 'Often ... is far superior to that which can be inferred from preserved material.'

The necessity of having a deposited holotype specimen for a new species has also been recently questioned by Donegan (2008); and



Table 5. Comparison of diagnostic characters of species in the genus *Bofinopsis*. Data derived from original descriptions plus Bigelow (1912), Mayer (1912) and Wrobel & Mills (1998).

	Lobe size	Body size	Comb rows	Sense organ	Colour	Other chars	Locality
<i>B. alata</i> (L. Agassiz, 1850)	Large, round	Not stated	SV about twice as long as ST; SV to level of the mouth (i.e., barely extending onto lobes)	Moderately sunken	Colourless	Complex lobe canals; ctenes heavy	New England
<i>B. chuni</i> (von Lendenfeld, 1885a)	Very large, nearly circular	11cm	Ctene rows extending halfway onto lobes; comb plates numerous	Embedded 1 cm	Transparent with violet lobe vessels	Lobe vessels simple; stomach broad	Sydney, NSW
<i>B. elegans</i> (Mertens, 1833)	Huge	Not described	SS nearly to apex of canal on lobes	Shallow	Body uniformly rose-coloured	Body covered with tubercles	South Sea
<i>B. hydatina</i> (Chun, 1880)	Large, round	2.5–4 cm long	Barely extending onto lobes, to level of mouth	Deeply sunken	Not described	Lobe vessels not complex	Naples, Italy
<i>B. indosinensis</i> Dawydoff, 1946	Small, short, about 1/3 body length	15–22 mm	SS only to base of lobes; 16–18 plates on ST, 20–22 plates on SS	Moderately embedded	Colourless and transparent	Large, broad auricles	Indochina
<i>B. infundibulum</i> (O.F. Müller, 1776)	Medium sized	15 cm	Comb rows extending less than halfway onto lobes	Very deeply sunken	Row of dark spots on lobes	Short, flat auricles	Greenland
<i>B. littoralis</i> (McCrady, 1859b)	Small, not expanded	Up to 50 mm	Not described	Not described	Not described	Not described	Charleston, South Carolina
<i>B. microptera</i> (A. Agassiz, 1865)	Short	50 mm length	Not described or figured	Not described	Transparent and colourless	Complicated windings of canals	Eastern coast of North America
<i>B. wikado</i> (Moser, 1907)	Medium size	Not described	Subventral very long, nearly to margin of lobes	Deeply sunken (1/5 as deep as the whole body)	Body transparent; canals rosy in life	Commonest ctenophore in the region	Japan
<i>B. norvegica</i> (Sars, 1835)	Huge, round	–	Subventral not extending onto lobes	Very deeply sunken	–	–	Norway
<i>B. ovalis</i> (Bigelow, 1904)	Small	50 mm length; half as wide	Sparsely arranged comb plates (15–18 on short rows; 30–35 on long rows)	In deep cleft; with radiating muscle fibers	Colourless	Auricles similar in shape to <i>B. vitrea</i> ; canals not complicated	Maldives

Table 5 (continued) ...

	Lobe size	Body size	Comb rows	Sense organ	Colour	Other chars	Locality
<i>B. paragastr</i> Ralph & Kaberry, 1950	Large (3/5 total length)	Up to 50 mm	Subventral slightly longer than subtentacular; subventral do not extend beyond mouth	Moderately sunken	Canals red; deep red-brown pigmented stomach	Branched paragastric canals join meridional canals; double tentacle bases	New Zealand
<i>B. rubripuncta</i> Tokioaka, 1964	Moderate	50 mm	50-60 on short rows; 120 on long rows	In deep cleft	4-6 reddish- orange spots along periphery of each lobe; canals reddish	Auricles wide	Seto, Japan
<i>B. septentrionalis</i> (Mertens, 1833)	Very short	Not described	Ctenes rows not extending onto lobes; comb plates distantly spaced	Shallow	Light blue-coloured	Lobe vessels straight	Bering Strait
<i>B. vitrea</i> (L. Agassiz, 1860)	Small, short	Narrow; length not stated	Subventral about 2x as long as subtentacular; more than halfway onto lobes	Deeply sunken	Remarkable in its transparency	Combs very small and fine, barely visible	Key West, Florida
<i>B. ashleyi</i> sp. nov.	Huge, round, about as broad as body is long	To 120 mm	Subventral extending nearly to edge of lobes, c. 2x subtentacular	Very deeply sunken	Crimson pigment marking the main canals	Thick comb rows	Southern Qld
<i>B. sp. 1</i>	Width equal to half body length or slightly less	To 70 mm	Subventral extending nearly to edge of lobes, c. 1.5x as long as subtentacular	Deeply sunken	Magenta canals	Elongate egg-shaped, extremely common	Southern Australia
<i>B. sp. 2</i>	Width narrow, but more than half total body length	To 70 mm	Subventral extending nearly to edge of lobes, c. 2x subtentacular	Deeply sunken	Completely colourless	Nearly perfectly egg-shaped; extremely common	Tropical Qld
<i>B. sp. 3</i>	Lacking	To 20 mm	(not noted)	Deeply sunken	Transparent and colourless body with two granular red dots along each side of body	Uncommon; generally found with dense gelatinous zooplankton bloom	Cairns region

while his argument against this process was primarily based on ethical and conservation issues, he also emphasised that superior information to assist identification can frequently be secured from non-corpse material. Our description of *Bolinopsis ashleyi* sp. nov. is thus primarily based on the excellent photographs that clearly illustrate the morphology of this species. If a suitable method of preservation is developed, designation of a neotype of *B. ashleyi* (as well as its congeners!) would probably be desirable.

The most striking feature of *Bolinopsis ashleyi* is its brilliant colouration. While colour is often regarded as of little taxonomic value because it cannot be studied in preserved specimens, many previous ctenophore workers have also used colouration (Mayer 1912; Bigelow 1912; Tokioka 1964; Harbison & Miller 1986; Mills 1987; Matsumoto 1988; Matsumoto & Gowlett-Holmes 1996; Matsumoto 1999). In the case of ctenophores, which often cannot be preserved at all, colour remains an invaluable tool to be used in combination with other characters.

*Bolinopsis ashleyi* differs from its congeners by the following (see also Table 5). Its broad, nearly hemispherical lobes, separate it from the narrow lobed species: *Bolinopsis microptera* (Agassiz, 1865), is more elongated, has very short lateral lobes, has complexly winding canals, and is transparent and colourless; *Bolinopsis indosinensis* Dawydoff, 1946, has small, short lobes and large, broad auricles; and *Bolinopsis ovalis* (Bigelow, 1904), has sparsely-arranged comb plates and is colourless.

Of the species with large lobes, *Bolinopsis ashleyi* can be distinguished by the following. *Bolinopsis rubripunctata* Tokioka, 1964, is about half the size, and has numerous conspicuous reddish orange spots along the periphery of the lobes. *Bolinopsis infundibulum* (Müller, 1776), has much shorter subsagittal comb rows, and rows of dark spots on the lobes, but lacks any trace of the brilliant red colouration of *B. ashleyi*. *Bolinopsis chuni* (von Lendenfeld, 1885a), has much shorter and less-dense subsagittal comb rows that are violet in the adult. *Bolinopsis elegans* (Mertens, 1833), is covered with tubercles. *Bolinopsis paragaster* Ralph & Kaberry, 1950, has bifurcated paragastric canals and double tentacle bases. Finally, *Bolinopsis alata* (Agassiz,

1850), has short comb rows that barely extend onto the lobes, and also a more complex form of lobe canals (see Agassiz, 1860: figs 88, 89).

Several other species are said to contain red pigment. First, Mayer (1912) stated that *Bolinopsis vitrea* sometimes displays intense pink colour in the peripheral parts of the chymiferous tubes, probably due to products of digestion or excretion. This is unlike *B. ashleyi*, in which the pigment granules are epithelial, not digestive. Second, like *B. ashleyi*, *B. paragaster* has red canals, but it also has a deep red-brown pigmented stomach, bifurcated paragastric canals, and double tentacle bases. Third, *B. mikado* (Moser, 1907) is said to be 'transparent and almost colourless; only the canals are rosy when living' (Komai, 1918: 455); however, there is another form of *Bolinopsis* in southern Australian waters which has rosy canals, but would not be easily mistaken for *B. ashleyi*, in which the red pigment might be more accurately likened to 'racing stripes'.

#### Family Leucotheidae Krumbach, 1925

##### *Leucothea* Mertens, 1833

##### *Leucothea filnersankeyi* sp. nov.

(Fig. 4A–D)

*Leucothea* sp. – Gershwin & Zeidler, 2003: 238 (Tas, SA).

**Material examined.** HOLOTYPE: QVM-20:4196, Stanley Jetty, Stanley, Tasmania [40°46'02.4"S, 145°18'19.1"E], 8.03.2009, at surface in 1 m of water, observed for 3 days in captivity then preserved in EtOH; 10 cm TL live. PARATYPE: QVM-20:4197, same coll. data as holotype; 13 cm TL live.

**Non-type material.** TAS: Same coll. data as holotype; 2 specs, 8–10 cm TL, observed in captivity for 2 days before spontaneous disintegration occurred. Same coll. data as holotype; 7 specs, 7–10 cm TL, observed in the field and released. Stanley Jetty, 3.09.2002 (GZ0210); one spec. torn beyond specific recognition, appeared to be approximately 15 cm TL; some tissue retained in 100% ethanol [SAM-XH445], some in liquid nitrogen [SAM-ABTC101331]. SA (probably identical): North Point, St Francis I. [32°29'33.9"S, 133°16'59.6"E], S. Murray-Jones, 23.02.2002 (GZ0549); fragmentary specimen in alcohol [SAM-XH449] and liquid nitrogen. Fenelon I., Nuyts Archipelago [32°34.474'S, 133°17.550'E], L. Gershwin, 25.02.2002 (GZ0559); 1 spec., about 15 cm TL, examined in the laboratory until disintegration. Several specs were observed at Masillon I. [32°33.581'S, 133°17.041'E], L. Gershwin, 25.02.2002.



**Diagnosis.** *Leucothea* with body to about 15 cm in length; with long, narrow, blind tentacular pits; with long, slender papillae; with ctene rows about 3/4 length of lobes, broad; with bimorphic diverticula beneath ctene rows; with pale orange tint to core of body, lacking other colouration.

