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Note

A novel benthopelagic ctenophore from 7,217 m depth in the Ryukyu Trench, Japan, with notes on the taxonomy of deep-sea cydippids

Dhugal J. Lindsay[1]* & Hiroshi Miyake[1,2,3]

[1] *Marine Biology and Ecology Research Program, Extremobiosphere Research Center, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2–15 Natushima-cho, Yokosuka, 237–0061, Japan*
[2] *New Enoshima Aquarium, 2–19–11 Katase-Kaigan, Fujisawa city, Kanagawa, 251–0035, Japan*
[3] *Present address: School of Fisheries Science, Kitasato University, Ofunato, Iwate, 022–0101, Japan*

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Abstract: Two tentaculate ctenophores were observed floating above the sediment at 7,217 m depth in the Ryukyu Trench, Japan, anchored by a pair of long, flexible filaments emerging from the end of the animal opposite the simple tentacles. Several characters suggest taxonomic affinities to the genus *Aulacoctena*, and the taxonomic placement of this genus is reviewed and discussed with reference to recently collected material. In the light of this re-examination a new family is proposed to contain the genus *Aulacoctena*. The exact taxonomic placement of the enigmatic benthopelagic ctenophore species remains pending due to the difficulty of procuring samples from such abyssal depths with the recent loss of the world's only submersible platform rated below 7,000 m—the ROV *Kaiko*.

Key words: benthopelagic, ctenophore, cydippid, ROV, submersible

Two large (5–8 cm wide, 10–20 cm long) gelatinous organisms were observed anchored to the muddy substrate of the gently sloping seafloor (14°) at 7,217 m bottom depth at 12 : 29 : 00 and 12 : 35 : 40, respectively, during dive number 233 of the ROV *Kaiko* on 5 April 2002 in the Ryukyu Trench, south of the main island of Okinawa (24°25.25′N, 127°21.75′E). Physico-chemical parameters in the benthopelagic layer were as follows: salinity 34.68, temperature 2.0°C. Size was estimated by reference to objects of known size on the ROV. Both animals were attached to the substrate by means of two long flexible filaments that extended from the surface of one end of the animal opposite to the end from which two long simple retractable tentacles emerged. This combination of tentacles and filaments caused them to somewhat resemble a twin-tailed box kite flying above the substrate by means of two stabilizing kite strings (Fig. 1A–D). The organisms possessed long white reflective structures arranged in pairs along the long edges of their rectangular box-shaped bodies (Fig. 1A–D). These eight structures resembled the comb rows of ctenophores and this, in combination with the presence of two retractable tentacles and a round to squarish/rectangular body with no lobe-like structures causes us to tentatively identify them as cydippid ctenophores under the common taxonomy, but perhaps more accurately merely as tentaculate ctenophores given the polyphyletic nature of the Order Cydippida (Podar et al. 2001). Unfortunately, the animals were not collected and the only material available for study is several photographs and two short video sequences.

Diverticula appeared to arise from the meridional canals (Fig. 1B) and the two tentacles were simple, with no tentilla (Fig. 1A–D). It is somewhat difficult to ascertain which end of this ctenophore is the oral end, and therefore whether the simple tentacles exit from the oral or aboral end. "Cydippid" ctenophores with simple tentacles are rare (Harbison 1985). If the tentacles exit orally, this enigmatic ctenophore might be placed within the family Bathyctenidae, as defined by Harbison (1985), or in the family Haeckellidae as defined by Harbison (1996). Each pair of comb rows seemed to either merge together or come into extremely close contact at the tentacular end of the animal (Fig. 1C). No "cydippid" ctenophores with simple tentacles that exit aborally are currently known to science (Harbison 1985).

The family Bathyctenidae, as defined by Harbison (1985), contains only two genera, *Aulacoctena* and *Bathyctena*, each with a single described species. The original description of *Bathyctena* (=*Mertensia*) *chuni* (Moser 1909) and almost all references to it in the literature thereafter (e.g. Mortensen 1932, Harbison 1985) are unclear with regard to the presence or absence of tentilla on the tentacles, although Harbison (1985) lists simple tentacles as one of the characters defining the fam-

