Ctenophora: Illustrated Guide and Taxonomy

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Chapter 2

Ctenophora: Illustrated Guide and Taxonomy

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Abstract

Ctenophores or comb jellies represent the first diverging lineage of extant animals – sister to all other Metazoa. As a result, they occupy a unique place in the biological sciences. Despite their importance, this diverse group of marine predators has remained relatively poorly known, with both the species and higher-level taxonomy of the phylum in need of attention. We present a checklist of the phylum based on a review of the current taxonomic literature and illustrate their diversity with images. The current classification presented remains substantially in conflict with recent phylogenetic results, and many of the taxa are not monophyletic or untested. This chapter summarizes the existing classification focusing on recognized families and genera with 185 currently accepted, extant species listed. We provide illustrative examples of ctenophore diversity covering all but one of the 33 families and 47 of the 48 genera, as well as about 25–30 undescribed species. We also list the 14 recognized ctenophore fossil species and note others that have been controversially attributed to the phylum. Analyses of unique ctenophore adaptations are critical to understanding early animal evolution and adaptive radiation of this clade of basal metazoans.

Key words Ctenophora, *Pleurobrachia*, *Mnemiopsis*, *Bolinopsis*, *Beroe*, *Cestum*, *Ocyropsis*, *Euplokamis*, Platyctenida, Benthic ctenophores, Feeding, Classification, Phylogeny, Fossils, Cambrian, Evolution

1 Introduction

Ctenophores or comb jellies (Figs. 1, 2, and 3) are the most likely candidates for the earliest-diverging lineage of animals – sister to the rest of Metazoa [1–6] (Fig. 4). As a result, they occupy a unique place in biological sciences, illuminating distinct paths of early animal evolution and origins of animal complexity [7–10].

Phylogenetic understanding of the relationships within the Ctenophora is still young but indicates that the traditional taxonomy will need to be substantially modified as it does not match recent molecular analyses. The two classes, most of the orders, and some of the families and genera for which phylogenetic data are available appear to be polyphyletic or nested within others [11–14] (Fig. 5), with multiple examples of gain and losses of particular traits [6, 15].

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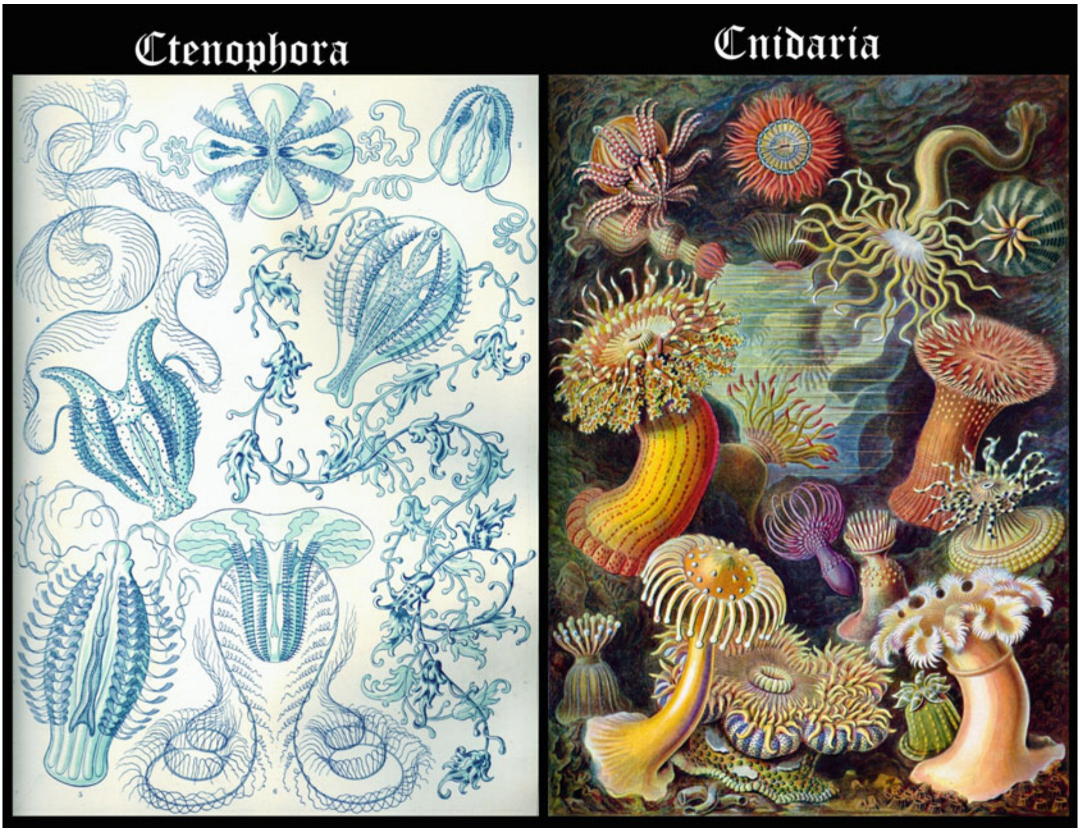


Fig. 1 Artistic Illustration of Ctenophore and Cnidarian diversity by Ernst Heinrich Philipp August Haeckel [86] (1899–1904; https:/commons.wikimedia.org/wiki/Kunstformen_der_Natur and https:/library.si.edu/digital-library/author/bibliographisches-institut-leipzig-germany). Left is the reproduction of plate 27 – Ctenophores: 1, 2 – *Haeckelia rubra*, Haeckeliidae; 3 – *Hormiphora foliosa* = *Hormiphora* sp., Cydippidae; 4 – *Callianira bialata*, Callianiridae; 5 – *Tinerfe cyanea*, Cydippidae; 6 – *Lampea pancerina*, Lampeidae

The species-level classification of ctenophores has not been reviewed in modern times, and the last genus-level overview was by Krumbach in 1925 [16], about 100 years ago. Dr. Claudia Mills (University of Washington, WA, USA) has initiated a summary of ctenophore taxa in 1998 and continues updating this ctenophore database [17] (https://faculty.washington.edu/cemills/Ctenolist.html). This became and was used as the basis for ctenophores in the World Register of Marine Species [WoRMS] (https://www.marinespecies.org/aphia.php?p=taxdetails&id=1248). In preparation for this chapter, GP reexamined the descriptions and synonymies of living ctenophore taxa from the primary literature and worked with Mills to reassess problematic ones. The results were used to update WoRMS and are presented below. Only published taxonomic information has been included. Numerous species and some higher taxa are poorly known, often based only on limited original descriptions, and should be considered *nomina dubia*.

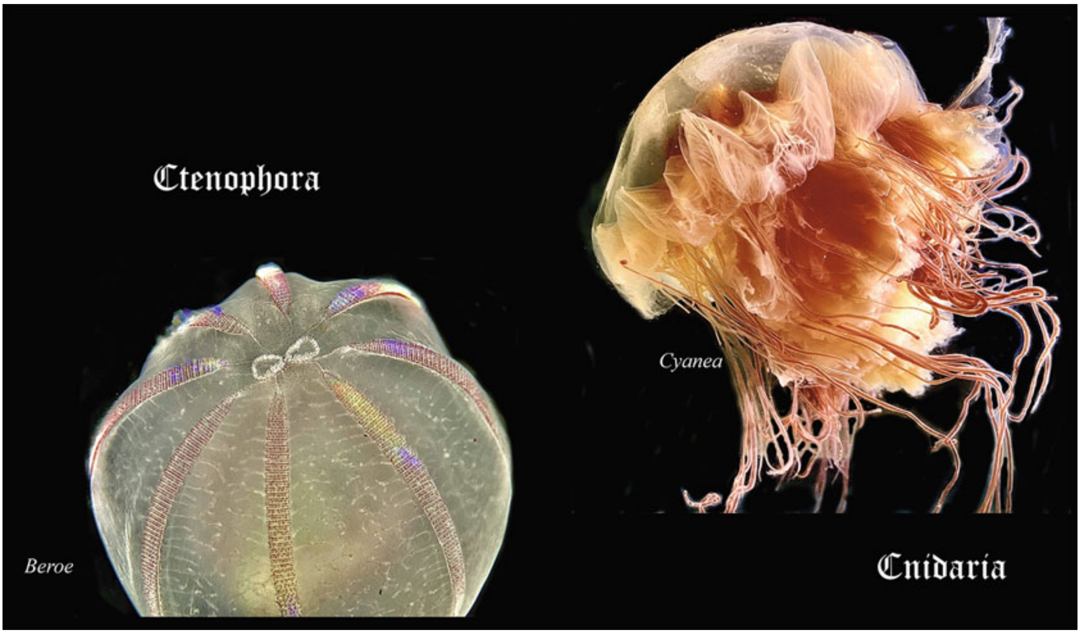


Fig. 2 Distinct body plans and locomotion modes in ctenophores vs. cnidarians. The left image is the top view of the comb jelly *Beroe abyssicola* with polar fields around the aboral organ and eight comb rows. The right image is the Lion's mane jellyfish, *Cyanea capillata* (Scyphozoa, Cnidaria). Both images are from Friday Harbor, WA, USA

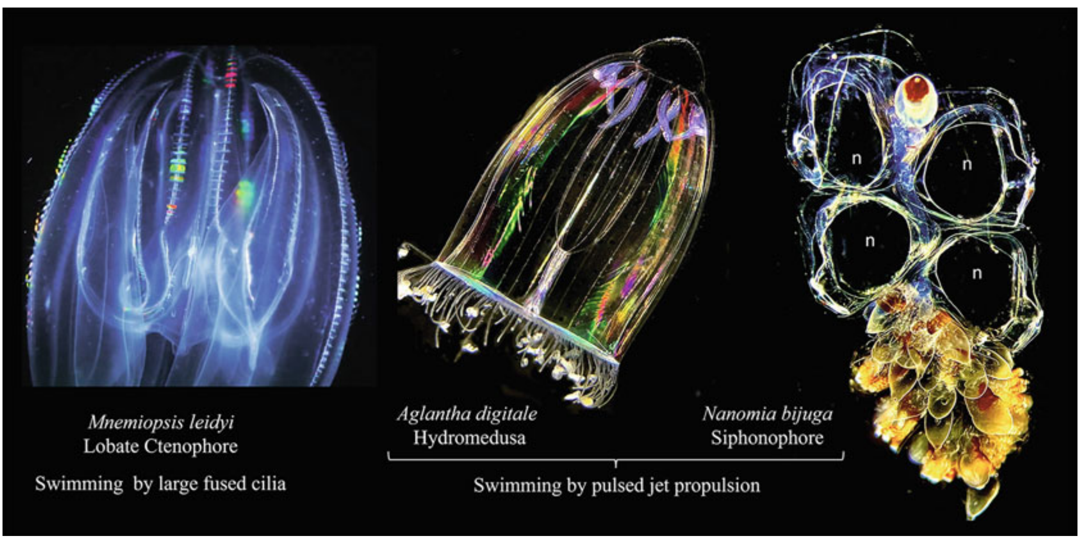


Fig. 3 Ctenophores primarily use their large ciliated plates for locomotion (e.g., the "sea walnut" *Mnemiopsis leidyi*, from Woods Hole, MA, USA). In contrast, cnidarians (e.g., *Aglantha* and *Nanomia*, both from Friday Harbor, WA, USA) primarily use muscular locomotion