**Description from living specimens.** Body highly compressed in the tentacular plane, flat along both broad sides; approximately 5 times as wide in the stomodaeal plane. Aboral end of body deeply cavernous, with statocyst further deeply embedded (Fig. 4A). Mouth small, inconspicuous, midway along narrow blade-like oral edge of body, concealed by lobes. Oral tentacles not observed. Tentacles 2, each located midway across each broad side, near mouth on oral edge of body, emitting from tentacular canals. Tentacular canals very long and narrow, about 1.5 mm wide, about 24 mm long, aboral-pointing portion about 3 times as long as oral-pointing portion, blind-ending in both directions; oral canal portion contains a linear internal structure of unknown function.

Lobes 2, relatively small compared to other species, comprising about half the total length (TL) of the ctenophore (Fig. 4A), attached to body such that approximately 1/2 of body and 3/4 of lobes overlap; with a broad figure-8 outline in normal posture, i.e., when lobes are curled in. When extended for feeding, lobes are broadly rounded in outline, about half as broad as the body is long, with a deeply incised midline notch along distal edge, appearing heart-shaped (Fig. 4B).

Auricles 4, attached to body somewhat oral to point of lobe attachment; long, slender, cylindrical, gradually tapered; held tightly coiled in a helical fashion most of the time (Fig. 4A), or, when relaxed and extended, movement by the animal causes ends of auricles to wave constantly, as if acting as lures.

Ctene rows 8, broad, arranged as follows: 4 substomodaeal ctene rows (SSCR) emanate from aboral end of body, extending to about 3/4 length of lobes, at point of divergence of meridional canals toward lobe margin; 4 subtentacular ctene rows (STCR) emanate from indented aboral end of body, extending somewhat beyond origin of auricles.

Tubercles prominent, numerous; most densely arranged and longest on aboral end and along long body corners, sparsely arranged and shorter on outer surfaces of lobes; slender, cylindrical, tapered, many reaching nearly 1 cm in length, about 1 mm diameter.

Canals: Infundibular canal short, elongated hourglass-shaped (Fig. 4D). Meridional canals straight, heavily diverticulated under comb rows, ovaries on opposite sides of adjacent canals. Diverticula bimorphic: those underlying subtentacular comb rows often alternate wide and narrow; those underlying substomodaeal rows typically of equally broad width. Beyond oral termination of substomodaeal comb rows, canals diverge at approximately 45° angles, extending in straight line nearly to distal edge of lobes (Fig. 4B). Lobe canals winding circuitously, forming large loops and smaller complex patterns (Fig. 4C), with left and right not necessarily in mirror image.

Colouration: pale orange in long spindle-shaped region of body core; lobes and auricles transparent ghostly whitish; tubercles mostly transparent and colourless.

**Etymology.** Named to honour Mr Patrick Filmer-Sankey, then Director of the Queen Victoria Museum and Art Gallery in Launceston, Tasmania, where the types are lodged. Patrick's enthusiastic approach to science and gentlemanly approach to life have been of great inspiration to the senior author.

**Field identification.** Body covered in narrow, gelatinous, retractable, flexible tubercles. Body shape very compressed in the tentacular plane, considerably longer than wide, with small lobes always held curled; forward margin of lobes with deep indentation. Colouration: pale orange body core, with transparent and colourless tubercles; auricles and lobes whitish. Size range: 6–15 cm long, with most specimens observed about 8–9 cm long.

**Distribution.** *Leucothea filmersankeyi* has only been confirmed hitherto from Stanley, in the far north-west of Tasmania, along Bass Strait. Samples from Nuyts Archipelago, SA, are also probably of this species, but more material is needed for positive identification.

**Behaviour.** Very active in captivity, spending most of its time just under the surface of the

water, hanging in a lobes-up orientation, frequently sinking to the bottom of the tank then bouncing back to the surface. On contact with the air-water interface, the lobes spread out somewhat, with no ripple whatsoever on the surface tension. Sometimes the animal begins to spin on its axis, which it may persist in doing for several minutes without ascending or descending from its position.

The animal is very responsive to mechanical stimulation. When touched gently on any side, it will recoil and immediately move away from the direction of stimulation. When a single tubercle is touched with a plastic probe, all neighbouring tubercles within about a 1.5 cm radius shoot out immediately in the direction of the probe, and stay extended for several seconds. The tubercles in a given area do not respond to continued stimulation, but will respond again if stimulated after another region.

Although no light-sensory apparatus was detected, it does respond to sudden illumination by immediately recoiling the body.

Bioluminescence was tested at night with a simple probe. Small flashes of blue light were emitted when stimulated along the canals; when stimulated near the base, all canals flashed simultaneously.

**Remarks.** *Leucothea filmersankeyi* differs from its congeners as summarised in Table 6. Structurally, *L. filmersankeyi* appears to be unique in having narrow, blind tentacular pits; the only other species for which the tentacular pits are well characterised is *L. pulchra*, in which they are broad. The gonadal regions of the meridional canals are bimorphic in *L. filmersankeyi*, whereas this pattern is undescribed for other species. Furthermore, the papillae are relatively narrower and longer than those figured for other species. For most species, the comb rows are described either as extending only halfway onto the lobes, or as 'very long'; in this respect,

*L. filmersankeyi* seems most similar to *L. japonica*, in that the comb rows extend about 3/4 the distance toward the margin of the lobes. However, *L. filmersankeyi* has no trace of red colouration, and does not squirt ink when poked, so it would be unlikely to be confused for *L. japonica*, which does.

In colouration, *L. filmersankeyi* is quite readily separated from all others, and its size separates it from many. Unfortunately, most structural features are not well described for the existing species of *Leucothea*, such that it is very difficult to compare across a range of features. However, logically, conspicuous differences in colouration may be indicative of other differences, which simply cannot be assessed at this time. For example, the striking colour pattern of *L. pulchra* has no counterpart in any other species; the spotted markings in *L. ochracea* and *L. tiedemannii*, while different from each other, are nonetheless not echoed in others; and finally, while most *Leucothea* species are yellowish, the presence of red pigment in *L. japonica* may be interpreted as a key difference.

We wonder about the relationship between *L. filmersankeyi* and a curious form from Little Waterfall Bay in southeastern Tasmania, further discussed in the next section. Both share the interesting characters of an elongate, narrow and largely colourless body, and tightly-held lobes. However, upon closer examination, the two have many differences. For example, the lobes of *L. filmersankeyi* comprise about half the total length of the ctenophore, whereas those of the southern form are nearly 2/3 the total length (compare this with the lobate family Bolinopsidae, in which a similar difference is used to separate the genera *Bolinopsis* and *Mnemiopsis*). In addition, the two Tasmanian forms of *Leucothea* have about the same density of tubercles, and they are quite slender in both forms, but the tubercles are

FIG. 4. A–D, *Leucothea filmersankeyi* sp. nov., holotype. A. Habitus, tentacular view. B. Stomodaeal view; note broad heart-shape lobes. C. Detail of lobe canal pattern. D. Detail of sense organ and infundibular canal. E, *Velamen* sp. (Tasmania), in life. Oral end orientated toward right. F–H, *Beroidea*, all specimens orientated with oral end 'up'. F, *Beroe* sp. A (North Queensland); completely transparent and colourless, in life. G, *Beroe* sp. B (North Queensland), with broad ctene rows and red pigmentation, in life. H, *Beroe* sp. C (Tasmania), with a pronounced neck lacking ctene rows, preserved. I, *Neis cordigera* (South Australia), in life. Photograph A by Karen Gowlett-Holmes; used with permission. Photograph E by Thierry Laperousaz (South Australian Museum); used with permission.



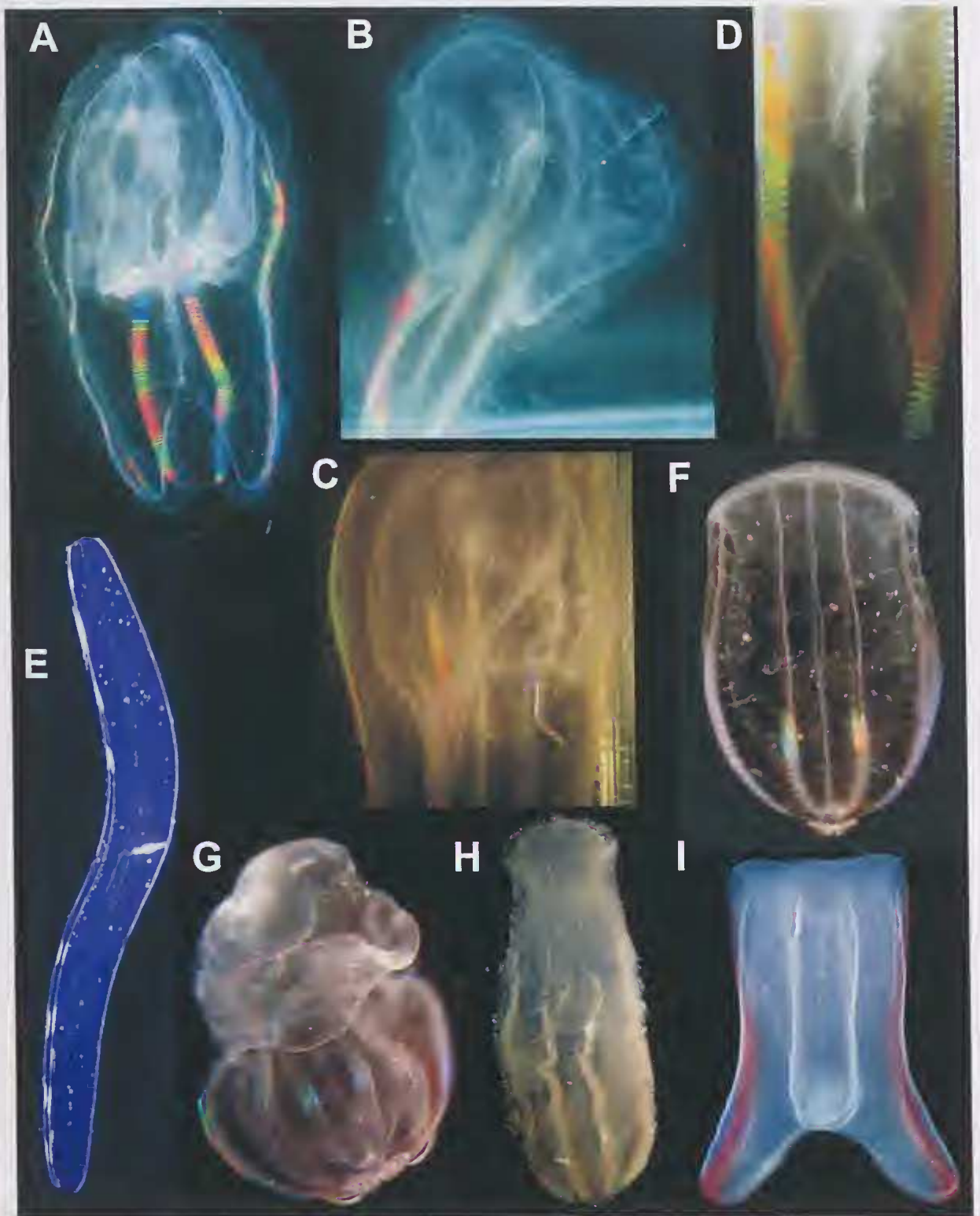




Table 6. Comparison of diagnostic characters of the species of *Leucolitea*. Data derived from original descriptions, plus Chun (1880). Abbreviations: Substomodaeal (SS), Subtentacular (ST), Comb row (CR).