* Corresponding author: Dhugal J. Lindsay; E-mail, dhugal@jamstec.go.jp

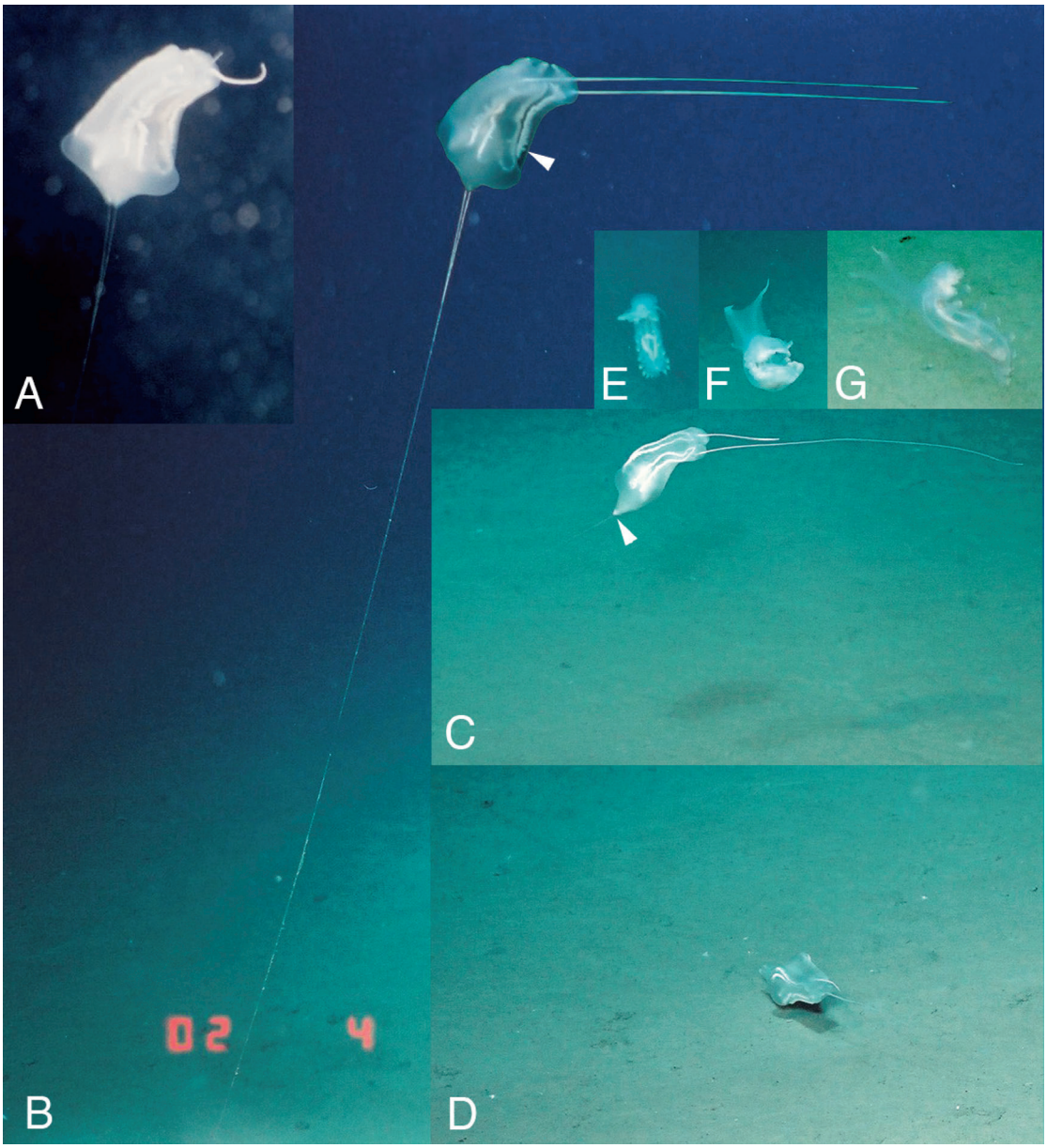

Fig. 1. Enigmatic benthopelagic ctenophore anchored by two filaments and floating high above the sediment with simple tentacles mostly retracted (A) and extended (B). Diverticula emergent from the meridional canals beneath the comb rows are easily visible (B, white arrowhead). The meridional canals seem to curve inwards some distance before reaching the end opposite the tentacles. The same ctenophore losing altitude as it reacts to the increased near-bottom water current caused by the ROV's thrusters (C–D). The attachment points of the filaments are visible as opaque white patches on horned projections (white arrowhead). Elasipodid holothurians were observed to swim and/or float past (E–G). Tentilla would not be necessary for the capture of such large, gelatinous prey with prominent body projections.