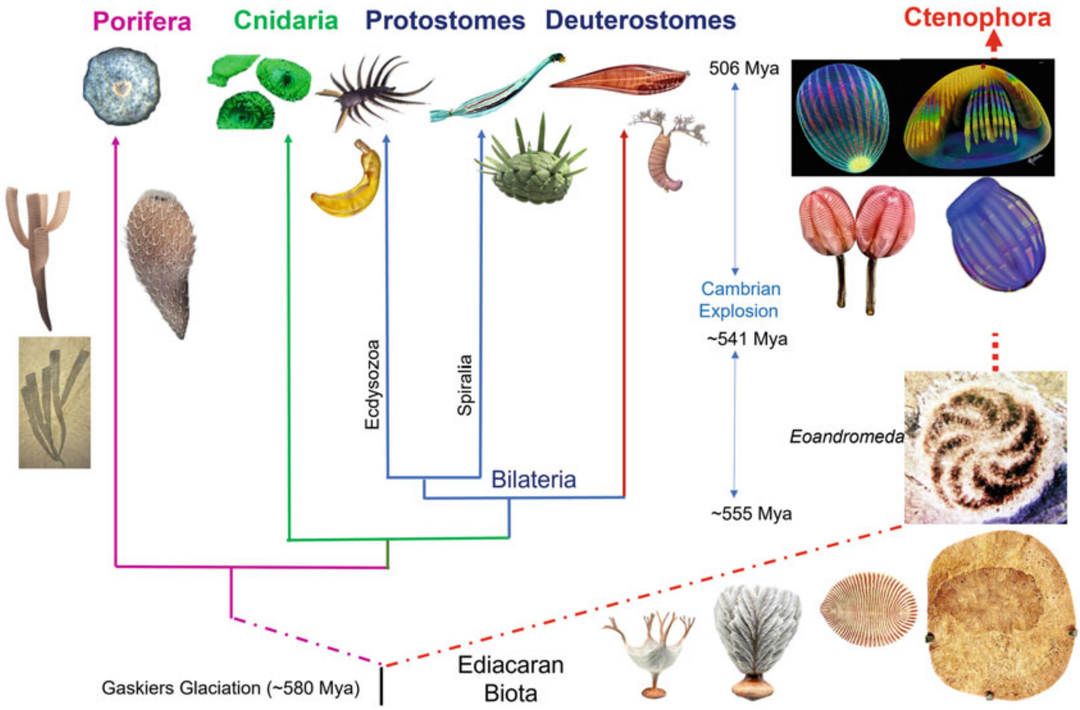


Fig. 4 Enigmatic origins of ctenophores as the sister lineage to all other Metazoa. Images of Cambrian animals are photos from reconstructions made by the Royal Ontario Museum© in Toronto, Canada. The ctenophore affinity of Ediacaran and many Cambrian fossils is disputed (*see* Subheading 4)

These are listed below, along with the well-known species, unless their status as *nomina dubia* has appeared in the literature and thus been captured in WoRMS. Synonymies of many species similarly remain contentious. The classification presented below reflects what is currently published and will undergo substantial changes as taxa are reassessed.

Traditionally [11, 13], two classes have been recognized in the phylum, but the paraphyly of the Tentaculata relative to the Nuda (ctenophores without tentacles) has long been suspected on morphological grounds [14] and confirmed by phylogenetics. Currently, nine orders are recognized (the two proposed by Ospovat [18] have not been assessed since their publication), with 33 families and 48 genera. Figure 5 summarizes relationships among selected ctenophore lineages, showing paraphyly of Cydippida and Lobata and placement of Nuda (Beroida). Cydippid-type organization (Figs. 6 and 7) is considered plesiomorphic, shared by many ctenophore lineages.

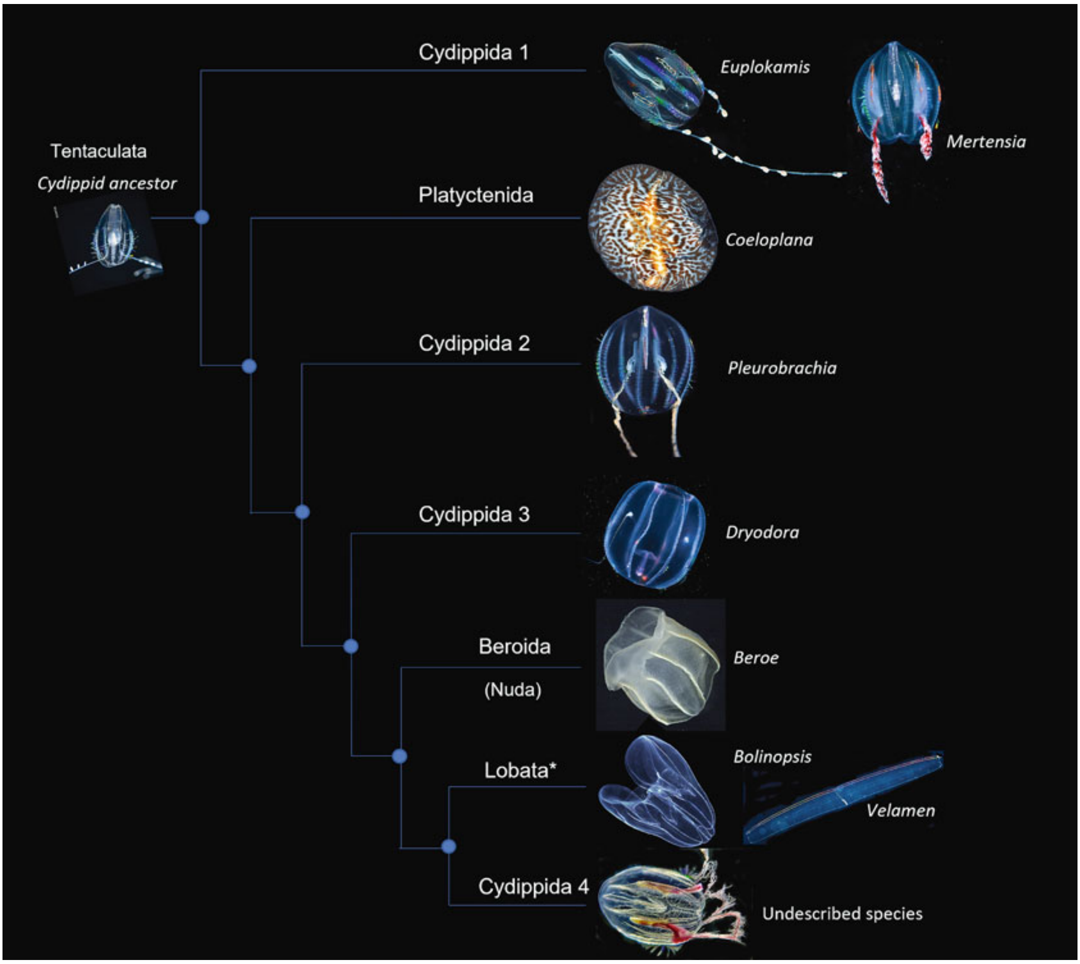


Fig. 5 Proposed phylogeny of several well-known ctenophore clades (based on [1, 6]). The revision of the higher-order taxonomy of ctenophores has not been systematically addressed, and we might suggest the name of the clade Euplokamida instead of Cydippida 1, as a tentative and representing one of the earliest branching lineages of ctenophores with unique adaptations in muscular and neural systems [65, 209]

2 List of Described Species and Illustrative Anatomy of the Phylum Ctenophora

Currently, 185 species of living ctenophores are recognized, although several dozen of these are too poorly known and should be considered *nomina dubia*. There are at least an additional 50 known but yet undescribed species and likely hundreds of ctenophore species (especially from deepwater habitats) awaiting discovery.

Below orders are arranged in order of decreasing species diversity: beginning with Cydippida with 62 described species (Figs. 6,

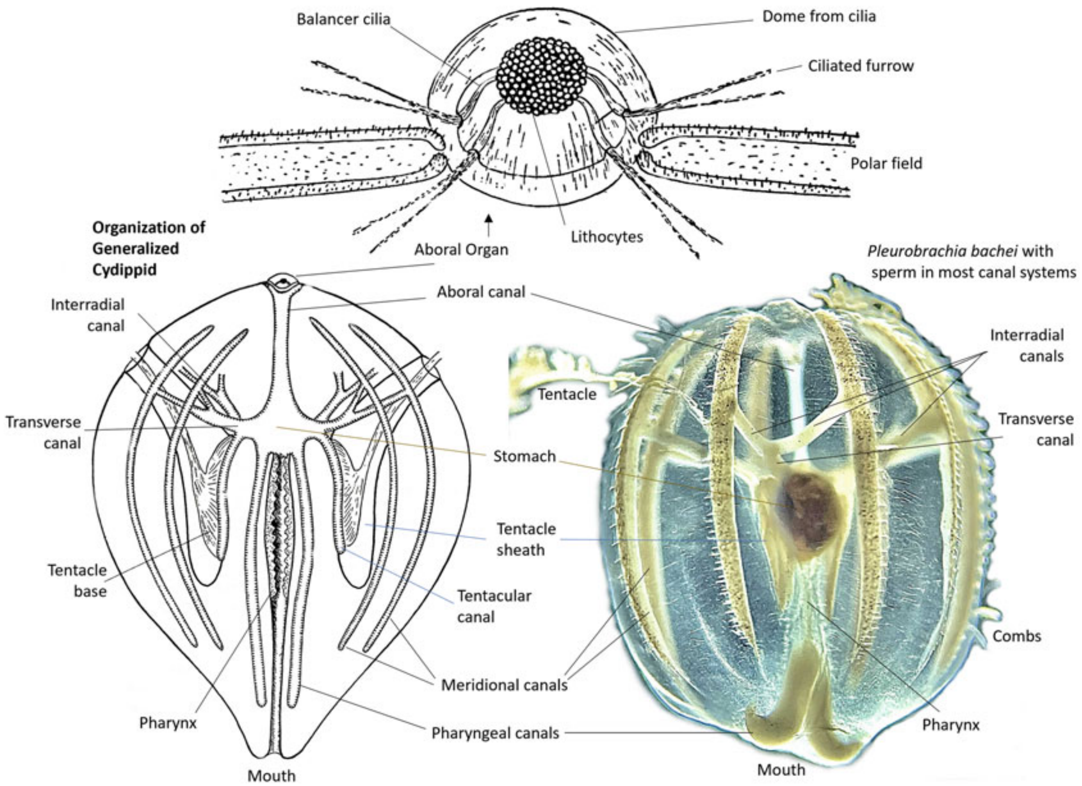


Fig. 6 General and microscopic anatomy of Cydippida with major organs and structures indicated (The left and top images are from [11]). The right image is *Pleurobrachia bachei*, with meridional canals filled with sperm. (The photo is taken in British Columbia, August 2023)

7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, and 89); Platyctenida, 49 species (Figs. 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, and 62); Lobata, 36 species (Figs. 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, and 89); and Beroida, 30 species (Figs. 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, and 101). Families are listed in alphabetical order. We also indicated the numbers of currently accepted species in each taxon.

Species with sequenced genomes are marked by #, while species with images in this chapter are bolded and referenced to appropriate figures.

For some taxa, we show multiple images to illustrate different aspects of morphology through ontogeny and by different types of illumination. We also provide illustrations of anatomy and selected ecological adaptations.

Several classical and recent manuscripts are useful in introducing details of ctenophore biology. These include monographic treatments from 1870 to 1940s focusing on ctenophore taxonomy and morphology with numerous illustrations [11, 19–27]. More recent reviews [28] summarize physiology [29–31], feeding [32], development [33, 34], and microscopic anatomy [35], as well as neurobiology [36–38]. Various aspects of ctenophore ecology and distribution can be found in the following publications: Harbison and colleagues [14, 39–41], Ospovat [18], Gershwin and colleagues about Australian ctenophores [42], as well as ctenophores in Antarctica [43], South Africa [44], New Zealand [45–47], Mexican seas [48], and many other regions worldwide [20, 24–26, 49–61].

3 Classification of Ctenophora

Phylum **Ctenophora** Eschscholtz, 1829 [62] (185 currently accepted species).

Marine, gelatinous, carnivorous animals with eight comb rows (or ctenes) formed by large fused cilia, biradial symmetry, true neurons, muscles, a gastrovascular system with canals in the mesoglea, an aboral organ with a statocyst that serves as an integrative center for locomotion, and other functions. As a result, the aboral organ is sometimes dubbed "an elementary brain" [1]. The aboral organ evolved independently from the analogous apical organs or sensory tufts in bilaterians and cnidarians, possesses a different organization [30, 31, 63–67], and should not be called "apical organ" in ctenophores.

Most ctenophores are simultaneous hermaphrodites with direct development and three embryonic layers (ectoderm, mesoderm, and endoderm). Most ctenophores are bioluminescent, and many that live in deep habitats are red-colored (Figs. 8, 9, 10, 35, and 75) to hide the animals in the darkness as red wavelengths are the first to be absorbed in water.

There are 199 species of ctenophores with valid names, including 185 extant and 14 fossils. Twelve other Cambrian and Ediacaran fossils were described as related to stem ctenophores, but their affinities are questionable and debated (*see* Subheading 4).

1. **"Cydippida"**: 13 families, 22 genera, 62 accepted species. A polyphyletic [1, 6] assemblage of pelagic ctenophores with well-developed tentacles that are retractible into specialized tentacle sheaths. Figures 6 and 7 provide overviews of typical representatives; Figs. 28 and 29 show some unusual feeding adaptations, and Figs. 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, and 37 illustrate diversity.