	Body size	Comb rows	Body colour	Other colour	Other notes	Locality
<i>L. multicornis</i> (Quoy & Gaimard, 1824) (largely based on Chun 1880)	20 cm	Long	Dull brownish, with brown tint on the lobe edges	N/A	N/A	Mediterranean
<i>L. grandiformis</i> Agassiz & Mayer, 1899	13.5 cm length	Very long, SSCR's nearly to the edge of lobes. No described or illustrated diverticula	Hyaline	Comb plates, stomach, and canals are cinnamon- yellow	Canals far less complex than <i>L. multicornis</i>	Suva Harbour, Fiji
<i>L. japonica</i> Komai, 1918	To 12 cm body length	Said to be short. SSCR's to about 2/3 distance on lobes. In 80 mm spec, 75 SS combs, and 110 ST combs	Faintly brick red	Canals deeper red; lappets amber-yellow	Squirts ink when poked!	Misaki, Japan
<i>L. ochracea</i> Mayer, 1912	9.6 cm	SSCR's to about 1/2 distance on lobes	Transparent with 4 opaque yellow spots on edges of lobes	Not described	Lateral filaments on principal tentacles	Tortugas, Florida, USA
<i>L. pulchra</i> Matsumoto, 1988	To 26 cm	Said to be long; SSCR's end about 1/2 way out onto the lobes	Translucent white; distinctive orange papillae	Lacking gut colouration	Broad pits	California, USA
<i>L. tiedemannii</i> Eschscholtz, 1829	18 cm	Very densely packed; rows very long	Surface sallow, brown	A dark point at each ctene	N/A	Sea east of Japan
<i>L. filicarsaukeyi</i> sp. nov.	15 cm	Ctene rows 3/4 length of lobes; broad; diverticula bimorphic	Pale orange tinted	None	Narrow blind pits; long, slender papillae	NW Tas, SA
<i>L. sp. 1</i>	9 cm	Ctene rows wide, long	Transparent yellowish	Pale orange gut	Large papillae	SE Qld
<i>L. sp. 2</i>	30–45 cm	Prominent diverticula	Transparent, colourless	Yellow-green gut	Large papillae	SE Tas
<i>L. sp. 3</i>	12 cm	Ctene rows narrow, long	Transparent, colourless	None	Short, slender papillae; long lobes	SE Tas

quite short in the southern form, and much longer in the northern *L. filuwersankeyi*. The exact relationship between the two forms remains unclear at this point, but it seems plausible that they represent different species. It also highlights the need for existing species to be re-examined across a range of structural characters, so that they can be properly compared.

#### *Leucothea* species

(Fig. 3G–H)

Other species of *Leucothea* that have been previously reported from Australia:

*Leucothea* spp. — Harbison & Miller, 1986: fig. 4 (Coral Sea); Edgar, 1997: 149 (Vic, NSW, Tas.); Edgar, 2000: 149 (Vic, NSW, Tas.).

**Material examined** [from photographs]. Qld: SAM-XH444, Pumicestone Passage, Moreton Bay, ethanol-preserved tissues from specimen in Fig. 3H, P. Petersen, Sept. 2000; about 9 cm TL. TAS: Little Waterfall Bay, Tasman Peninsula, K. Gowlett-Holmes, 2.03.1998; about 12 cm TL. Dog Leg Cave, Waterfall Bay, M. Baron, 18.11.1998; 30–45 cm TL.

**Field identification.** Body covered in gelatinous, retractable, movable tubercles; body usually longer than wide, with large or small lobes. Colourless and transparent, or yellowy, orangy, or greenish; medium-sized or massive.

**Distribution.** *Leucothea* was reported from Victoria to New South Wales, including Tasmania by Edgar (1997, 2000). We have also found *Leucothea* species of uncertain identity in South Australia (Gershwin & Zeidler 2003) and Queensland (unpublished data).

**Remarks.** *Leucothea* urgently needs revision. A good (though brief) summary of species was given by Matsumoto (1988), who recognised six species (Table 6). In Australian waters, it seems that several additional species may be present, based on our limited observations of specimens collected or photographed. However, any formal descriptions beyond those herein will require additional specimens with better photographs and/or preservation techniques.

Notes on the Australian forms are as follows. A specimen photographed by Karen Gowlett-Holmes on 2.03.1998 at Little Waterfall Bay on the Tasman Peninsula is about 12 cm long, and is characterised by having a very elongate, totally transparent and colourless body, with

short, slender papillae; the lobes comprise much more than half the total length (Fig. 3G). No specimens were captured.

A second form, comparable to *L. multicornis* (Quoy & Gaimard, 1824), was caught by Puk Petersen in Moreton Bay in September 2000 (Fig. 3H). Unfortunately, specimens could not be preserved intact. From the photographs, and from first-hand accounts, it can be described as: body length c. 9 cm, with prominent gelatinous extensions at the aboral corners; extensively covered by large papillae (c. 5 mm tall); ctene rows wide, running the entire length of the animal; colouration transparent yellowish with pale orange gut. The auricles were thick, cylindrical, tapered and long, most often held coiled in a conical form, but occasionally unreeling into long, writhing, tentacle-like appendages. These characters are similar to *L. multicornis*, described from the Mediterranean by Quoy & Gaimard (1824) and Chun (1880). However, given the different biogeographic provinces it is unlikely that these two populations will be conspecific. In colouration, the Moreton Bay form is different from *L. grandiformis* (Agassiz & Mayer, 1899), which is cinnamon-yellow on the ctene rows, canals, and gastric cavity; from *L. ochracea* Mayer (1912), which has lateral filaments on the tentacles in the adult stage, and also has conspicuous opaque yellow areas on the sides of the oral lobes; from *L. japonica* Komai (1918), which has a faintly brick-red body, deeper red canals, and yellow-edged lobes; and from *L. pulchra* Matsumoto (1988), which has a very large body with large lobes, and the body is opaque whitish with prominent orange papillae.

A third large Australian form was videod by Mick Baron at Dog Leg Cave, Waterfall Bay, Tasmania on 18.11.1998. While no specimens were retained, they were 30–45 cm long, with large papillae, a yellow-green gut, and prominent diverticula beneath the ctene rows.

Family Ocyropsidae Harbison & Miller, 1986

#### *Ocyropsis* Mayer, 1912

##### *Ocyropsis* species

(Fig. 3E–F)

The following *Ocyropsis* species have been previously reported from Australia:



*Ocyropsis maculata immaculata* Harbison & Miller, 1986: 413–424 (Heron I., Qld).

*Ocyropsis maculata maculata* Harbison & Miller, 1986: 413–424 (Heron I., Qld).

*Ocyropsis crystallina crystallina* Harbison & Miller, 1986: 413–424 (Heron I., Qld).

**Material examined (mostly unpreservable).** Qld: Palm Cove, 29.12.1999, during rich bloom of gelatinous zooplankton; many specs, c. 5 mm across, lacking spots, with shallowly indented stomach, with ctene rows starting beyond polar plates. Palm Cove, 24.01.2000; 2 cm across. Palm Cove, 19.02.2000; in thick jelly bloom. Palm Cove, 22.02.2000; 3 small specs in rich zooplankton bloom. Cairns Harbour, 25.12.2005, during rich jelly bloom (Fig. 3F). NT: Stokes Hill Wharf, Darwin Harbour, 6.08.1998; 1 stout spec. 19°13.021S, 121°15.399E, off Eighty Mile Beach, 16.04.2004; numerous c. 1 cm, some with spots, some without. WA: SAM-XH428 (= GZ0055), Port of Dampier, NW side of King Bay, 30.11.2000; 2 specs with 2 black spots on top end of each lobe above gonad; 1 in EtOH, 1 in liquid nitrogen.

**Field identification.** Body resembling the general shape of two hands held together in prayer, i.e., two large lobes connected at the bottom. The lobes are massive, and used for clapping together for rapid escape. Generally transparent and colourless, may also have two large diffuse brown spots, or two small black spots on each lobe. Most specimens are small, but may reach up to about 8 cm across.

**Distribution.** In Australia, the species *O. maculata immaculata*, *O. maculata maculata*, and *O. crystallina crystallina* were reported at Heron I., Qld, by Harbison & Miller (1986).

*Ocyropsis* of uncertain affinity were also found at Palm Cove, Qld, in the summer of 1999–2000. Found in abundance, the largest specimen was never more than about 1 cm. They were active swimmers, and readily luminesced at night when gently stimulated. Despite great effort, specimens were impossible to preserve.

**Remarks.** Like most other ctenophores, *Ocyropsis* are difficult to preserve. The genus needs formal revision, but we tentatively recognise eight species (Table 7), including *O. vance* sp. nov.

In addition to the new species, there seems to be at least three other species/forms of *Ocyropsis* in Australian waters: 1) a small, transparent form with a shallowly indented stomach and no spots (? = *O. crystallina*; Fig. 3F); 2) *Ocyropsis maculata* with large diffuse brown

spots and a deeply-indented stomach as reported by Harbison & Miller (1986) from Heron I., and 3) a small form from tropical North Queensland with a deeply-indented stomach and two small black spots near the margin of each lobe.