ily. The only references to tentacle type found in the literature were Harbison (1986) and Wrobel & Mills (1998). The latter work introduces a single, extremely good, photograph of a "cydippid" ctenophore identified as *B. chuni* and states that the species has "tentacles with many fine side branches." The credit and copyright for the photograph is recorded as belonging to Mills, so presumably the identification was done by this author on the animal while it was still in fresh, pristine condition. However, it is not clear whether it was the individual in the photograph that had tentilla-bearing tentacles or if the presented information came from multiple individuals, as the description of the pigmentation on the inside of the mouth obviously comes from at least three individuals. This book describes the pelagic invertebrates of the Pacific Coast. However, it is unclear whether the collection location of the photographed individual is from the Pacific Coast of the United States of America, whether it is from one of the localities referred to in the original species description (Indian Ocean sec-

tor of Southern Ocean, recorded as southwest of Kerguelen but figured as southeast, or tropical east Atlantic, west of Cape Verde), or whether it was collected from some other location. The senior author recently had the opportunity to examine a specimen of *B. chuni* captured in the tropical western Atlantic (*R/V Ronald H. Brown* CmarZ Cruise Station 5: 14°06′N, 54°30′W) from the 1,000–2,000 m depth layer using a MOCNESS net of 10 m^2 mouth area and a mesh size of 334 μm. This location is relatively close to that of the second individual referred to by Moser (1909) and the individual had a milky white coloration to the body with a darkly pigmented stomach and lips, as well as a general aspect resembling that of Figure 4 as recorded in the original description. This individual did indeed have tentacle bases that lay obliquely, close to the stomach, had tentilla on its tentacles, and resembled closely the animal identified by Wrobel & Mills (1998) as *B. chuni*. Unfortunately, the internal canal structure could not be determined because of the damaged condition of the specimen, and the canal structure is also not described in the short diagnosis by Wrobel & Mills (1998). The original figure of *B. chuni* is unclear as to the internal canal structure and shows the adradial canals bifurcating after leaving the vicinity of the tentacle bulb on the right side, but on the left side only one adradial canal is seen in this position (Moser 1909).

Harbison (1986) introduces a photograph of a "cydippid" labeled as *B. chuni* that has distinct tentilla on the orally-exiting tentacles. This photograph is in black and white, and the internal anatomy, as well as the presence or absence of diverticula, is not clear. The *B. chuni* of Wrobel & Mills (1998) has rows of spots lying midway between the comb rows, and these are also visible in a photograph of *B. chuni* identified by Dr. Steven Haddock and accessible through the electronic internet document "Phylum Ctenophora: List of all valid species names" published by Dr. Claudia Mills*. The *B. chuni* of Harbison (1986) lacks these rows of spots, is more transparent, and has spots instead at the oral ends of the comb rows, suggesting that it may belong to a different species. A species of ctenophore that closely resembles the "*B. chuni*" of Harbison (1986) occurs in large numbers in Sagami Bay, Japan (Hunt & Lindsay 1999; as *Pleurobrachia* sp.), has a heavily pigmented gut, paragastric canals with diverticula, and tentilla-bearing tentacles that leave near the oral end of the comb rows. Based on these characters, this animal was recently reported as an undescribed species belonging to the family Bathyctenidae (Lindsay & Hunt 2005). The internal canal structure of this *Bathyctena* sp. resembles that of Figure 6.2 (a) in Harbison (1985), ostensibly the canal structure of a pleurobrachiid, rather than that of Figure 6.2 (c), which is that of "a mertensiid, bathyctenid or platyctene." At this time Harbison had only studied personally *Aulacoctena acuminata* and had yet, it seems, to see a specimen of *Bathyctena* (p. 88, Harbison 1985). Harbison (1996) has since redefined the family Bathyctenidae to include only the genus *Bathyctena* with the following characters: Spherical body, tentacles with tentilla that emerge through sheaths near the oral edges of the comb rows; stomodeum with dark pigment. Presumably this redefinition was based on unpublished personal observations as we have been unable to locate any published evidence to support it, other than the observation by Wrobel & Mills (1998) which is poorly documented. To this definition we would add the following character: all adradial canals bifurcate from interradial canals (Fig. 2A). The species *Pleurobrachia latipharyngea* (Dawydoff 1946) may now be moved to this family within the genus *Bathyctena* based on the above characters. It can be distinguished from *B. chuni* by the translucent brown coloration of the body and the position of the tentacle bulbs far from the stomach, and from the undescribed *Bathyctena* sp. from Harbison (1986) and Lindsay & Hunt (2005) by the greatly enlarged reddish-purple pharynx and aboral position of the interradial canals.