1.1. Aulacoctenidae Lindsay & Miyake, 2007 (**1**) [68]
Aulacoctena Mortensen, 1913 (**1**)

Aulacoctena acuminata Mortensen, 1913 [69] (Fig. 9)

1.2. Bathyctenidae Mortensen, 1913 [70] (**2**)
Bathyctena Mortensen, 1912 [25] (**2**)

Bathyctena chuni (Moser, 1909) [71] (Fig. 10)

Bathyctena latipharyngea (Dawydoff, 1946) [72] (Fig. 11)

1.3. Callianiridae Eschscholtz, 1829 [62] (**4**)
Callianira Lamarck, 1816 (**4**) [73] (Fig. 12)

Callianira antarctica Chun, 1897 (Fig. 13) [74]

Callianira bialata Delle Chiaje, 1841 [75] (Fig. 1)

Callianira cristata Moser, 1909 [71]

Callianira ficalbi Curreri, 1900 [76]

1.4. Cryptocodidae Leloup, 1938 (**1**)
Cryptocoda Leloup, 1938 (**1**)

Cryptocoda gerlachi Leloup, 1938 [77] (Fig. 14)

1.5. Ctenellidae C. Carré & D. Carré, 1993 (**1**). Monotypic family without colloblasts but with labial suckers [78].
Ctenella C. Carré & D. Carré, 1993 (**1**)

Ctenella aurantia C. Carré & D. Carré, 1993 [78] (Fig. 15)

1.6. Cydippidae Gegenbaur, 1856 [79] (**28**)
Attenboroughctena Ceccolini & Cianferoni, 2020 [80] (**1**)

Attenboroughctena bicornis (C. Carré & D. Carré, 1991) [81] (Fig. 16)

Hormiphora L. Agassiz, 1860 (**16**) (Fig. 17) [82]

Hormiphora australis (Benham, 1907) [213]

Hormiphora californensis# (Torrey, 1904) [83]

Hormiphora cilensis (Ghigi, 1909) [84]

Hormiphora cucumis (Mertens, 1833) [85]

Hormiphora elliptica (Eschscholtz, 1829) [62]

Hormiphora foliosa Haeckel, 1904 (Fig. 1) [86]

Hormiphora hormiphora (Gegenbaur, 1856) [87] (Fig. 18)

Hormiphora luminosa Dawydoff, 1946 [72]

Hormiphora ochracea (A. Agassiz & Mayer, 1902) [88]

Hormiphora octoptera (Mertens, 1833) [85]

Hormiphora palmata Chun, 1898 [89]

Hormiphora piriformis Ghigi, 1909 [84]

Hormiphora polytrocha Dawydoff, 1946 [72]

Hormiphora punctata Moser, 1909 [71]

Hormiphora sibogae Moser, 1903 [90]

Hormiphora spatulata Chun, 1898 [89]

Minictena C. Carré & D. Carré, 1993 (**1**)

Minictena luteola C. Carré & D. Carré, 1993 [91, 92] (Fig. 19)

Pleurobrachia Fleming, 1822 (**8**) [93] (Figs. 6, 17, 20, 21, 22, and 23)

Pleurobrachia bachei# A. Agassiz, 1860 [82] (Figs. 6, 17, 20, 21, and 22)

Pleurobrachia brunnea Mayer, 1912 [24]

Pleurobrachia cyanea (Chun, 1889) [94]

Pleurobrachia globosa Moser, 1903 [90]

Pleurobrachia pigmentata Moser, 1903 [90]

Pleurobrachia pileus (O. F. Müller, 1776) [95] (Fig. 23)

Pleurobrachia rhodopis Chun, 1879 [74]

Pleurobrachia striata Moser, 1908 [96]

Tinerfe Chun, 1898 [89] (**1**)

Tinerfe cyanea (Chun, 1889) [94] (Fig. 24)

1.7. Dryodoridae Harbison, 1996 [41] (**1**)
Dryodora L. Agassiz, 1860 (**1**) [82]

Dryodora glandiformis (Mertens, 1833) [85] (Fig. 25).

1.8. Euplokamididae Mills, 1987 (**5**) [97]
Euplokamis Chun, 1879 (**5**) [74]

Euplokamis crinita (Moser, 1909) [71]

Euplokamis dunlapae Mills, 1987 (Figs. 7 and 26) [98]

Euplokamis evansae Gershwin, Zeidler & Davie, 2010 [42]

Euplokamis helicoides (Ralph & Kaberry, 1950) [46]

Euplokamis stationis Chun, 1879 [74]

1.9. Haeckeliidae Krumbach, 1925 [99] (**4**)
Haeckelia Carus, 1863 [100] (**4**)

Haeckelia beehleri (Mayer, 1912) [24] (Fig. 27)

Haeckelia bimaculata C. Carré & D. Carré, 1989 [101]

Haeckelia filigera (Chun, 1880) [20]

Haeckelia rubra (Kölliker, 1853) (Fig. 28) [102]

1.10. Lampeidae Stechow, 1921 (**5**) [103]
Lampea Stechow, 1921 (**5**) (Fig. 28)

Lampea dimidiata (Eschscholtz, 1829)

Lampea elongata (Quoy & Gaimard, 1833) [104]

Lampea komai (Dawydoff, 1937) [105]

Lampea lactea (Mayer, 1912) [24] (Fig. 29)

Lampea pancerina (Chun, 1879) [74] (Fig. 1)

1.11. Mertensiidae L. Agassiz, 1860 (**3**) [82]
Mertensia Lesson, 1829 (**2**) (Fig. 13)

Mertensia groenlandica Lesson, 1829 [106]

Mertensia ovum (Fabricius, 1780) [107, 108] (Figs. 7, 30, 31, and 32)

Charistephane Chun, 1879 (**1**)

Charistephane fugiens Chun, 1879 [74] (Fig. 33)

1.12. Pukiidae Gershwin, Zeidler & Davie, 2010 (**2**) [42]
Pukia Gershwin, Zeidler & Davie, 2010 (**2**)

Pukia falcata Gershwin, Zeidler & Davie, 2010 (Fig. 34)

Pukia ohtsukai Lindsay, 2017 [68] (Fig. 34)

1.13. Vampyroctenidae Townsend, Damian-Serrano & Whelan, 2020 (**1**)
Vampyroctena Townsend, Damian-Serrano & Whelan, 2020 (**1**)

Vampyroctena delmarvensis Townsend, Damian-Serrano & Whelan, 2020 [109] (Fig. 35)

Cydippida *incertae sedis* (of uncertain placement) (**4** species)

Duobrachium Ford, Bezio & Collins, 2020 (**1**)

Duobrachium sparksae Ford, Bezio & Collins, 2020 [56] (Fig. 36)

Paracelsia Dawydoff, 1946 (**1**)

Paracelsia quadriloba Dawydoff, 1946 [72] (Fig. 19)

Thoe Chun, 1879 (**1**)

Thoe paradoxa Chun, 1879 [74] (Fig. 37)

Tizardia Dawydoff, 1946 (**1**)

Tizardia phosphorea Dawydoff, 1946 [72] (Fig. 19)

2. **Order Platyctenida** Bourne 1900: Five families and six genera with 49 accepted species (Figs. 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, and 62). A well-defined clade of benthic ctenophores, with two well-developed tentacles, differentiated aboral and oral sides, the latter a creeping sole derived from the stomodaeum. Comb rows lost in adults, except in the Ctenoplanidae; embryos brooded. The aboral organ can be reduced, and the statocyst is lost in *Savangia*. Most species epifaunal on invertebrates or algae [1, 6, 110, 111].

   2.1. Coeloplanidae Willey, 1896 [112] (**33**)

   Coeloplana Kowalevsky, 1880 [113] (**32**) (Figs. 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, and 56).

   Coeloplana agniae Dawydoff, 1930 [114]

   Coeloplana anthostella Song & Hwang, 2010 [115]

   Coeloplana astericola Mortensen, 1927 [116] (Fig. 39)

   Coeloplana bannwarthii Krumbach, 1933 [117] (Fig. 40)

   Coeloplana bocki Komai, 1920 [118]

   Coeloplana duboscqui Dawydoff, 1930 [114]

   Coeloplana echinicola Tanaka, 1932 [119]

   Coeloplana fishelsoni Alamaru, Brokovich & Loya, 2016 [120] (Fig. 41)

   Coeloplana gonoctena Krempf, 1921 [121]

   Coeloplana huchonae Alamaru, Brokovich & Loya, 2016 [120]

   Coeloplana indica Devanesen & Varadarajan, 1942 [122]

   Coeloplana komaii Utinomi, 1963 [123]

   Coeloplana krusadiensis Devanesen & Varadarajan, 1942 [122] (Fig. 42)

   Coeloplana lineolata Fricke, 1970 [61]

   Coeloplana loyai Alamaru & Brokovich, 2016 [120] (Figs. 43 and 44)

   Coeloplana mellosa Gershwin, Zeidler & Davie, 2010 [42]

   Coeloplana mesnili Dawydoff, 1938 [124]

   Coeloplana meteoris Thiel, 1968 [125] (Figs. 45 and 46)

   Coeloplana metschnikowii Kowalevsky, 1880 [113]

   Coeloplana mitsukurii Abbott, 1902 [126] (Fig. 47)

   Coeloplana perrieri Dawydoff, 1930 [114]

   Coeloplana punctata Fricke, 1970 [61]

Coeloplana reichelti Gershwin, Zeidler & Davie, 2010 [42]

Coeloplana scaberiae Matsumoto & Gowlett-Holmes, 1996 [127] (Fig. 42)

Coeloplana sophiae Dawydoff, 1938 [124]

Coeloplana tattersalli Devanesen & Varadarajan, 1942 [122]

Coeloplana thomsoni Matsumoto, 1999 [128]

Coeloplana waltoni Glynn, Bayer & Renegar, 2014 [129]

Coeloplana weilli Dawydoff, 1938 [124]

Coeloplana willeyi Abbott, 1902 [126] (Fig. 48)

Coeloplana wuennenbergi Fricke, 1970 [61] (Fig. 49)

Coeloplana yulianicorum Alamaru, Brokovich & Loya, 2016 [120] (Fig. 50)

Vallicula Rankin, 1956 (**1**)

Vallicula multiformis Rankin, 1956 [130] (Fig. 57)

2.2. Ctenoplanidae Willey, 1896 [112] (**12**)
Ctenoplana Korotneff, 1886 (**12**) [131] (Figs. 38, 58, 59, and 60)

Ctenoplana agniae Dawydoff, 1929 [132]

Ctenoplana bengalensis Gnanamuthu & Nair, 1948 [133]

Ctenoplana caulleryi (Dawydoff, 1936) [134]

Ctenoplana duboscqui Dawydoff, 1929 [132]

Ctenoplana korotneffi Willey, 1896 [112]

Ctenoplana kowalevskii Korotneff, 1886 [131]

Ctenoplana maculomarginata Yosii, 1933 [135]

Ctenoplana maculosa Yosii, 1933 [135]

Ctenoplana neritica Fricke & Plante, 1971 [136]

Ctenoplana perrieri Dawydoff, 1936 [134]

Ctenoplana rosacea Willey, 1896 [112]

Ctenoplana yuri Dawydoff, 1929 [132]

2.3. Lyroctenidae Komai, 1942 (**2**) [137–140]
Lyrocteis Komai, 1941 (**2**) (Fig. 61)

Lyrocteis imperatoris Komai, 1941 (Fig. 62) [141]

Lyrocteis flavopallidus Robilliard & Dayton, 1972 [142]

2.4. Savangiidae Harbison & Madin, 1982 (**1**) [40].
Savangia Dawydoff, 1950 (**1**), no illustrations available; no specimens were recorded since the original description more than 70 years ago [143].

Savangia atentaculata Dawydoff, 1950 [143].

This truly enigmatic ctenophore species has only been found in the China Sea; it has six symmetrical aboral papillae beset with small tubercles; neither an aboral organ nor anal pores were reported. The oral part of the stomodaeum is permanently everted, forming a creeping sole as in other Platyctenida. *Savangia* is chocolate brown and can reach 2.5 cm [40, 143].