The last form is of interest, because it does not seem to match any known species. In colouration, it is most similar to *O. crystallina guttata*, described by Harbison & Miller (1986) with small brown to black spots closely associated with the substomodaeal meridional canals, located at the ends of the gonads where the substomodaeal meridional canals make a sharp bend to begin their windings on the oral lobes. However, in this last form, there are exactly two small black spots very near the margin. We have seen this form from time to time, but it is unpreservable and short-lived.

### *Ocyropsis vance* sp. nov.

(Fig. 3E)

**Material Examined.** HOLOTYPE: SAM-H935 (PH0322), Waterfall Bay, Tasman Peninsula, Tasmania, drifting in 2–4 m, K.L. Gowlett-Holmes, 28.03.1999.

**Diagnosis.** Hermaphroditic *Ocyropsis* lacking tentacular bulbs or canals, pigment spots, and warts; with 26–27 ctenes per subtentacular row, 53–54 ctenes per substomodaeal row; with deeply indented hourglass-shaped stomodaeum; with long substomodaeal ctene rows, originating well before polar plates and extending to the level of the stomodaeal indentation; with gonads in diverticula on both sides of the meridional canals, ovaries facing one another, with testes projecting in opposite direction.

**Description.** Body 29.8 mm (aboral pole to mouth); 47.7 mm total length preserved (aboral pole to lobe tip), lacking warts or pigmentation. Tentacular canals and bulbs absent.

Lobes large, glove-like around mouth in preserved specimen; 41.3 mm long. Lobe musculature densely crowded, in distinct pattern of approx. every second longitudinal fibre heavier than those between; cross-fibres minute.

Auricles 15.0 mm long, nearly reaching level of mouth distally; long narrow triangles with straight edges.

Subtentacular ctene rows proximally joining at centerpoint of aboral 'edge' of body; distal terminus at level of lobe origination; with 26–27

ctenes, arched obliquely over raised row. Substomodaeal ctene rows parallel along aboral side; proximally well beyond polar plates but not adjoining; distal terminus approximately half again longer than subtentacular rows; with 53–54 ctenes, mostly perpendicular over raised rows.

Stomodaeum 26.3 mm long, deeply indented hourglass-shaped, 13.3 mm wide at mouth, 13.5 mm at widest part of base, 3.1 mm wide at constriction; mouth approx. 2/3 distance to tips of lobes.

Canals underlying ctene plates diverticulated, but appear to lack gonadal material. Lobe canals complexly looped. Paragastric canals fine, narrow, long.

Gonads in diverticula on both sides of the substomodaeal meridional canals, apparently confined to lobe regions distal to ctene terminus; diverticulations alternate and opposite, with ovaries in diverticula facing adjacent canals, testes facing away; pattern irregular, with those toward outer edge of lobe simple and short, approximately 1/3 to 1/2 as long as those toward center axis of lobe, which are somewhat branched.

Statocyst in shallow aboral cavity about half depth to level of subtentacular rows; polar plates each 9.6 mm long, very narrow.

Colour in life: transparent and colourless.

**Etymology.** The specific name '*vance*' is derived from a Category 5 cyclone that destroyed the town of Exmouth in Western Australia in the autumn of 1999 (while the senior author happened to be visiting). After wiping out Exmouth, the cyclone then went on to travel southward across Western Australia, emerging in the Southern Ocean, and never losing cyclone-rating the whole journey over nearly 1,000 km of land. Upon reaching the Southern Ocean, it regathered its strength and moved east towards South Australia and Victoria. Like Cyclone Vance, *Ocyropsis vance* seems nearly indestructible. Noun in apposition.

**Remarks.** *Ocyropsis vance* is most similar in overall appearance to *O. maculata immaculata* Harbison & Miller, 1986, in having a deeply indented, hourglass-shaped stomodaeum, gonads on both sides of the meridional canals and the comb rows originating well before the end of

the polar plates, and in lacking spots; however, *O. vance* lacks tentacular canals and bulbs, as in *O. crystallina*. Primary characters of the species of *Ocyropsis* are summarised in Table 7.

Mayer (1900) described 'wart-like protuberances upon the surface of the ctenophore' for *O. crystallina* (legend, pl. 31), but in fig. 105 (pl. 31) these appear to be the internal gonads. Fewkes (1882) described *Ocyropsis* from the Tortugas two decades earlier, but did not note surface warts. Harbison & Miller (1986, fig. 1b, p. 415) also show what might be mistaken for protruding gonads in their *O. maculata immaculata*, but these appear to be encased within a nearly-invisible envelope. If Mayer's Tortugas form does indeed have surface warts, this would separate it readily from the Australian *O. vance*.

Despite *Ocyropsis* being notoriously difficult to preserve, the holotype is in excellent condition (preserved without special effort in 10% formalin/propylene glycol in seawater); whether there is any structural or physiological feature behind this should be investigated further. *Ocyropsis vance* is a cold-temperate species whereas all other ocyropsids inhabit warm, tropical waters.

ORDER CESTIDA Gegenbaur, 1856

Family Cestidae Gegenbaur, 1856

*Velamen* Krumbach, 1925

*Velamen* species

(Fig. 4E)

Only one *Velamen* species has been previously reported from Australia:

*Velamen parallelum* (Fol, 1869) — Gowlett-Holmes, 2008: 54 (Australia-wide).

**Material examined.** Qld: Palm Cove, Cairns District, L. Gershwin, summer of 1999–2000; several specs, c. 1 cm BL, caught during routine plankton tows, in cooler water believed to be of an oceanic current, with a rich diversity of other gelatinous zooplankton. Tas: SAM-XH448 (=GZ 0128), Bicheno [41° 52' 24.5" S, 148° 18' 39.2" E], W. Zeidler and L. Gershwin, 25.01.2002; 2 spec. approximately 3 mm BL, tissues preserved in EtOH. Photograph K. Gowlett-Holmes, south of The Thumbs, Tasman Peninsula, 4.03.1998, c. 14 C; c. 9 cm, no spec. retained.



Table 7. Comparison of the characters of species of *Ocyropsis*. Information collated from original descriptions, newly collected material, and Rang (1828a, 1828b).

	Body size	Tentacle bulbs	Stomodaeum	Comb rows	Other characters	Locality
<i>O. unaculata unaculata</i> (Rang, 1828a)	70 mm stomodaeal axis length	Present	Deeply indented in hourglass shape	SS extend almost to statocyst; comb plates numerous	Large diffuse yellow brown to brownish black spots on inner surface of oral lobes	N Atlantic, Amazon, Heron I.
<i>O. unaculata immaculata</i> Harbison & Miller, 1986	35 mm stomodaeal axis length	Present	Deeply indented in hourglass shape	SS extend almost to statocyst	Lacking spots	Southern Sargasso Sea, N Atlantic, Amazon, Heron I.
<i>O. cristallina cristallina</i> (Rang, 1828a)	75 mm length	Absent	Only slightly indented	SS only to ends of polar plates; comb plates sparse	Lacking spots	Equatorial; Southern Sargasso Sea, Heron I.
<i>O. cristallina guttata</i> Harbison & Miller, 1986	Not described	Absent	Only slightly indented	SS only to ends of polar plates	With small brown to black spots on oral lobes in association with meridional canals at oral ends of gonads	N Atlantic slope
<i>O. pterocessa</i> (Bigelow, 1904)	25 mm polar diameter	Not described	Large, variable in form; not normally lobed	Short, with only a few combs	Auricles short; spots absent; canals simpler than <i>O. cristallina</i>	Maldives
<i>O. bruite</i> (Rang, 1828a)	150–200 mm length	Not described	Not described	SS to end of polar plates	Body uniformly brown in colour; lobes very big transversely but not thick	Cape Verde
<i>O. lactea</i> (Rang, 1828a)	250–350 mm length	Not described	Not described	SS to end of polar plates	Big, thick lobes with 2 big dark brown spots	Antilles
<i>O. vaice</i> sp. nov.	30 mm stomodaeal axis length; ~50 mm total length	Absent	Deeply indented hourglass-shaped	SS twice as long as ST; nearly to statocyst	Transparent and colourless, lacking spots	Cold-temperate Tasmania

**Diagnosis.** Ribbon-like ctenophore, with the sides of the body drawn out to the extreme. In *Velamen*, the canals arise straight off the axial canal system toward the lobes, whereas in *Cestum*, the canals parallel the stomach for a short distance then curve sharply outward along the lobes.

**Field identification.** Body ribbon-like or belt-like, with the sides of the body drawn out to the extreme. In *Velamen*, the canals arise straight off the axial canal system toward the lobes, whereas in its close relative *Cestum*, which reaches about 1 m in length, the canals parallel the stomach for a short distance then curve sharply outward along the lobes.

**Remarks.** *Velamen parallelum* (Fol, 1869) was originally described from the Mediterranean and tropical Atlantic; it has subsequently been reported from the Indian Ocean (Harbison *et al.* 1978) and off California and the Sea of Cortez in the North Pacific (Stretch 1982). Ralph & Kaberry (1950) documented the closely related *Cestum* in cold New Zealand waters. It was recently reported in Australian waters for the first time by Gowlett-Holmes (2008).

The taxonomy of *Velamen* is in need of reassessment. Currently, most workers consider that there is only one species of *Velamen*, namely *V. parallelum*; the same has often been said for the closely related genus *Cestum*, although Harbison *et al.* (1978) thought differently. With the ctenophores of most of the world's regions poorly studied, not to mention the difficulty in their capture and preservation (Harbison *et al.* 1978), it is plausible that there may be additional species in either or both genera awaiting discovery. Specifically, we believe it is possible that there are species differences yet to be elucidated between our cold-water Tasmanian form and the warm-water Mediterranean *V. parallelum*; thus, we have not identified our form to species, in hope of stimulating further study. Thus, it seems unwise to assign these Australian forms to any particular species without closer examination and comparison with overseas material, especially since the Tasmanian specimen was much larger than those that we typically see in Australia, although still within the size-range reported for the species (see Harbison & Madin 1982).

## CLASS NUDA Chun 1879

## ORDER BEROIDA Eschscholtz, 1825

## Family Beroidae Eschscholtz, 1825

*Beroe* Browne, 1756*Beroe* species

## (Fig. 4F–H)

The following *Beroe* species have been previously reported from Australia:

*Beroe ovale* Bosc, 1802 – Quoy & Gaimard, 1824: 575 (Sydney).