"Cydippids" with simple tentacles that exit orally seem to be currently placed in the family Haeckellidae (Harbison 1996, Mills & Haddock 2002). This placement must be based on tra-

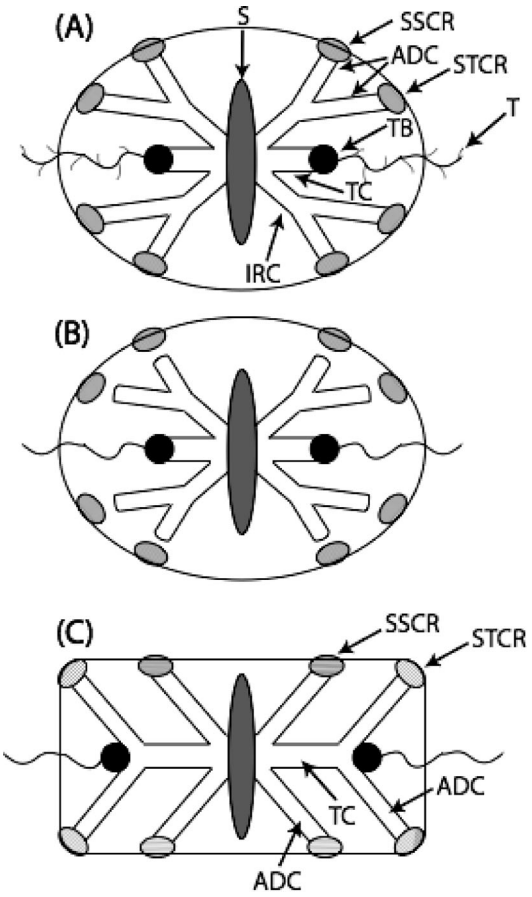

Fig. 2. The internal canal structure of (A) bathyctenid and pleurobrachiid ctenophores, (B) *Haeckelia*, and (C) aulacoctenid, tjalfiellid, mertensiid, and euplokamidid ctenophores (note although not figured the latter two families have tentilla). Abbreviations are S: stomodeum, SSCR: sub-stomodeal comb row, ADC: adradial canal, STCR: sub-tentacular comb row, T: tentacle, TB: tentacle bulb, TC: tentacular canal, and IRC: interradial canal.

* http://faculty.washington.edu/cemills/Ctenolist.html. Published by the author, web page established March 1998, last updated April 5, 2005.

dition rather than accumulated evidence as the type for the family, *Haeckelia* (=*Euchlora*) *rubra* Kölliker, has an internal canal structure that differs considerably from that of *A. acuminata* Mortensen 1932. In *H. rubra*, as figured by Komai and Tokioka (1942) and Chiu (1980), the subtentacular and substomodeal adradial canals do not supply the comb rows directly but are separated spatially from the comb rows by the mesogleal matrix (Fig. 2B). Carré and Carré (1989) interpret these canals to be meridional canals that lack an aboral caecum. These adradial/meridional canals arise from interradial canals that in turn arise from perradial canals leaving the stomodeum, similar to the canal structure observed in the undescribed *Bathyctena* species and in pleurobrachiid ctenophores in Figure 6.2 (a) in Harbison (1985). Although visible in *H. rubra*, in *Haeckelia bimaculata* the perradial canals were unable to be resolved (Carré & Carré 1989), perhaps due to the small size of the animal. Perradial canals are sometimes short and unresolvable as separate canals in smaller animals (see Podar et al. (2001) on *Haeckelia*), and as such are omitted in Figure 2. However, the internal canal structure of "cydippid" ctenophores would seem to be an important trait in determining their taxonomic affinities and it is recommended that more attention be paid to it in subsequent investigations.

In *Aulacoctena acuminata*, the sole described representative of this genus, Mortensen (1932) described and figured the substomodeal adradial canals to arise from the stomodeum while the subtentacular adradial canals arose from the continuation of the perradial canal, the tentacular canal, that left the stomodeum (Fig. 2C). *A. acuminata* has both lateral diverticula arising from the meridional canals and simple tentacles, while *H. rubra* lacks true meridional canals, rather having canals that are more of a hybrid of the adradial and meridional canals found in other ctenophores, and it also lacks the lateral diverticula that would arise from them. Another reference to the genus *Aulacoctena* with an accompanying photograph was made by Deborah Kovacs & Kate Madin (1996), and this undescribed "cydippid" (identified by Dr. Larry Madin) has the same branching pattern of the internal canals as in *A. acuminata*, the substomodeal adradial canals supply the substomodeal meridional canals directly from the stomodeum, it has lateral diverticula arising from the meridional canals, and has simple tentacles that exit orally. The body shape of this undescribed *Aulacoctena* resembles the present enigmatic benthopelagic ctenophores in that it is rather angular and box-shaped.