2.5. Tjalfiellidae Komai, 1922 (**1**)

Tjalfiella Mortensen, 1910 (**1**)

Tjalfiella tristoma Mortensen, 1910 [25] (Fig. 38)

3. **Order Lobata:** 9 families and 11 genera with 34 accepted species (Figs. 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, and 89). A paraphyletic group of fragile pelagic ctenophores with reduced tentacles, body compressed in the tentacle plane, two large oral lobes and four auricles, and oral ends of gastrovascular canals anastomosing [1, 6].

3.1. Bathocyroidae Harbison & Madin, 1982 (**3**) [144]

Bathocyroe Madin & Harbison, 1978 (**3**)

Bathocyroe fosteri Madin & Harbison, 1978 [145] (Fig. 64)

Bathocyroe longigula Horita, Akiyama & Kubota, 2011 [146] (Figs. 64 and 65)

Bathocyroe paragaster (Ralph & Kaberry, 1950)

3.2. Bolinopsidae Bigelow, 1912 [147] (**12**)

Bolinopsis L. Agassiz, 1860 [82] (**10**)

Bolinopsis ashleyi Gershwin, Zeidler & Davie, 2010 [42] (Fig. 66)

Bolinopsis chuni (von Lendenfeld, 1884) [148]

Bolinopsis elegans (Mertens, 1833) [85]

Bolinopsis indosinensis Dawydoff, 1946 [72]

Bolinopsis infundibulum (O.F. Müller, 1776) [95] (Figs. 67 and 68)

Bolinopsis microptera# (A. Agassiz, 1865) [149] (Fig. 70)

Bolinopsis mikado (Moser, 1907) [150] (Fig. 69)

Bolinopsis ovalis (Bigelow, 1904) [151]

Bolinopsis rubripunctata Tokioka, 1964 [152]

Bolinopsis vitrea (L. Agassiz, 1860) [82] (Fig. 70)

Mnemiopsis L. Agassiz, 1860 [82] (**2**)

Mnemiopsis gardeni L. Agassiz, 1860 [82]

Mnemiopsis leidyi# A. Agassiz, 1865 [149] (Figs. 63 and 70)

3.3. Eurhamphaeidae L. Agassiz, 1860 [82] (**2**)
Deiopea Chun, 1879 [74] (**1**)

Deiopea kaloktenota Chun, 1879 (Fig. 71).

Eurhamphaea Gegenbaur, 1856 [87] (**1**)

Eurhamphaea vexilligera Gegenbaur, 1856 [153] (Figs. 72 and 73)

3.4. Kiyohimeidae Komai & Tokioka, 1940 [154] (**2**)
Kiyohimea Komai & Tokioka, 1940 (**2**)

Kiyohimea aurita Komai & Tokioka, 1940 [154] (Fig. 74)

Kiyohimea usagi Matsumoto & Robison, 1992 [155, 156] (Fig. 74)

Or ref. 85, Video: https://www.youtube.com/watch?app=desktop&v=WNX8xcAvSEY

3.5. Lampoctenidae Harbison, Matsumoto & Robison, 2001 (**1**)
Lampocteis Harbison, Matsumoto & Robison, 2001 (**1**) (Fig. 75)

Lampocteis cruentiventer Harbison, Matsumoto & Robison, 2001 [157] (Fig. 76)

3.6. Leucotheidae Krumbach, 1925 [16] (**6**)
Leucothea Mertens, 1833 [85] (**6**) (Fig. 77)

Leucothea filmersankeyi Gershwin, Zeidler & Davie, 2010 [42]

Leucothea grandiformis (Agassiz & Mayer, 1899) [158]

Leucothea japonica Komai, 1918 [159]

Leucothea multicornis (Quoy & Gaimard, 1824) [160] (Figs. 78, 79, and 80)

Leucothea ochracea Mayer, 1912 [24] (Fig. 81)

Leucothea pulchra Matsumoto, 1988 [161] (Fig. 77)

3.7. Lobatolampeidae Horita, 2000 (**1**)
Lobatolampea Horita, 2000 (**1**)

Lobatolampea tetragona Horita, 2000 [162, 163] (Fig. 82)

3.8. Ocyropsidae Krumbach, 1925 [99] (**5**). At least two species (*O. maculata* and *O. crystallina*) are dioecious rather than hermaphroditic [164].

Ocyropsis Mayer, 1912 [24] (**5**)

Ocyropsis crystallina (Rang, 1827) [165] (Figs. 83, 84, and 85)

Ocyropsis fusca (Rang, 1827) [165]

Ocyropsis maculata (Rang, 1827) [165] (Figs. 86 and 87)

Ocyropsis pteroessa Bigelow, 1904 [151]

Ocyropsis vance Gershwin, Zeidler & Davie, 2010 [42]

3.9. Pterygioctenidae Mills & Dubois, 2023 (**2**) [166]
Pterygiocteis Mills & Dubois, 2023 (**2**)

Pterygiocteis nigrolimbatus Mills & Dubois, 2023 [166] (Fig. 88)

Pterygiocteis pinnatus (Ralph & Kaberry, 1950) [46]

Lobata *incertae sedis*. The following species (*Axiotima gaedii*, Eschscholtz, 1825, 1829) has not been recognized after its original description [62, 167]; the original drawing is not interpretive.

4. **Order Beroida** Eschscholtz, 1825 (Class Nuda) [167]: One family, two genera with 30 accepted species (Figs. 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, and 101). Muscular pelagic predators that typically feed on other ctenophores. There are no tentacles during any time in their development. The aboral organ is well-developed with numerous papillae. All species have a very wide mouth; the stomodeum (pharynx) occupies most of the body; meridional canals in most species have numerous side branches.

4.1. Beroidae Eschscholtz, 1825 (**30** species) [168]; (Figs. 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, and 100).
Beroe Müller, 1776 [95] (**29**)

Beroe abyssicola Mortensen, 1927 [116] (Figs. 90, 91, 92, 93, 94, and 95).

Beroe australis Agassiz & Mayer, 1899 [158]

Beroe baffini Kramp, 1942; the original description is not documented

Beroe basteri Lesson, 1829 [106]

Beroe beroe (Linnaeus, 1758) [169]

Beroe campana Komai, 1918 [159]

Beroe chiaji Lesson, 1836 [170]

Beroe compacta Moser, 1909 [71]

Beroe constricta Chamisso & Eysenhardt, 1821 [171]

Beroe cucumis Fabricius, 1780 [172] (Figs. 96, 97, and 98)

Beroe cyathina (A. Agassiz, 1860) [82]

Beroe fallax Lesson, 1836 [170]

Beroe flemingii (Eschscholtz, 1829) [62]

Beroe forskalii Milne Edwards, 1841 [173] (Fig. 99)

Beroe gracilis Künne, 1939 [174]

Beroe hyalina Moser, 1907 [150]

Beroe macrostomus Péron & Lesueur, 1807 [175]

Beroe mitraeformis Lesson, 1829 [106]

Beroe mitrata (Moser, 1907) [150] (Fig. 89)

Beroe ovata Bruguière, 1789 [176] (Fig. 100)

Beroe pandorina Moser, 1903 [90]

Beroe penicillata (Mertens, 1833) [85]

Beroe quoyi Lesson, 1836 [170]

Beroe ramosa Komai, 1921 [177]

Beroe roseus Quoy & Gaimard, 1824 [160]

Beroe rufescens (Eschscholtz, 1829) [62]

Beroe santonum Lesson, 1843 [178]

Beroe scoresbyi Lesson, 1836 [170]

Beroe shakespeari Benham, 1907 [47]

Neis Lesson, 1829 (**1**)

Neis cordigera Lesson, 1829 [106] (Fig. 101)

5. **Order Cestida (4)**. One family, two genera, four accepted species. These pelagic ctenophores are highly compressed in the tentacular plane with a long ribbon-like body (10–150 cm); four comb rows and the tentacles are reduced, but they have two rows of small tentilla along their oral margin.

5.1. Cestidae Gegenbaur, 1856 [79] (**4**)

Cestum Lesueur, 1813 [179] (**3**)

Cestum mertensii L. Agassiz, 1860 [82]

Cestum najadis Eschscholtz, 1829 [62]

Cestum veneris Lesueur, 1813 [179] (Fig. 102)

Velamen Krumbach, 1925 (**1**)

Velamen parallelum (Fol, 1869) [180] (Fig. 103)

6. **Order Cryptolobiferida** (**2**). Order with one family proposed by Ospovat [18] for two genera and species of poorly known tropical ctenophores; no recent photos.

6.1. Cryptolobatidae Ospovat, 1985 [18]

Cryptolobata Moser, 1909 (**1**)

Cryptolobata primitiva Moser, 1909 [71] (Fig. 104)

Lobocrypta Dawydoff, 1946 (**1**)

Lobocrypta annamita Dawydoff, 1946 [72] (Fig. 105a)

7. **Order Ganeshida**. One family and genus, two accepted species. Tropical ctenophores of intermediate form between cydippid and lobate body plan [14], with large mouth, body compressed in tentacular plane, tentacles with sheaths and tentilla, and circumoral canal. Known from earlier morphological observations; no recent photos.

7.1. Ganeshidae Moser, 1907 [150] (**2**)
Ganesha Moser, 1907 [150] (**2**)

Ganesha annamita Dawydoff, 1946 [72] (Fig. 105d)

Ganesha elegans (Moser, 1903) [90] (Fig. 105c)

8. **Order Cambojiida.** Monotypic order proposed by Ospovat for a poorly known tropical ctenophore known from two specimens [18]; no recent photos.

8.1. Cambojiidae Ospovat, 1985 [18] (**1**)
Cambodgia Dawydoff, 1946 (**1**)

Cambodgia elegantissima Dawydoff, 1946 [72] (Fig. 105b)

9. **Order Thalassocalycida** (**1**). Monotypic. Extremely fragile pelagic ctenophores with medusa-bell shape and unique feeding strategy [181, 182]. Tentacles (without sheaths) are near the mouth.

9.1. Thalassocalycidae Madin & Harbison, 1978 (**1**).
Thalassocalyce Madin & Harbison, 1978 (**1**)

Thalassocalyce inconstans Madin & Harbison, 1978 [181] (Fig. 106).

4 Fossil Ctenophora

Fragile ctenophores left a very limited fossil record, and the affinity of early fossils is often questionable. The middle Cambrian (~506–510 MA) *Fasciculus vesanus*, *Xanioascus canadensis*, *Ctenorhabdotus capulus* [183], *Ctenorhabdotus campanelliformis* and *Thalassostaphylos elegans* [184] from the Burgess Shale had multiple comb plates but no tentacles. The only known specimen of *Fasciculus vesanus* (114 mm) appears to have possessed ~80 comb rows and had bilaterial-like symmetry. *Xanioascus* and *Ctenorhabdotus* both had 24 comb rows (maximum sizes: 122 mm and 77 mm, respectively), and *Thalassostaphylos* had 16 rows [184] (but *see* [185] for evidence of tentacles in Cambrian ctenophores).

Class Scleroctenophora † (extinct) (**6**).

Armored, probably sessile, ctenophore-like animals from the early Cambrian Chengjiang biota (ca. 520 Ma) with oral-aboral axis, aboral sense organ, and eight ctene rows [186].

1. *Batofasciculus ramificans* Hou, Bergstöm, Wang, Feng & Chen, 1999† [187]. Chengjiang Biota, Lower Cambrian: Yunnan, China (see also [188] for the fossil affinity discussion).
2. *Galeactena hemispherica* Ou, Xiao, Han, Sun, Zhang, Zhang & Shu, 2015† Chengjiang Biota, Lower Cambrian: Yunnan, China
3. *Gemmactena actinala* Ou, Xiao, Han, Sun, Zhang, Zhang & Shu, 2015† Chengjiang Biota, Lower Cambrian: Yunnan, China
4. *Maotianoascus octonarius* Chen and Zhou, 1997†. Chengjiang Biota, Lower Cambrian: Yunnan, China [189]; see also [190] for possible embryos.
5. *Thaumactena ensis* Ou, Xiao, Han, Sun, Zhang, Zhang & Shu, 2015†. Chengjiang Biota, Lower Cambrian: Yunnan, China
6. *Trigoides aclis* Luo and Hu, 1999† [191] Chengjiang Biota, Early Cambrian: Yunnan, China (see also [192]).

Cydippida (**2**)

7. *Archeocydippida hunsrueckiana* Stanley & Stürmer, 1987† [193], Devonian: from Hunsrück Slate, Germany. The fossil with (two proposed tentacles) was reinterpreted as not a ctenophore [194] but then accepted [183] and again challenged [17].
8. *Paleoctenophora brasseli* Stanley & Stürmer, 1983† [195], from Devonian: Hunsrück Slate, Germany, also independently accepted as a ctenophore [183].