*Beroe macrostomus* Péron & Lesueur, 1808 – Lesson, 1829: 105–106 (south of New Guinea).

*Beroe cucumis* Fabricius, 1780 – Stiasny, 1931: 40 (Watson Bay, Port Jackson, NSW); Edgar, 1997: 150 (southern Australia WA to NSW, including Tas.); Edgar, 2000: 150 (southern Australia WA to NSW, including Tas.).

*Beroe ovata* Bruguière, 1789 – Greenwood, 1980: 93 (Moreton Bay); Goy, 1990: 110 (Shark Bay, WA); Steene, 1990: 86 (Lizard I., GBR).

*Beroe* spp. – Péron, 1807: 105; WA. – Dakin & Colefax, 1933: 198 (NSW); Dakin & Colefax, 1940: 211 (NSW); Hamond, 1971: 27 (Moreton Bay, Qld); Zeidler & Gowlett-Holmes, 1998: 117–118 (amphipod association in Port Phillip Bay, Vic.); Gowlett-Holmes, 2008: 53 (southern Australia).

*Beroe* "n. sp." – Dakin & Colefax, 1933: 198, pl. 7, fig. 1 (NSW).

**Material examined.** Qld: SAM-H1574, Palm Cove, L. Gershwin, 23.02.2000; 2 spec., 2–3 mm, with red dots on stomach and red lines. Gershwin coll., Palm Cove, L. Gershwin, 19.12.1999; 2 spec.: 6.88 mm BL with red granules under combs; 3.53 mm BL with yellowish comb rows. Gershwin coll., Palm Cove, L. Gershwin, 29.12.1999, during rich bloom of gelatinous zooplankton; several spec., incl. one pink c. 2 cm BL; not preserved. Gershwin coll., Palm Cove, L. Gershwin, 22.01.2000; 6 spec. in rich zooplankton bloom. Gershwin coll., Buchen's Cove, L. Gershwin, 10.02.2000; 3 spec. Gershwin coll., Palm Cove, L. Gershwin, 22.02.2000; 2 spec. c. 1 cm BL, plus several 2–3 mm juvs., in rich jelly bloom. Cullen Bay Marina, Darwin Harbour, K. Gowlett-Holmes, 18.08.1998; 1 large purple spec., disintegrated prior to preservation. SA: SAM-GZ0537, Ceduna, W. Zeidler & L. Gershwin, 20.02.2002; 3 tiny spec. WA: SAM-H1284 (GZ0054), Port of Dampier, NW side of



King Bay, W. Zeidler & L. Gershwin, 30.11.2000; 1 spec. with wide flared mouth. Tas: TMAG K1726, Slopen main beach, Tasman Peninsula, L. Turner, May 1999, in very shallow water; 1 spec. TMAG K1727, same data as K1726; 6 spec. SAM-H1577, 'Sloping Main', Tasman Peninsula, J. Cossum, 29 Apr [no year stated]; 2 spec., 34.72 mm BL and 36.44 mm BL. TMAG 602/K32, Maria I. West, QVMAG, photograph by C. Reid, washed up on beach near Musselroe Bay, far NE, 8.05.2009; conspicuous red pigment under ctene rows, no specimen retained. Vic: SAM-PH0082, Portsea, Port Phillip Bay, 5.07.1993, with commensal amphipods.

**Field identification.** Body very soft and mucous, bag-like, typically flattened, with a very large open mouth at one end; usually colourless and transparent, but may be faintly coloured yellowish, purplish, or reddish, especially along the ctene rows. Body of some species may get quite large, but most specimens are about 1–6 cm long.

**Remarks.** *Beroe* is common in Australian waters. There are several easily distinguishable forms, although matching these up to existing species has proven difficult. One form from Darwin is large, about the size of a man's fist, faintly purple throughout with bright purple ctene rows, with comb rows almost to the mouth, with two oval rings of papillae near the apical organ; unfortunately, both specimens disintegrated prior to study. A second form, from tropical Queensland, always 1–2 cm or less in body length, is transparent throughout (Fig. 4F). A third, also from tropical Queensland, only about 2 cm long, has numerous bright red pigment granules around quite heavy comb rows and at the aboral end of the body, along with large, branched aboral papillae (Fig. 4G). A fourth, from Tasmania, has a long, narrow body with flared lips, and short, unbranched aboral papillae along both sides of a prominent conical cap over the statocyst (Fig. 4H). A fifth, also from Tasmania, has a fairly short, stout body, with conspicuous red pigment beneath the ctene rows. Two others have been identified as *B. cucumis* and *B. ovata* by Edgar (1997, 2000) and Steene (1990), respectively; the former has a more sloping aboral body contour, whereas this is more squared off in the latter. Without doubt, there are additional forms as well, yet to be elucidated, pending more field work and a formal review of the genus.

*Neis* Lesson, 1829

*Neis cordigera* Lesson, 1829

(Fig. 4I)

*Neis cordigera* Lesson, 1829: 103–104, pl. 16, fig. 2 (Port Jackson); Lesson, 1843: 97–98 (summary); von Lendenfeld, 1885b: 968–976 (comprehensive redescription); von Lendenfeld, 1885c: 673–682, pl. 33 (detailed description); Whitelegge, 1889: 197 (Port Jackson); Stiasny, 1931: 40 (Gunnamatta Bay, Port Hacking, NSW; reg. no. AM-P12946).

**Material examined.** WA: WAM-Z4694, west side of groin, Cockburn Sound Power Boat Association Beach, Cockburn Sound, J. Fromont, 6.03.1999; 33.75 mm BL, 37.98 TL, mouth 25.4 mm wide. WAM-Z4695, South Mole, Fremantle, c. 1 m water depth, J. Fromont, 8.03.1999; 11 cm BL, 7 cm wide. Gershwin coll., 19°13.021S, 121°15.399E, off Eighty Mile Beach, WA, L. Gershwin, 16.04.2004; numerous at sunset only. SA: SAM-H1070, North Arm Marina, Commercial Fishing Harbour, Fisherman's Wharf, Port River, Adelaide, T. Laperousaz & K. Phillips, 24.05.2000; 6 spec.: 25.86 mm BL, 19.33 mm BW; 23.74 mm BL, 17.7 mm BW; 33.23 mm BL, 39.4 mm BW; 34.83 mm BL, 33.2 mm BW; 62 mm BL, 46.1 mm BW; 77.22 mm BL, 58.45 mm BW. SAM-XH233, same collection data as H1070; 3 spec.: 19.4 mm BL, 13.76 mm BW; 24.46 mm BL, 16.4 mm BW; 17.98 mm BL, 11.83 mm BW. SAM (GZ0523), Cowell, L. Gershwin & T. Laperousaz, 20.02.2002; 1 spec. Qld: Reefworld pontoon, Hardy Reef, Whitsundays, Great Barrier Reef Marine Park, 3.11.2008, photographs by Emily Smart / Fantasea Adventure Cruising; 1 specimen, 8 cm TL (note that this species is said to be sighted every year by Fantasea staff, and reaches up to 15 cm long).

**Other material.** SA: Streaky Bay, 5–7.03.08; approx. 30–40 individuals per 2 hours each day, varied from 10 cm to 20 cm; observed and videotaped by T. Laperousaz, SAM; no spec. retained.

**Diagnosis.** *Beroidea* with pronounced aboral lobes; with canal network uninterrupted across the midline.

**Redescription.** Body dimensions of largest specimen (ex SAM-H1070): length along center axis 77.2 mm, total length including wings 96.5 mm; width between oral ridges 58.5, between mouth corners 52.0 mm; von Lendenfeld (1885b) reported specimens up to 250 mm, with general measurements being 2–2.5 times as long as broad, and 4–5 times as long as thick. The body is thickest in the centre region when viewed from the narrow sides. General shape square to slightly rectangular (excluding the wings),

quite compressed, with distinct large, triangular aboral wings protruding to the posterior on either side of the statolith and center axis, edged by a prominent ridge, creating a hollowed-out appearance of the two narrow sides. Laterally, the oral edge flares into a ridge positioned along the midpoint of either narrow side, which ends about 2/3 back between the ridges of the wings.

Ctene rows along the entire length of the body; the four peripheral rows running from approx. 2 mm either side of the statocyst, along the aboral margin, around the edge of the wings, and up the side edge to the corner where the mouth opens. The four axial rows run from adjacent to the statocyst, flaring outward slightly, up toward the mouth, ending on the outer portion of the lip. Thus, the peripheral ctene rows are considerably longer than the axial ctene rows.

Mouth large, encompassing the entire leading edge of the animal, though not flared. Stomach vase shaped, largest at the oral end, spanning from corner to corner, tapering back to a point at statocyst; not extending into the aboral wings.

Gonads not observed.

Gastrovascular system forms a continuous network, i.e., it is not divided side to side. Canals of two types: some continuous between ctene rows, with anastomoses to adjacent canals, to the stomach, and possessing blind branches; others, singly or doubly between continuous canals, unbranched and ending blindly.

Aboral statocyst small, embedded shallowly in a cup-shaped pit in the 'saddle' between the two large aboral wings. Polar fields could not be found.

Aboral papillae of two types: lateral ones simple and short; axial ones biforked and approx. double the length of the lateral ones.

Colouration: The SA specimens were slightly cloudy with carmine red side edges (along nearly the entire length of the short sides). The bodies of the WA specimens were, in contrast, colourless with a slightly cloudy translucency, except for the ctene rows, under each of which runs a line of fine red points.

**Bioluminescence.** Bioluminescence was observed in the smaller of the two WA specimens.

Several times throughout the first night following capture, tapping of the jar was found to produce a single response, approximately 1 x 1 mm. The exact point of light production could not be established prior to the death of the specimen.

**Biology.** At present, nothing is known about the reproductive or ecological biology of this species. In Western Australia, it was found at around midday, in about 0.5 m depth, where the water was about 3 m bottom-depth, over a sandy area beside a rocky groin, in windswept seas; in South Australia, large numbers were found in the harbour during the day; von Lendenfeld (1885b) repeatedly found single specimens accompanying swarms of *Bolinopsis* in Sydney Harbour. Its behaviour was not observed in situ in either case. In the laboratory, specimen number WAM-Z4694 vigorously avoided light, attempting to dive into the bottom of the observation dish and remaining curled until the water level was lowered. During observation, the aboral 1/3 of the sides of the stomach could be seen repeatedly undulating peristaltically within the body.