The present benthopelagic ctenophores have both simple tentacles and lateral diverticula arising from the vicinity of the comb rows (Fig. 1B), both features being shared with *Aulacoctena* but only the first being shared with *Haeckelia*, which lacks lateral diverticula. It also seems that the present enigmatic ctenophore, although being quadrate, is somewhat flattened in the tentacular plane—a feature shared with *A. acuminata* as recorded in the original description by Mortensen (1932) and verified in a live specimen captured by manned submersible at 959 m in Sagami Bay during *Shinkai* 2000 dive 1055 (3.4°C, 34.82PSU, dissolved oxygen 1.2 ml/L). On the basis of the internal canal structure, which differs from that in *Haeckelia*, and the presence of orally-exiting simple tentacles, where those of *Bathyctena* are equipped with tentilla, we recommend that the genus *Aulacoctena* be placed in a new family, the Aulacoctenidae, with the following characters: Body quadrate to somewhat flattened in tentacular plane; substomodeal adradial canals arise directly from the stomodeum; subtentacular adradial canals arise from tentacular canal; meridional canals with lateral diverticula; simple tentacles without tentilla emerging orally; stomodeum with dark pigment.

The possibility exists that the present enigmatic ctenophore has aborally-exiting simple tentacles (Fig. 1C). The only ctenophore that is presently recorded in the literature as having simple tentacles that appear to exit aborally (although their true condition is in fact oral) is the benthic ctenophore *Tjalfiella tristoma* Mortensen 1910. This ctenophore has a "cydippid larva" stage, and the branching pattern of the internal canals is similar to that observed in *Aulacoctena* and the mertensiid ctenophores (Mortensen 1912, unpublished observations), although in the mertensiids the tentacles do in fact truly exit aborally. This internal canal structure is shared too by the euplokamidid (Mills 1987) ctenophores (Fig. 2C), though they, like the mertensiids, have tentilla-bearing rather than simple tentacles. The structure of the tentillum in euplokamidids is unlike that of any other ctenophore reported to date (Mills 1987), and they were not included in the phylogeny proposed by Podar et al. (2001). The mertensids and the Platyctene (incl. *Tjalfiella*) ctenophores are currently considered to be the most primitive ctenophores based on both molecular and morphological evidence (Podar et al. 2001). It may well be that other as-yet-undiscovered ctenophores, such as the present benthopelagic species, are the most basal and ancestral in the Phylum Ctenophora.

It has been concluded in the present study that the character of simple tentacles seems to be plesiomorphic, given that it is shared by such unrelated genera as *Aulacoctena*, *Haeckelia* and *Tjalfiella*. This, in combination with the presence of long terminal filaments on the end of the animal opposite the tentacles, and the peculiar ecology of this animal, suggests that it would be prudent to await the collection of specimens to determine the correct taxonomic position of this enigmatic ctenophore.

Long flexible filaments on a ctenophore have only thus far been reported in the lobate ctenophore *Eurhamphaea vexilligera* (Harbison & Madin 1982) and there are no reports of these being used for attachment to a substrate. Observations by the first author on live individuals of *E. vexilligera* captured at 33°33′N, 69°40′W and 19°49′N, 54°43′W during the *R/V Ronald H. Brown* CmarZ cruise in April 2006 did not suggest that they were able to attach to anything as no "stickiness" was evident. Long simple tentacles with no tentilla have been proposed to imply predation on tentaculate prey (Harbison 1985). Although tentaculate medusae have been reported from depths below 6,000 m (Lindsay 2005), none were observed in the benthopelagic layer where the present enigmatic ctenophore occurred. Other large, potential gelatinous prey in the form of

benthopelagic holothurians were observed at this site (Fig. 1E–G) and, although these holothurians were not tentaculate, we propose that this ctenophore feeds by anchoring itself to the substrate using the filaments and employing its long, simple tentacles to capture large gelatinous prey that are swept past in the current.

The benthopelagic habitat of these animals precludes the use of plankton nets for their collection, and their expected fragility and habitat depth makes their successful collection in a benthic trawl very unlikely. Furthermore, the loss of the world's deepest diving submersible platform, the ROV *Kaiko*, in May 2003 has ensured that procuration of specimens of this enigmatic ctenophore will only be possible following the development of a new submersible platform with the capability of reaching depths of over 7,000 m or the discovery of populations living at shallower depths.

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