Others (**6**)

Family **Ctenorhabdotidae (6)** Conway Morris and Collins, 1996 [183], 24 comb rows.

9. ***Ctenorhabdotus capulus*** Conway Morris and Collins, 1996† [183]. Middle Cambrian: Burgess Shale, British Columbia, Canada (Fig. 107c)
10. *Ctenorhabdotus campanelliformis* Parry, Lerosey-Aubril, Weaver and Ortega-Hernandez, 2021† [184], Middle Cambrian: House Range of western Utah, USA

Family **Fasciculidae** Conway Morris and Collins, 1996 [183].

11. ***Fasciculus vesanus*** Simonetta and Della Cave, 1978† [183]. 80 comb rows. Middle Cambrian: Burgess Shale, British Columbia, Canada (Fig. 107b)

Family **Xanioascidae** Conway Morris and Collins, 1996 [183].

12. ***Xanioascus canadensis*** Conway Morris and Collins, 1996† [183]. 24 comb rows. Middle Cambrian: Burgess Shale, British Columbia, Canada (Fig. 107a)

Family is not defined for the species belows.

13. *Thalassostaphylos elegans* Parry, Lerosey-Aubril, Weaver and Ortega-Hernandez, 2021† [184]. Middle Cambrian: House Range of western Utah, USA; 16 comb rows.
14. *Daihuoides jakobvintheri* Klug, Kerr, Lee & Cloutier, 2021 † Later Devonian ctenophore-type organism; it is suggested to be a sister lineage to *Fasciculus* as a later surviving representative of stem-ctenophores [196].

Questionable Cambrian ctenophore-like fossils: (**8**)

15. ***Siphusauctum gregarium*** O'Brien and Caron, 2012† [197]. Middle Cambrian, Burgess Shale, ~510 million years old. A stalked, sessile fossil (*see also* Fig. 107d) with six radial parts with comb-like elements that surround an internal body cavity with a large stomach, conical median gut, and straight intestine. *The* animal was probably an active filter-feeder, with water passing through the calyx openings, capturing food particles with its comb-like elements. More than 1100 specimens were collected [197].
16. *Dinomischus isolatus*† – Proposed as a sessile stem-group ctenophore, Middle Cambrian, Burgess Shale [198].
17. *Dinomischus venustus*† – Proposed as a sessile stem-group ctenophore, Chengjiang Biota, Lower Cambrian [198].
18. *Daihua sanqiong*† – Proposed as a sessile stem-group ctenophore, Chengjiang Biota, Lower Cambrian, [198].
19. *Xianguangia sinica*† – Proposed as a sessile stem-group ctenophore, Chengjiang Biota, Lower Cambrian [198], with possible tentaculate-type structures [199].
20. *Sinoascus papillatus* Chen and Zhou, 1997†. Chengjiang Biota, Lower Cambrian: Yunnan, China. The fossil was initially interpreted as an early ctenophore, but this affinity is uncertain [188].
21. *Yunnanoascus haikouensis* Hu et al. 2007† [188]. Chengjiang Biota, Lower Cambrian: Yunnan, China. The fossil

was initially interpreted as a ctenophore [200], but later it was assigned to Cnidaria as a jellyfish with rhopalia [201].

22. *Stromatoveris psygmoglena* Shu, 2006† [202]. Chengjiang Biota, Lower Cambrian: Yunnan, China. The fossil has been interpreted as an early stem-group ctenophore; it can be a potential "link" between Ediacaran and Cambrian biotas [203]

Questionable Precambrian ctenophore fossils (4)

23. *Eoandromeda octobrachiata*† Ediacaran Biota, South China. The fossil has been interpreted as a ctenophore-like organism due to apparent spiral comb-like structures (4 pairs) and octoradial symmetry or as an early stem-group ctenophore [204].
24. *Dickinsonia* spp.† Ediacaran Biota. Interpreted as a possible ctenophore due to biradial symmetry [205].
25. *Rangea schneiderhoehni*, Gurich, 1930†. Dzik (2002) argues for possible ctenophore affinities of this Precambrian sea-pen-like organism [206].
26. *Namacalathus hermanastes*†† [207]; a biomineralized fossil similar to *Siphusauctum*, but also interpreted as lophotrochozoan [208].

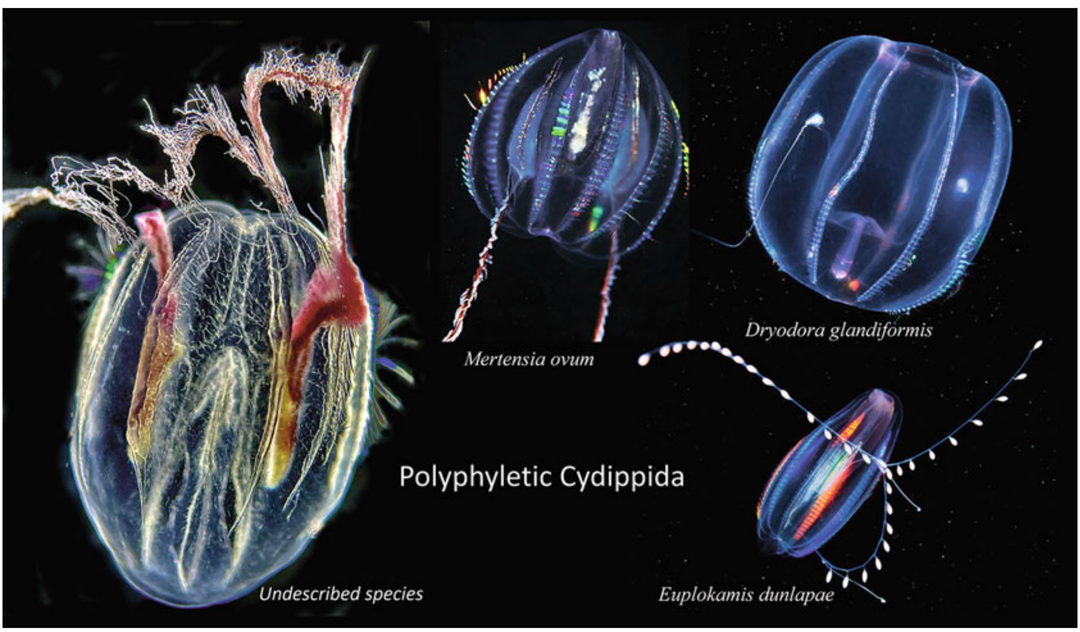


Fig. 7 Illustrated examples of different cydippid species. (The photo of an undescribed cydippid was taken at Friday Harbor Laboratories, Washington, USA. *Mertensia*, *Dryodora*, and *Euplokamis* are from Arctic photos by Alexander Semenov© (https:/www.flickr.com/photos/a_semenov/40592507363/in/photostream/))

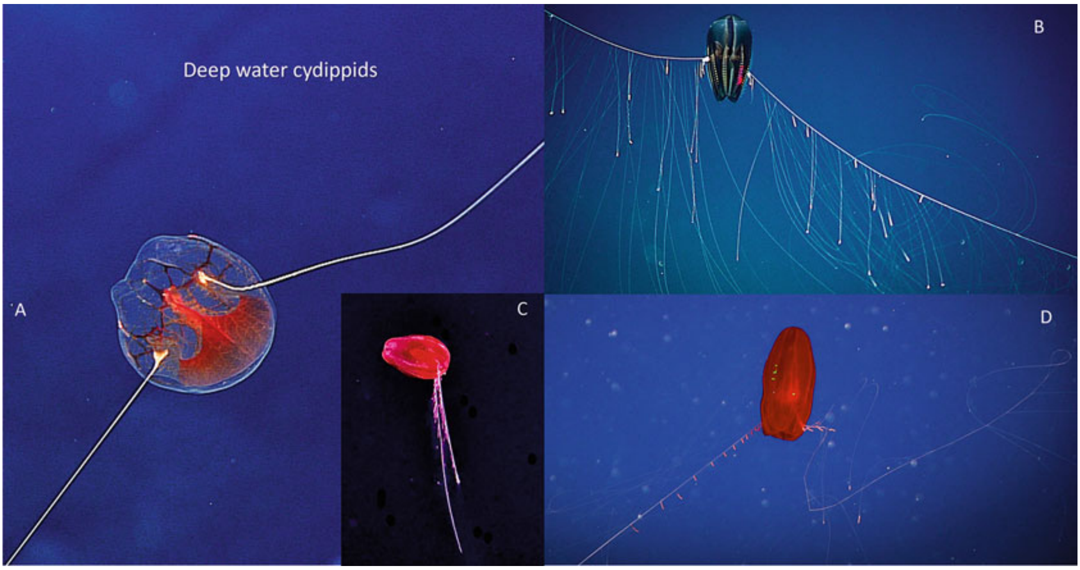


Fig. 8 Deepwater cydippids with red/black coloration. Their pigments hide the animals in the darkness as red light is the first wavelength to be absorbed in water from the visible spectrum. (**a**) A ctenophore with long tentacles (Aulacoctenidae) was collected at Southernmost Cone within the Pacific Remote Islands Marine National Monument. (Image courtesy of the NOAA Office of Ocean Exploration and Research, 2015 Hohonu Moana (https:/oceanexplorer.noaa.gov/okeanos/explorations/ex1504/logs/sept27/sept27.html; or https:/www.flickr.com/photos/oceanexplorergov/22568727927/in/photostream/)). (**b**) This dark cydippid was observed ~1460 m deep in an area of the Western Gulf of Mexico. (Image courtesy of the NOAA Office of Ocean Exploration and Research, Gulf of Mexico, 2018 (https:/www.flickr.com/photos/oceanexplorergov/40959988584/in/photostream/)). (**c**) Undescribed deepwater cydippid from the public exposition at the Monterey Bay Aquarium. (**d**) Undescribed cydippid. (Courtesy of the NOAA Office of Ocean Exploration and Research, Deep Connections 2019 (https:/www.flickr.com/photos/oceanexplorergov/48976460707/in/photostream/))

Fig. 9 Deep (**a**–**c**) *Aulacoctena acuminata*, its body can be up to 30 cm long with white tentacles; observed at depths of 500 to over 3000 m. (For *Aulacoctena* photos, credits go to Marsh Youngbluth/MAR-ECO, Census of Marine Life (https:/ocean.si.edu/ocean-life/invertebrates/red-mid-water-comb-jelly); (https:/oceanexplorer.noaa.gov/explorations/05arctic/logs/july19/media/aulacoctena.html); see also *video courtesy of The Hidden Ocean 2016: Chukchi Borderlands, Oceaneering-DSSI* (https:/oceanexplorer.noaa.gov/explorations/16arctic/logs/video/combjelly/combjelly_video.html)). However, these three ctenophores might also represent three different species

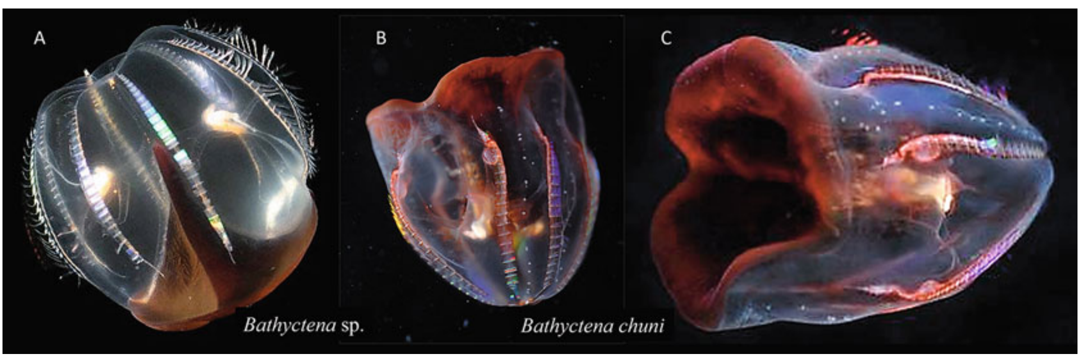


Fig. 10 (**a**) Deepwater *Bathyctena* sp. (?), Arctic Ocean, and (**b**, **c**) *Bathyctena chuni.* (Sources of images: (**a**) *Arctic Ocean diversity by* Russ Hopcroft – public domain: http:/www.arcodiv.org/watercolumn/ctenophores/Bathyctena.html; (**b**) public domain: https:/forums.unknownworlds.com/discussion/154142/arctic-jellyfish; (**c**) Photo: Steven Haddock© MBARI 2006. That animal was caught May 2006 at a depth of 697 meters off the California coast. https:/www.eurekalert.org/multimedia/929241. Photo Credit: Steve Haddock; see also [32]. *See additional images of Bathyctena chuni*, from [32], and undescribed cydippids (from [15]). Additional sources for deepwater ctenophore images: http:/www.coml.org/census-arts/the-deep/; https:/twitter.com/Emma_Hollen/status/965871500590043136/photo/1; https:/cflas.org/2015/05/13/comb-jellyfish/; https:/twitter.com/Emma_Hollen/status/965871500590043136; https:/imgur.com/gallery/BL8gS/comment/297275655, MBARI© and Academic Press© [15])