**Distribution.** Subsequent to Lesson's (1829) description from Port Jackson, *Neis* has been reported several times in the Sydney area: von Lendenfeld (1885b, 1885c) found it at Sydney Harbour, and Stiasny (1931) found it at Port Hacking. We here broaden the distribution to include Adelaide, the west coast of South Australia, Western Australia from the southernmost Indian Ocean sector to the tropics, and the Whitsunday region of the Great Barrier Reef. Because of its broad distribution as now known, it seems likely that *Neis* may be found in Northern Territory and Tasmanian waters. This is the first tropical report of *Neis*. It has not yet been found outside Australian waters.

**Field identification.** Body similar to *Beroe*, i.e., flattened, bag-like, with large mouth at one end, but with the aboral end extending past the statocyst on both sides into lobes. Characterised by brilliant red pigmentation, particularly along the two narrow sides.

**Remarks.** Although Lesson's (1829) description was relatively brief, the figure is a perfect rendition of the species, making it immediately recognisable. A good account of the morphology



and behaviour of the species was given by von Lendenfeld (1885b). *Neis cordigera* remains today a relatively common ctenophore in temperate Australian waters, and may occasionally occur in large swarms.

There has been debate as to whether *Neis* is merely a *Beroe*. Chun (1880: 307) regarded *Neis* and *Beroe* to be identical. Von Lendenfeld (1885b) quite forcefully asserted that *Neis* is not identical with *Beroe*, and further remarked that *Neis* seems to represent a transition from *Beroe* to the Lobata. As elucidated by von Lendenfeld (p. 969), the vascular system of *Beroe* is divided in the two halves of the body, whereas no such separation is present in *Neis*.

KEY TO THE CTENOPHORES OF AUSTRALIA

1. Body globular or ribbon-like, gelatinous and planktonic. . . . . 2
  - Body flatworm-like, creeping on algae, echinoderms, or other substrate. Benthic ctenophores. . . . . 18
2. Body more or less spherical or egg-shaped, with or without lobes. . . . . 3
  - Body highly compressed, and sac-like or ribbon-like. . . . . 16
3. Body lacking conspicuous lobes; more or less spherical; with two conspicuous retractable tentacles issuing from cylindrical bulbs between stomach and body wall. . . . . 4
  - Body with conspicuous lobes; more or less egg-shaped; lacking tentacles. . . . . 6
4. With two conspicuous tentacles issuing from crescentic-shaped bulbs. . . . .
  - . . . . . *Pukia falcata* gen. nov., sp. nov.
  - With two conspicuous tentacles issuing from cylindrical-shaped bulbs. . . . . 5
5. Tentacles with distantly-spaced tentilla, usually held tightly coiled with a 'beehive' appearance, like droplets along the tentacle; mouth protruding. . . . .
  - . . . . . *Enplokamis evansae* sp. nov.
  - Tentacles with closely-spaced tentilla, usually held relaxed out with a comb-like or feather-like appearance. . . . .
    - . . . . . *Plenrobrachia* species
6. Body surface smooth, lacking tubercles. 10
  - Body covered in gelatinous tubercles. [*Leucothea* spp.] . . . . . 7

7. Body (including lobes) to about 15cm in length, elongate. . . . . 8
  - Body about 30–45cm long, with large papillae; gut yellow-green. . . . .
    - . . . . . *Leucothea* sp. A
8. Body overall yellowish, with large papillae (Qld). . . . . *Leucothea* sp. B
  - Body overall transparent and colourless, with small papillae (Tas). . . . . 9
9. Body densely covered with long, slender tubercles; lobes 1/2 total length (north-western Tas, SA). . . . .
  - . . . . . *Lencothea filmersankeyi* sp. nov.
  - Body sparsely covered with short, slender tubercles; lobes approximately 2/3 total length (south-eastern Tas). . . . .
    - . . . . . *Leucothea* sp. C
10. Lobes one-half total animal length or less. [*Bolinopsis* spp.] . . . . . 11
  - Lobes massively long, much greater than one half total animal length; animal moves with a hand-clapping motion when disturbed. [*Ocyropsis* spp.] . . . . . 13
11. Lobes small, giving the whole animal a compact egg-shape appearance; pigment lacking or inconspicuous (e.g., fine canals coloured, but not body). . . . . 12
  - Lobes broad and wing-like; with crimson pigment marking the cteno rows. . . . .
    - . . . . . *Bolinopsis ashleyi* sp. nov.
12. Body colourless; canals violet. . . . .
  - . . . . . *Bolinopsis chuni*
  - Body colourless; canals finely magenta-coloured. . . . . *Bolinopsis* sp. A
13. Stomach deeply indented into a strongly pronounced hourglass shape; with or without spots. . . . . 14
  - Stomach not deeply indented, more shallowly hourglass-shaped, lacking spots. . . . .
    - . . . . . *Ocyropsis crystallina*
14. Body small (c. 1 cm), found in the tropics. 15
  - Body large (c. 5 cm long), transparent, lacking spots; found in temperate waters. . . . .
    - . . . . . *Ocyropsis vance* sp. nov.
15. Transparent, with large diffuse brownish or blackish spots on inner surfaces of lobes. . . . .
  - . . . . . *Ocyropsis maculata*
  - Transparent, with two small black spots near edge of lobes. . . . . *Ocyropsis* sp.
16. Body compressed, sac-like, with large mouth at one end. . . . . 17

- Body highly compressed, ribbon-like or belt-like. . . . . *Velamen* sp.
- 17. Body with rounded lobe extensions on ‘corners’ of aboral end; oral end broad and square; conspicuous crimson pigment on lobes. . . . . *Neis cordigera*
- Body with smoothly rounded aboral end; oral end broad or pursed; colourless or sometimes purplish or pinkish. . . *Beroe* spp.
- 18. Benthic ctenophores found on algal or seagrass host. . . . . 19
- Benthic ctenophores found on animal host or free-living in tropical waters. . . . . 22
- 19. Benthic ctenophores found on algal host in temperate waters. . . . . 20
- Benthic ctenophores found on algal or seagrass host in tropical waters; body transparent with numerous green specks, with branched papillae, about 20 mm long. . . . . *Coeloplana reichelti* sp. nov.
- 20. Body colour red, pink, or orange. . . . . 21
- Body colour green or white, found on *Jania* sp. (coralline alga) at Rottneest I.; about 10mm long. . . . . *Coeloplana thomsoni*
- 21. Found on *Scaberia agardhii* (brown alga) in South Australia; body bright red or orange, 25 mm long. . . . . *Coeloplana scaberiae*
- Found on red and green algal hosts in Port Philip Bay; body dark pink to orange-red with transparent or whitish areas, 10–50 mm long. . . . . *Coeloplana willeyi*
- 22. Found on animal host, e.g., starfish or soft coral. . . . . 23
- Free-living on muddy sand on the Great Barrier Reef; body with yellowish-white reticulate pattern and red pigment, about 36 mm long. . . . . *Coeloplana meteoris*
- 23. On *Sarcophyton* sp. (soft coral) on Great Barrier Reef; body colourless, mottled with ectodermal pale reddish-brown blotches, about 25 mm long. . . . . *Coeloplana mellosa* sp. nov.
- Found on *Acanthaster planci* (Crown-of-thorns starfish) on Great Barrier Reef; body transparent and colourless, about 5 mm long. . . . . *Coeloplana* sp. A

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LITERATURE CITED

Abbott, J.F. 1902. Preliminary notes on *Coeloplana*. *Annotationes Zoologicae Japonenses* 4: 103–108.

1907. The morphology of *Coeloplana*. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 24: 41–70, pls 8–10.

Agassiz, A. 1865. North American Acaleph. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 1(2): 1–234.

Agassiz, A. & Mayer, A.G. 1899. Acalephs from the Fiji Islands. *Bulletin of the Museum of Comparative Zoology at Harvard University* 32(9): 157–189, 17 pls.

Agassiz, L. 1850. Contributions to the Natural History of the Acalephae of North America. Part II. On the beroid medusae of the shores of Massachusetts, in their perfect state of development. *Memoirs of the American Academy of Arts and Sciences, New Series* 4 (2): 313–374, pls 1–8.