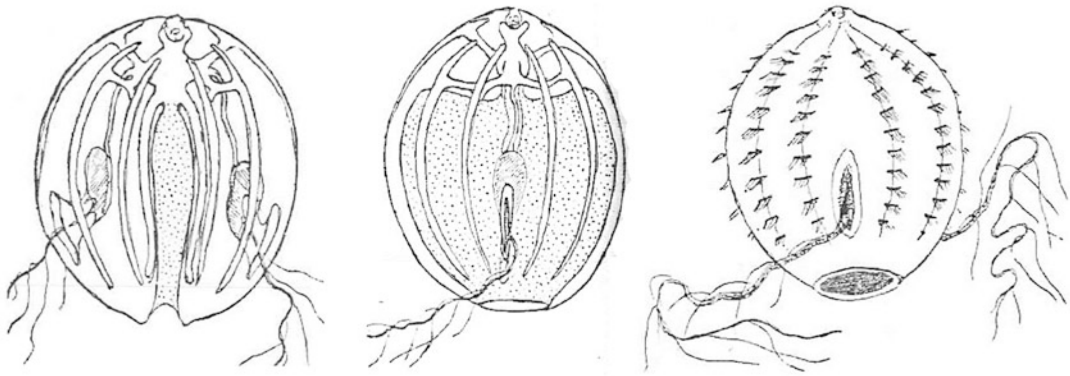


Fig. 11 Deepwater *Bathyctena latipharyngea* (Dawydoff, 1946). (from [72])

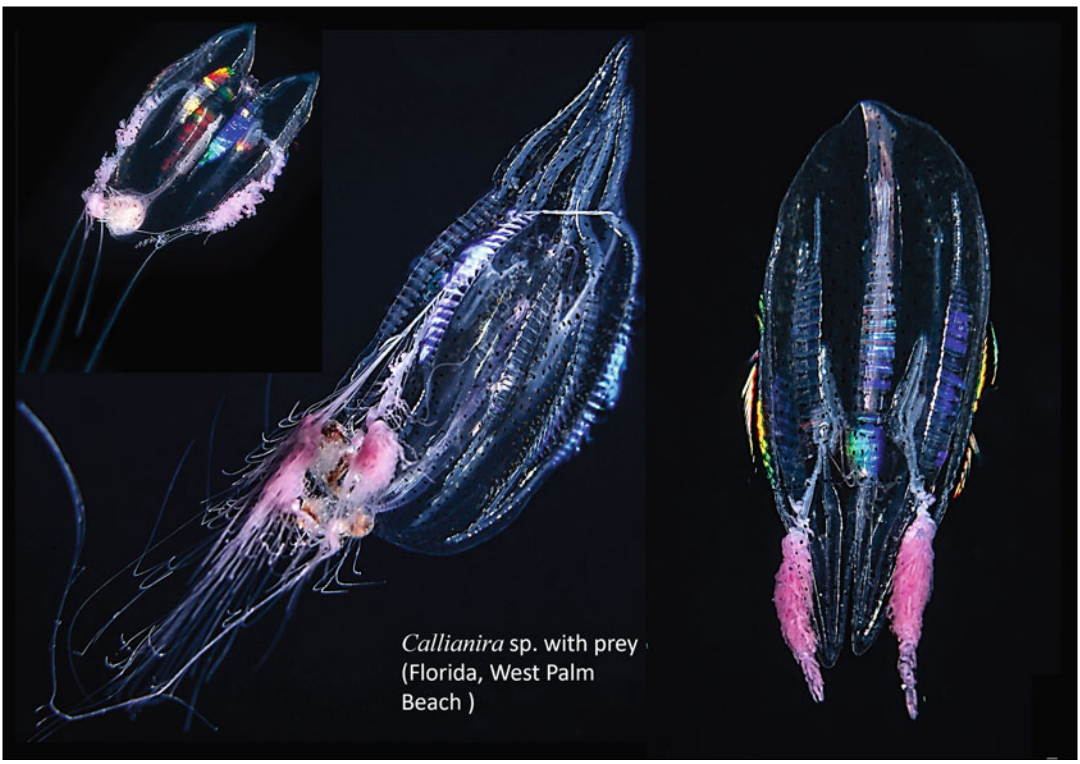


Fig. 12 *Callianira* spp. Florida, West Palm Beach, USA. Possible *Callianira cristata*

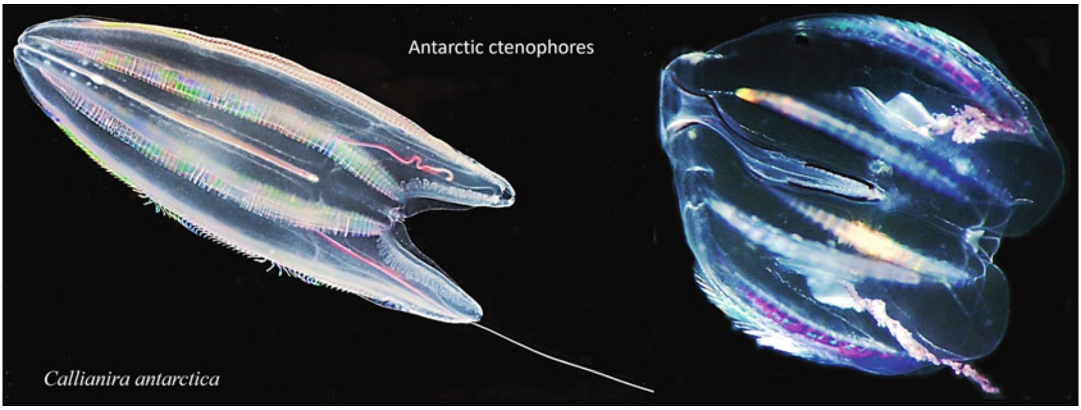


Fig. 13 *Callianira antarctica* and undescribed cydippid, Weddell Sea, Antarctica

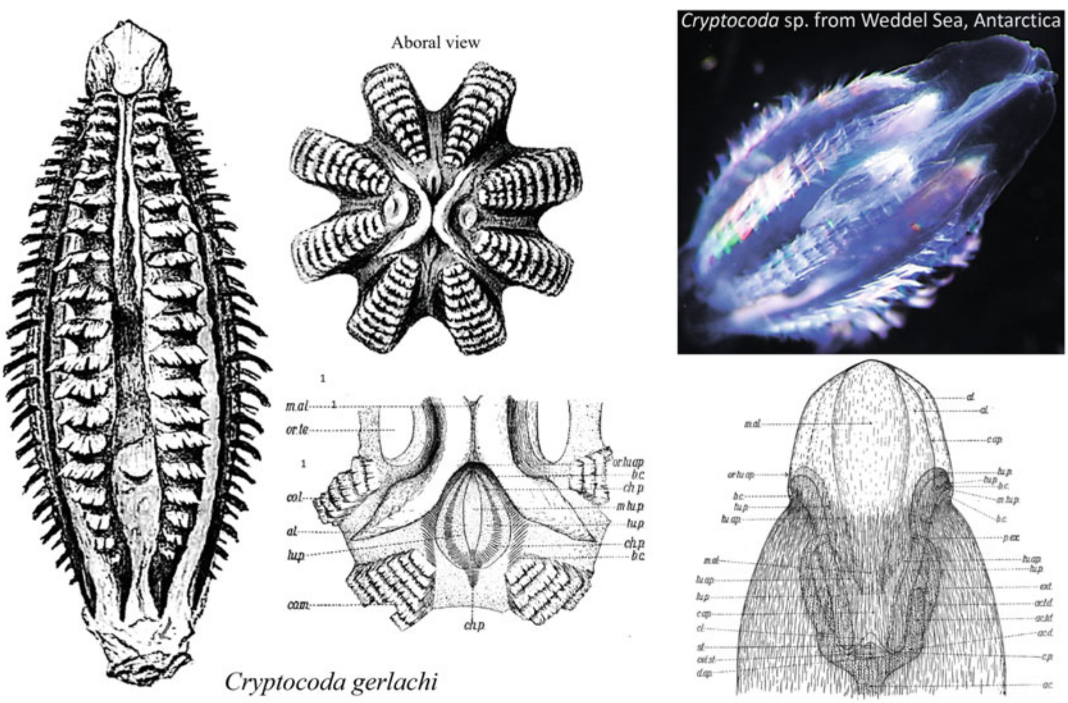


Fig. 14 *Cryptocoda gerlachi* Leloup, 1938. (from [77] with original abbreviations). The top right image might be *Cryptocoda* sp. from Weddel Sea, Antarctica

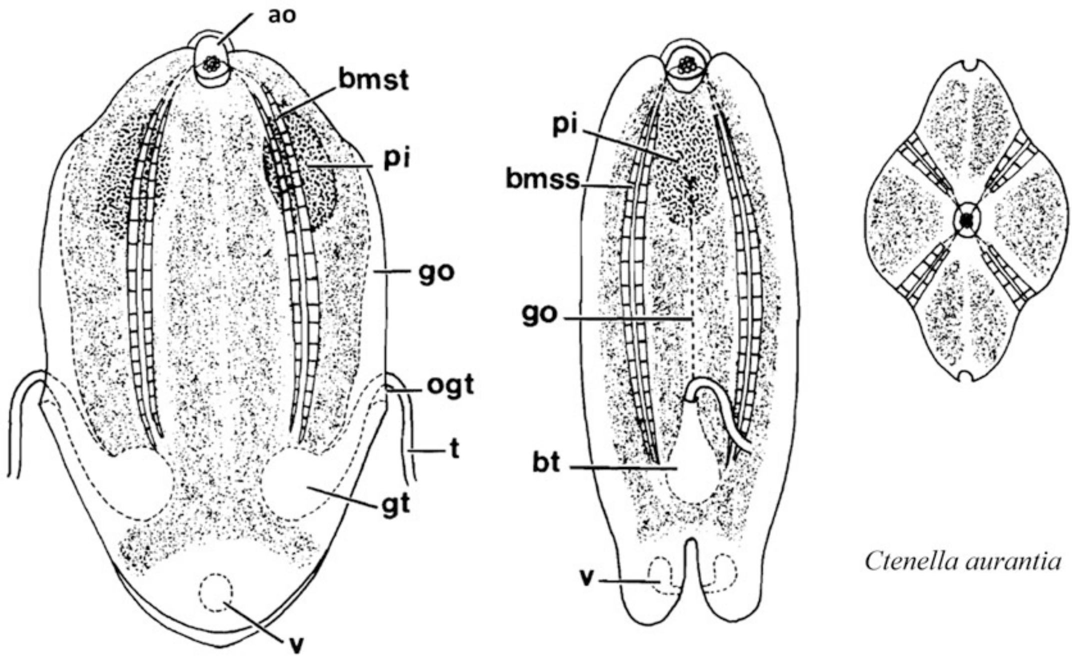


Fig. 15 *Ctenella aurantia* C. Carré & D. Carré, 1993. (from [78] with original abbreviations)