1860. *Contributions to the Natural History of the United States of America*. vol. III. pt. I. Acalephs in general. pt. II. Ctenophorae. (Little Brown: Boston).
- Arnold, P. 1993. First record of ctenophore *Coeloplaua* (*Benthioplana*) *meteoris* (Thiel, 1968) from Australia. *Memoirs of the Queensland Museum* 33(1): 16.
- Bigelow, H.B. 1904. Medusae from the Maldive Islands. *Bulletin of the Museum of Comparative Zoology at Harvard University* 39: 245–269.
1912. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer Albatross, from October 1904, to March 1905, Lieutenant Commander L.M. Garrett, U.S.N., commanding, XXVI. The ctenophores. *Bulletin of the Museum of Comparative Zoology at Harvard College* 54(12): 369–408.
- Bosc, L.A.G. 1802. Histoire naturelle des vers, contenant leur description et leurs mœurs, avec figures dessinées d'après nature. Medusozoa. Pp. 130–168. In, Buffon, G.L.L. (Ed.) *Histoire Naturelle de Buffon*, classée d'après le système de Linne par R. R. Castel. Vol. 2. (Déterville: Paris).
- Bourne, G. 1900. Chapter 7, The Ctenophora. Pp. 1–25. In, Lankester, R.A. (Ed.), *A Treatise on Zoology*. Part 2 The Porifera and Coelenterata (Adam and Charles Black: London).
- Brown, R.W. 1956. *Composition of Scientific Words*. (Smithsonian Institution Press: Washington, DC).
- Browne, P. 1756. *The Civil and Natural History of Jamaica*. (Osborne and Shipton: London).
- Bruguière, M. 1792. *Histoire naturelle des vers*. 757 pp. In, D'Alembert, M.D.E. (Ed.) *Encyclopédie Méthodique*. Vol. 1. (Chez Panckoucke: Paris).
- Carré, C. & Carré, D. 1991. *Ceroctea bicornis*, new genus new species of ctenophore (Cydippida, Pleurobrachiidae) from the Mediterranean. *Comptes Rendus de l'Académie des Sciences Serie III Sciences de la Vie* 313(12): 559–564.
- 1993a. *Ctenella aurautia*, new genus and species of a Mediterranean tentacled ctenophore (Ctenellidae fam. nov.) without colloblasts and with labial suckers. *Canadian Journal of Zoology* 71(9): 1804–1810.
- 1993b. *Minicteta luteola*, new genus and new species of Mediterranean Cydippida ctenophore with five types of colloblasts. *Beaufortia* 43(10): 168–175.
- Carus, J.V. 1863. *Handbuch der Zoologie* (W. Engelmann: Leipzig).
- Chun, C. 1879. Die im Golfe von Neapel erscheinenden Rippenquallen. *Mittheilungen aus der Zoologischen Station zu Neapel Tome I* (2 Heft): 180–217, Pl. 6.
1880. Die ctenophoren des Golfes von Neapel und der angrenzenden Meeres-abschnitte. *Fauna und Flora des Golfes von Neapel* 1: 313 pp., 16 pls.
1898. *Die Ctenophoren der Plankton-expedition*. (Lipsius & Tischer: Kiel).
- Costello, J.H. & Coverdale, R. 1998. Planktonic feeding and evolutionary significance of the lobate body plan within the Ctenophora. *Biological Bulletin (Woods Hole)* 195(2): 247–248.
- Dakin, W.J. & Bennett, I. 1987. *Australian Seashores* (Angus & Robertson: North Ryde, NSW).
- Dakin, W.J. & Colefax, A.N. 1933. The marine plankton of the coastal waters of New South Wales. *Proceedings of the Linnæan Society of New South Wales* 58: 186–222, pl. 7.
1940. *The plankton of the Australian Waters off New South Wales* (The Australasian Medical Publishing Co.: Sydney).
- Davie, P. 1998. *Wild Guide to Moreton Bay* (Queensland Museum: Brisbane).
- Dawydoff, C. 1930a. Sur une nouvelle Coeloplanide (*Coeloplaua perrieri* n. sp.) provenant du Golfe de Siam. *Archives de zoologie expérimentale et générale* 70 (Notes et Revue, Numéro 2): 52–54.
- 1930b. Une nouvelle Coeloplanide de la côte sud d'Annam (*Coeloplaua agniae* nov. sp.). *Archives de zoologie expérimentale et générale* 70 (Notes et Revue, Numéro 3): 83–86.
- 1930c. *Coeloplana dubosqui* nov. sp., Coeloplanide provenant du Golfe de Siam, commensale des Pennatules. *Archives de zoologie expérimentale et générale* 70 (Notes et Revue, Numéro 3): 87–90.
1938. Les Coeloplanides Indochinoises. *Archives de zoologie expérimentale et générale* 80: 125–162, pl. 1.
1946. Contribution la connaissance des ctenophores pélagiques des eaux de l'Indochine. *Bulletin Biologique de la France et de la Belgique* 80(2): 113–170.
- Devanesen, D.W. & Varadarajan, S. 1942. On three new species of *Coeloplaua* found at Krusadai Island marine biological station, Gulf of Manaar. *Journal of Madras University* 14: 181–188.
- Donegan, T.M. 2008. New species and subspecies descriptions do not and should not always require a dead type specimen. *Zootaxa* 1761: 37–48.
- Edgar, G.J. 1997. *Australian Marine Life* (Reed Books: Kew, Victoria).
2000. *Australian Marine Life*, Revised Edition (Reed New Holland: Sydney).
- Eschscholtz, F. 1825. *Bericht über die zoologische Ausbeute während der Reise von Kroustadt bis St. Peter und Paul*. Isis (Oken) XVI: 733–747, Pl. V.

1829. *System der Acalephen. Eine ausführliche Beschreibung aller medusenartigen Strahlthiere* (F. Dümmlert: Berlin).
- Fabricius, O. 1780. *Fauna Groenlandica*. (Impensis Ioannis Gottlob Rothe: Hafniae et Lipsiae).
- Fewkes, J.W. 1882. Notes on acalephes from the Tortugas, with a description of new genera and species. *Bulletin of the Museum of Comparative Zoology at Harvard University* 9(7): 251–289, 7 pls.
- Fleming, J. 1822. *The philosophy of zoology, or a general view of the structure, functions, and classification of animals* (Archibald Constable: Edinburgh).
- Fol, H. 1869. *Ein Beitrag zur Anatomie und Entwicklungsgeschichte einiger Rippenquallen*. Berlin, Medicinischen Facultat der Friedrich-Wilhelms Universität: 12 pp., 4 pls.
- Fricke, H.W. 1970. Neue kriechende Ctenophoren der Gattung *Coeloplana* aus Madagascar. *Marine Biology* 5: 225–238, 16 pls.
- Gegenbaur, C. 1856. Studien über organisation und systematik der Ctenophoren. *Archiv für Naturgeschichte* 22(1): 163–205, pls 7, 8.
- Gershwin, L.-A. & Zeidler, W. 2003. Encounter 2002 expedition to the Isles of St Francis, South Australia: Medusae, siphonophores and ctenophores of the Nuyts Archipelago. *Transactions of the Royal Society of South Australia* 127(2): 205–241.
- Ghigi, A. 1909. Raccolte planctoniche fatte dalla R. Nave "Liguria" nel viaggio di circonvallazione del 1903–1905. I. Ctenofori. *Pubblicazioni del R. Istituto di Studi Superiori Pratici e di Perfezionamento in Firenze Sezione di Scienze Fisiche e Naturali* 2(1): 1–24, pl. 1.
- Gorman, N. 1988. Planktonic Cnidaria and Ctenophora of Moreton Bay. MS Thesis, Department of Zoology, Brisbane, University of Queensland: 82 pp.
- Gowlett-Holmes, K. 2008. *A field guide to the marine invertebrates of South Australia* (Notomares: Tasmania).
- Goy, J. 1990. Preliminary observations on the zooplankton of Shark Bay, Western Australia, with emphasis on medusae and description of a new rhizostome jellyfish (Cnidaria, Scyphozoa). Pp. 107–113. In, Berry, P.F. et al. (Eds), *Research in Shark Bay. Report of the France-Australe Bicentenary Expedition Committee*. (WA Museum: Perth).
- Greenwood, J.G. 1980. Composition and seasonal variations of zooplankton populations in Moreton Bay, Queensland. *Proceedings of the Royal Society of Queensland* 91: 85–103.
- Haddock, S.H.D. & Case, J.F. 1995. Not all ctenophores are bioluminescent: *Plenrobrachia*. *Biological Bulletin (Woods Hole)* 189(3): 356–362.
- Hamond, R. 1971. Some medusae from near Brisbane. *Search* 2(1): 27.
- Harbison, G.R. 1996. Ctenophora. Pp. 101–147. In, Gasca, R. & Suárez, E. (Eds), *Introducción al Estudio del Zooplankton Marino* (ECOSUR: Chetumal, Mexico).
- Harbison, G.R. & Madin, L.P. 1982. Ctenophora. Pp. 707–715, pls 68, 69. In, Parker, S.P. (Ed.), *Taxonomy and classification of living organisms*, Vol. 1. (McGraw-Hill: New York).
- Harbison, G.R., Madin, L.P. & Swanberg, N.R. 1978. On the natural history and distribution of oceanic ctenophores. *Deep-sea Research* 25(3): 233–256.
- Harbison, G.R. & Miller, R.L. 1986. Not all ctenophores are hermaphrodites. Studies on the systematics, distribution, sexuality and development of two species of *Ocyropsis*. *Marine Biology* 90: 413–424.
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature* (International Trust for Zoological Nomenclature: London).
- Kasuya, T., Ishimaru, T. & Murano, M. 1994. Feeding characteristics of the lobate ctenophore *Bolinopsis mikado* Moser. *Bulletin of Plankton Society of Japan* 41(1): 57–68.
- Kideys, A.E. 2002. Fall and rise of the Black Sea ecosystem. *Science (Washington DC)* 297(5586): 1482–1484.
- Komai, T. 1918. On ctenophores of the neighborhood of Misaki. *Annotationes Zoologicae Japonenses* 9: 451–474, 1 pl.
1920. Notes on *Coeloplana bocki* n. sp. and its development. *Annotationes Zoologicae Japonenses* 9: 577–584.
- Korotneff, A. 1886. *Ctenoplana kowalevskii*. *Zeitschrift für Wissenschaftliche Zoologie* 43: 242–251, pl. viii.
- Kowalevsky, A. 1880. Über *Coeloplana metschnikowii*. *Zoologischer Anzeiger* 3: 140–141.
- Kremer, P. 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries* 2(2): 97–105.
- Kremer, P., Reeve, M.R. & Syms, M.A. 1986. The nutritional ecology of the ctenophore *Bolinopsis vitrea*: comparisons with *Mnemiopsis mccradyi* from the same region. *Journal of Plankton Research* 8(6): 1197–1208.
- Krempf, A. 1920. Sur un Ctenophore planariforme nouveau *Coeloplana gonoctena* (nov. sp.). *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris)* 171: 438–440.
- Krumbach, T. 1925. Ctenophora. Pp. 905–995. In, Kukenthal, W. & Krumbach, T. (Eds), *Handbuch der Zoologie* (W. de Gruyter: Berlin). Vol. 1.