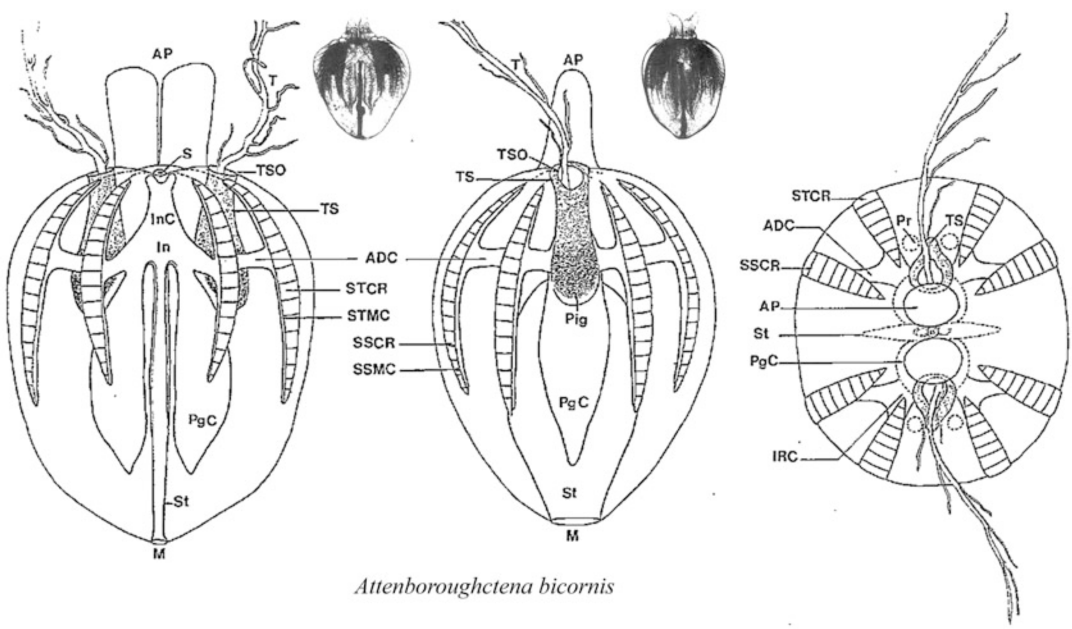


Fig. 16 *Attenboroughctena bicornis* (C. Carré & D. Carré, 1991). (from [81])

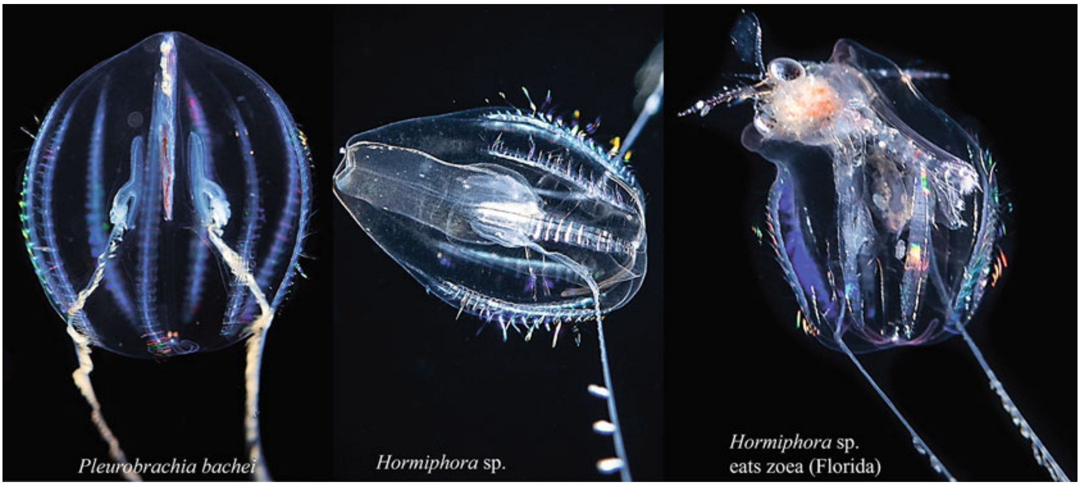


Fig. 17 A comparison of cydippids: *Pleurobrachia bachei*, San Juan Archipelago, vs. *Hormiphora* sp., Florida, USA

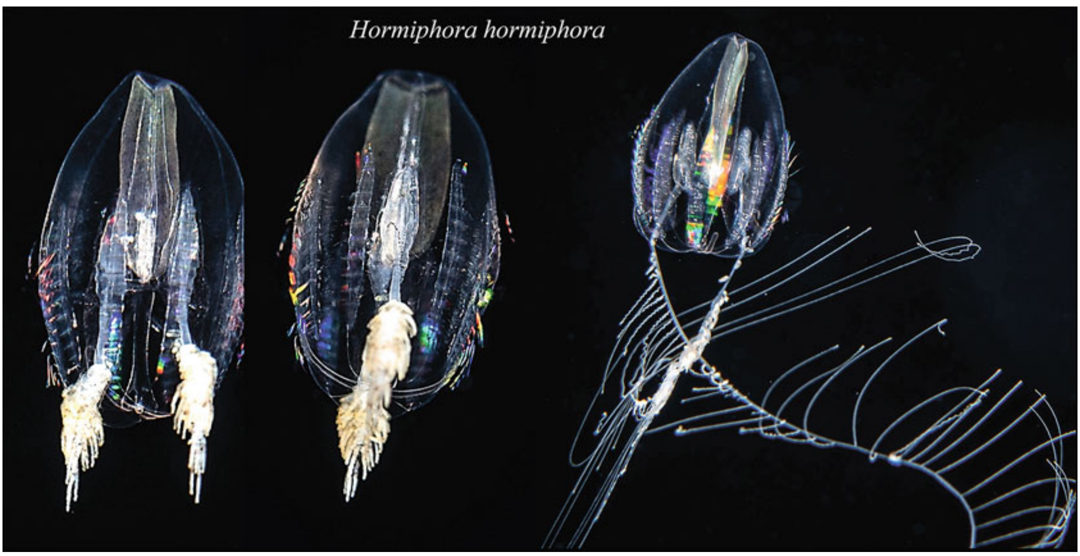


Fig. 18 *Hormiphora hormiphora*, Florida, USA

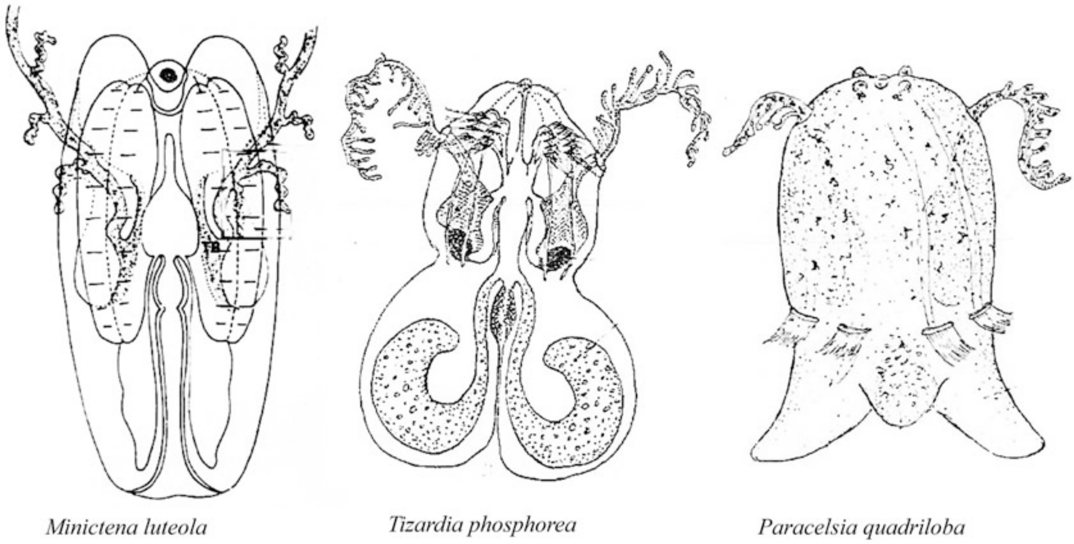


Fig. 19 *Minictena luteola* C. Carré & D. Carré, 1993. (from [91, 92]). *Tizardia phosphorea* Dawydoff, 1946. (Modified from [72]). *Paracelsia quadriloba* Dawydoff, 1946. (from [72])

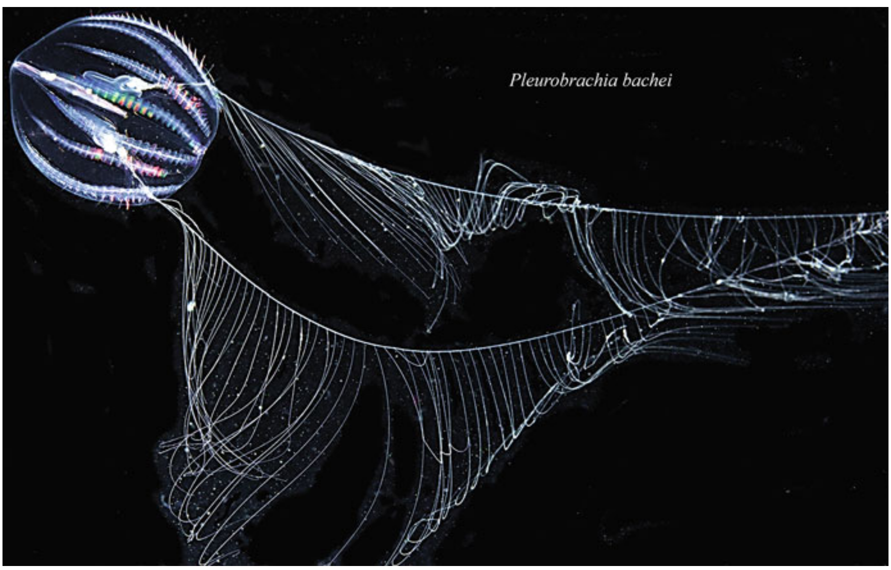


Fig. 20 *Pleurobrachia bachei* is one of the most common ctenophores in the Northeast Pacific

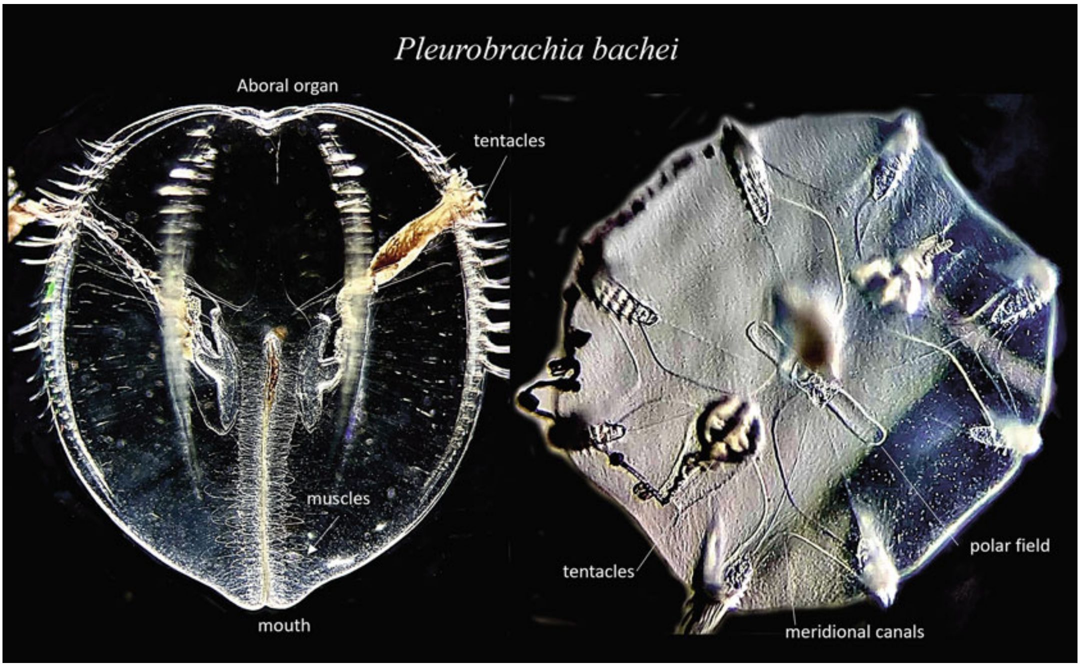


Fig. 21 *Pleurobrachia bachei*. The left image shows the animal in the tentacle plane with mouth and circular muscles around the pharynx. The right image is the aboral view of this transparent animal