1933. Ueber eine kriechende Ctenophore aus dem Golfe von Suez und ein paar Thesen über die Architektonik der Rippenquallen. *Mittheilungen aus dem Zoologischen Museum in Berlin* 19: 475–479.
- Leoup, E. 1938. Siphonophores et ctenophores. *Résultats du voyage du S.Y. Belgica en 1897–1898–1899 sous le commandement de A. de Gerlache de Gomery ... Rapports scientifiques Expedition Antarctique Belge* (J.E. Buschmann: Anvers.).
- Lesson, R.P. 1829. *Voyage de la Coquille. Zoophytes.* (A. Bertrand: Paris).
1836. Mémoire sur la famille des Béroïdes. *Annales des Sciences Naturelles, Paris (Zoology), Series 2* 5: 235–266 [pls 1–2 referenced, but could not be located].
1843. *Histoire Naturelle des Zoophytes. Acalèphes* (Librairie Encyclopédique de Roret: Paris).
- Main, R.J. 1928. Observations on the feeding mechanism of a ctenophore, *Mnemiopsis leidyi*. *Biological Bulletin (Woods Hole)* 55: 69–78.
- Matsumoto, G.I. 1988. A new species of lobate ctenophore, *Leucothea pulchra* sp. nov., from the California Bight. *Journal of Plankton Research* 10(2): 301–311.
1999. *Coeloplana thomsoni* sp. nov., a new benthic ctenophore (Ctenophora: Platyctenida: Coeloplaniidae) from Western Australia. Pp. 385–393. In: Walker, D.I. & Wells, F.E. (Eds), *The Seagrass Flora and Fauna of Rottneest Island, Western Australia*. (Western Australian Museum: Perth).
- Matsumoto, G.I. & Gowlett-Holmes, K.L. 1996. *Coeloplana scaberiae* sp. nov., a new benthic ctenophore (Ctenophora: Platyctenida: Coeloplaniidae) from South Australia. *Records of the South Australian Museum* 29(1): 33–40.
- Matsumoto, G.I. & Robison, B.H. 1992. *Kiyohimea usagi* sp. nov., a new lobate ctenophore from the Monterey Submarine Canyon. *Bulletin of Marine Science* 5(1): 19–29.
- Mayer, A.G. 1900. Some medusae from Tortugas, Florida. *Bulletin of the Museum of Comparative Zoology at Harvard College* 37(2): 13–82, 44 pls.
1912. *Ctenophores of the Atlantic coast of North America* (Carnegie Inst. Washington Publ.: Washington D.C.).
- McCrary, J. 1859a. Notes from the Meeting of the Elliott Society, September 1st, 1857. *Proceedings of the Elliott Society of Natural History of Charleston, South Carolina* 1: 239–240.
- 1859b. On the development of two species of Ctenophora found in Charleston Harbor. *Proceedings of the Elliott Society of Natural History of Charleston, South Carolina* 1: 254–271, pl. 14.
- Mertens, H. 1833. Beobachtungen und untersuchungen über die beroeartigen akalephen. *Mémoires de l'Académie Impériale des Sciences de St. Petersburg Series 6, 2*: 479–544, Pls 1–13.
- Mills, C.E. 1987. Revised classification of the genus *Euplokamis* Chun, 1880 (Ctenophora: Cydippida: Euplokamidae n. fam.) with a description of the new species *Euplokamis dunlapae*. *Canadian Journal of Zoology* 65(11): 2661–2668.
2001. Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451: 55–68.
2007. Phylum Ctenophora: list of all valid species names. Electronic internet document available at <http://faculty.washington.edu/cemills/Ctenolist.html> Published by the author, web page established March 1998, last updated 13 May 2007.
- Mortensen, T. 1912. Ctenophora. *Danish Ingolf-Expedition* 5(2): 1–95, pls 1–10, 1 chart.
1927. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. XXXIX. Two new ctenophores. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening* 83: 277–288.
1932. Ctenophora. *Report on the Scientific Results of the "Michael Sars" North Atlantic Deep Sea Expedition, 1910* 3 (Part 2, No. 1): 1–12, 1 pl.
- Moser, F. 1907. Neues ueber Ctenophoren. II. *Zoologischer Anzeiger* 32: 449–454.
1909. Die Ctenophoren der Deutsche Sudpolar-Expedition 1901–1903. *Deutsche Sudpolar-Expedition, XI. Zoologie III*: 116–192, 3 pls.
- Müller, O.F. 1776. *Zoologiae Danicae prodromus, seu animalium Danicae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium* (Impensia auctoris, typis Hallageriis: Havniae).
- Nagabhushanam, A.K. 1959. Feeding of a ctenophore, *Bolinopsis infundibulum* (O.F. Muller). *Nature, London* 184 (4689): 829.
- Péron, F. 1807. *Voyage de découvertes aux terres Australes, exécuté par ordre de sa Majeste l'Empereur et Roi, sur les Corvettes le Geographe, le Naturaliste, et la Goelette le Casuarina, pendant les années 1800, 1801, 1802, 1803 et 1804. Historique: Tome 1* (de l'Imprimerie Impériale: Paris).
- Péron, F. & Lesueur, C.A. 1810. Histoire de la famille des mollusques ptéropodes. *Annales du Muséum d'histoire naturelle, Paris* 15: 57–69, pl. 2, fig. 16.
- Purcell, J.E. 1990. Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasii*) at herring spawning grounds in British Columbia [Canada]. *Canadian Journal of Fisheries and Aquatic Sciences* 47(3): 505–515.

1991. A review of cnidarians and ctenophores feeding on competitors in the plankton. *Hydrobiologia* **216/217**: 335–342.
- Purcell, J.E. & Arai, M.N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* **451**: 27–44.
- Quoy, J.R.C. & Gaimard, J.P. 1824. Voyage autour du monde ... exécuté sur l'Uranie et la Physicienne, pendant ... 1817–20. Zoologie. 12 pp., plus Atlas. In, Freycinet, M.L.D. (Ed.) *Voyage de l'Uranie* (Paris).
- Ralph, P.M. 1950. Ctenophores from the waters of Cook Strait and Wellington Harbour. *Transactions of the Royal Society of New Zealand* **78**(1): 70–82.
- Ralph, P.M. & Kaberry, C. 1950. New Zealand Coelenterates: Ctenophores from Cook Strait. *Zoology Publications from Victoria University College* **3**: 1–11.
- Rang, P.C.A.L. 1828a. Etablissement de la famille des Beroides dans l'ordre des Acalèphes libres, et description de deux genres nouveaux qui lui appartiennent. *Mémoires de la Société d'Histoire naturelle Paris* **4**: 166–173, pls 19, 20.
- 1828b. Description d'un nouveau genre de la classe des acalèphes. *Bulletin d'Histoire naturelle de la Société linnéenne de Bordeaux* **1**: 314–319.
- Reeve, M.R., Walter, M.A. & Ikeda, T. 1978. Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. *Limnology and Oceanography* **23**(4): 740–751.
- Robilliard, G.A. & Dayton, P.K. 1972. A new species of platyctenean ctenophore, *Lyrocteis flavopallidus* sp. nov., from McMurdo Sound, Antarctica. *Canadian Journal of Zoology* **50**: 47–52.
- Sars, M. 1835. *Beskrivelser og iagttagelser over nogle mærkelige eller nye i havet ved den bergenske kyst levende dyr af polypernes, acalèphernes, radiaternes, annelidernes, og molluskernes classer, med en kort oversigt over de hidtil af forfatteren sammesteds fundne arter og deres forekommen.* (T. Hallager: Bergen).
- Schulze-Röbbecke, A.C. 1984. Functional morphology of *Bolinopsis infundibulum* (Ctenophora). *Helgoländer Meeresuntersuchungen* **38**(1): 47–64.
- Shiganova, T.A. 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fisheries Oceanography* **7**(3–4): 305–310.
- Smith, B.J. & Plant, R.J. 1976. A creeping ctenophoran (Platyctenea: Ctenophora) from Victoria, Australia. *Memoirs of the National Museum of Victoria* **37**: 43–46.
- Stechow, E. 1921. Neue genera und species von hydrozen und anderen evertebraten. *Archiv für Naturgeschichte Jahrg.* **87**, Sect. A (Part 3): 248–265.
- Steene, R. 1990. *Coral Reefs: Nature's richest realm* (Crawford House Press: Bathurst, Australia).
- Stephenson, T.A., Stephenson, A., Tandy, G. & Spender, M. 1931. The structure and ecology of Low Isles and other reefs. *Scientific Reports of the Great Barrier Reef Expedition* **3**: 17–112, 27 pls.
- Stiasny, G. 1931. Über einige coelenterata von Australien. *Zoologische Mededelingen* **14**(1–2): 27–42.
- Stretch, J.J. 1982. Observations on the abundance and feeding behavior of the cestid ctenophore, *Velamen parallelum*. *Bulletin of Marine Science* **32**: 796–799.
- Tanaka, H. 1932. *Coeloplana echnicola* n. sp. *Memoirs of the College of Science, University of Kyoto, Series B* **7**: 247–250, 1 pl.
- Thiel, H. 1968. *Coeloplana meteroris* nov. spec. (Ctenophora, Platyctenea): Beschreibung und systematische stellung mit einem vergleich der gastrovaskularsysteme in dieser ordnung. *Sonderdruck aus "Meteor" Forschungsergebnisse*, **D 3**: 1–13.
- Tokioka, T. 1964. *Bolinopsis rubripunctata* n. sp., a new lobatean ctenophore from Seto. *Publications of the Seto Marine Biological Laboratory* **12**(1): 93–99.
- Utinomi, H. 1963. *Coeloplana komaii*, a new creeping ctenophore from Sagami Bay. *Japanese Journal of Zoology* **14**(1): 15–19.
- Uye, S.-I. & Kasuya, T. 1999. Functional roles of ctenophores in the marine coastal ecosystem. Pp. 57–76 (Japanese with English Abstract) In, Okutani, T. et al. (Eds), *Update Progress in Aquatic Invertebrate Zoology* (Tokai University Press: Tokyo) [not seen].
- Von Lendenfeld, R. 1885a. The metamorphosis of *Bolina chuni* nov. spec. *Proceedings of the Linnean Society of New South Wales* **9**: 929–931, pls 44, 45.
- 1885b. Notes on a beroid of Port Jackson. *Proceedings of the Linnean Society of New South Wales* **9**: 968–976.
- 1885c. Über coelenteraten der Sudsee, VI: *Neis cordigera* Lesson, eine australische Beroide. *Zeitschrift für Wissenschaftliche Zoologie* **41**: 673–682, pl. 33.
- Whitelegge, T. 1889. List of the marine and freshwater invertebrate fauna of Port Jackson and the neighborhood. *Journal and Proceedings of the Royal Society of New South Wales* **23**: 163–324 [coelenterates pp. 187–197, 306].
- Willey, A. 1896. On *Ctenoplana*. *Quarterly Journal of Microscopical Science* **39**(155): 323–343, pl. 21.
- Wrobel, D. & Mills, C. 1998. *Pacific Coast Pelagic Invertebrates: A Guide to the Common Gelatinous Animals* (Sea Challengers and Monterey Bay Aquarium: Monterey, CA).
- Zeidler, W. & Gowlett-Holmes, K.L. 1998. Confirmation of the association of the hyperiidean amphipod genus *Hyperia* (Crustacea: Amphipoda: Hyperiidea: Hyperiidae) with ctenophores. *Records of the South Australian Museum* **31**(1): 117–118.