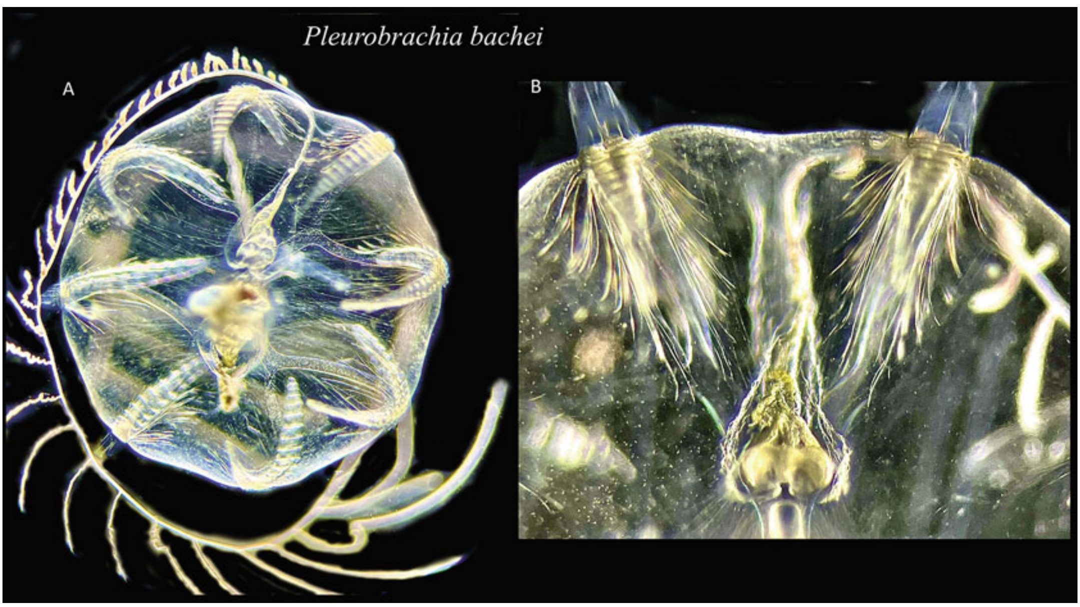


Fig. 22 *Pleurobrachia bachei*. (**a**) A view from the oral side shows tentacles with sheaths and meridional canals. (**b**) Side view of two comb plates with cilia and muscles. The bottom of the image shows a tentacle retracted in the tentacle pocket (sheath)

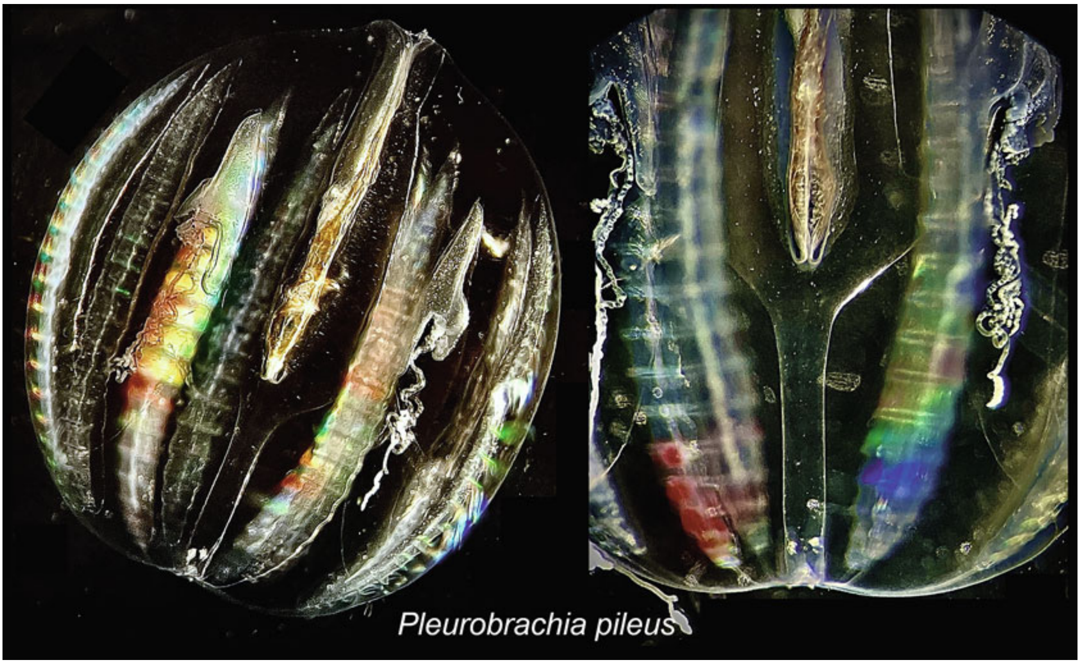


Fig. 23 *Pleurobrachia pileus*, Maine, USA

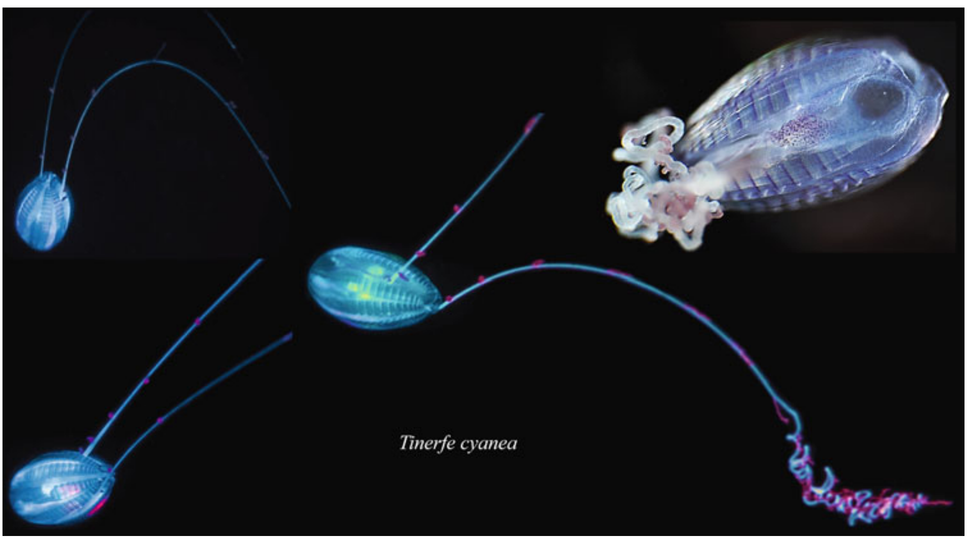


Fig. 24 *Tinerfe cyanea*, Florida, USA

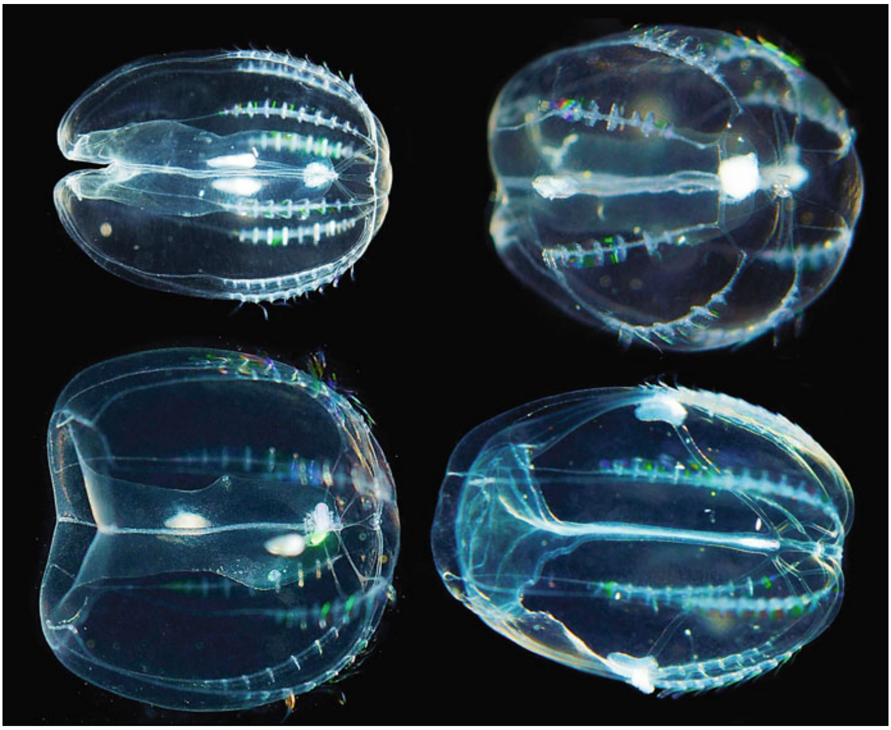


Fig. 25 These images are of an unidentified juvenile lobate from New Caledonia

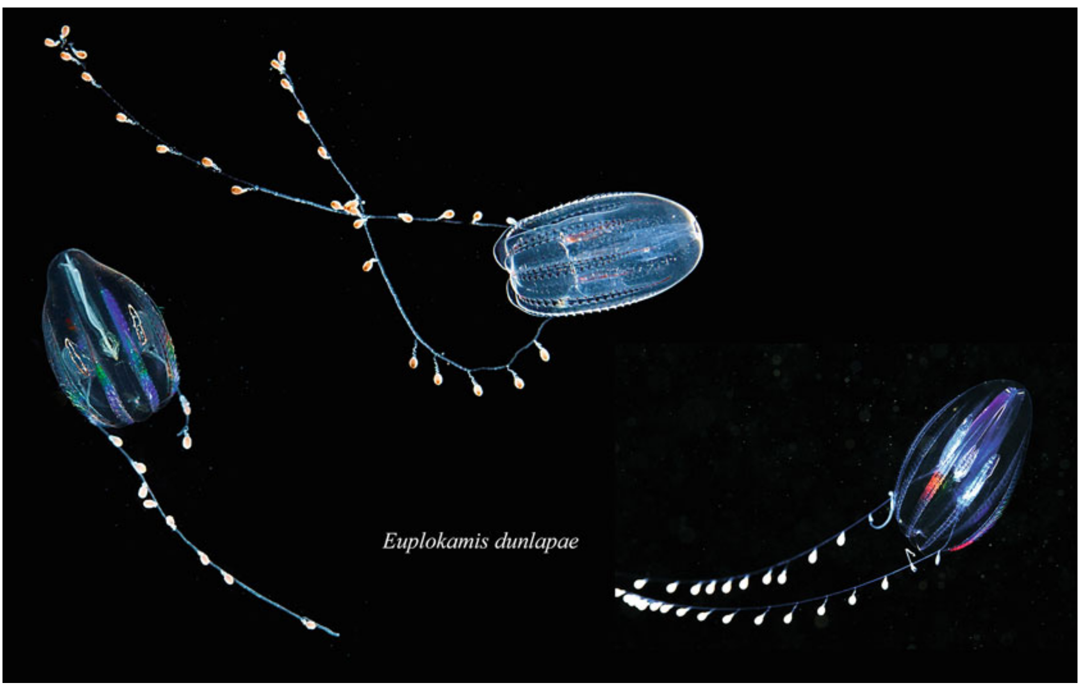


Fig. 26 *Euplokamis dunlapae* (Friday Harbor, Washington, USA, and Arctic Ocean) (Right Photo: Alexander Semenov©). *Euplokamis* also has unusual feeding because its rapidly coiling tentillae have unique striated muscles among ctenophores

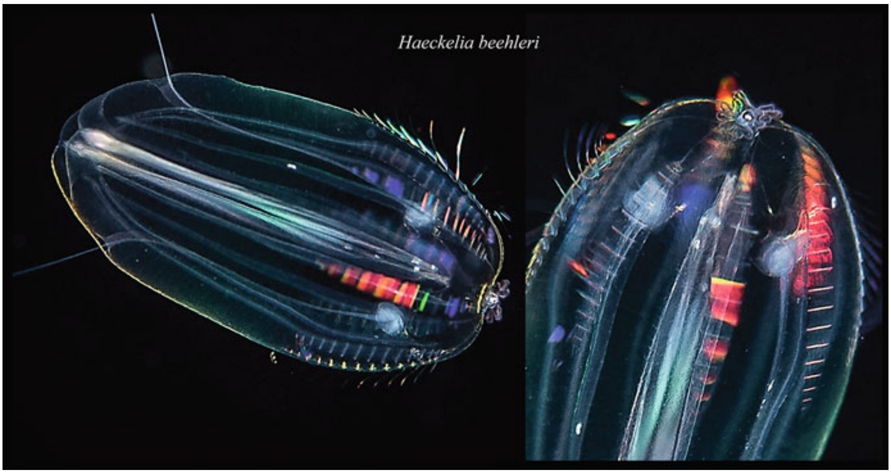


Fig. 27 *Haeckelia beehleri*, Florida, USA

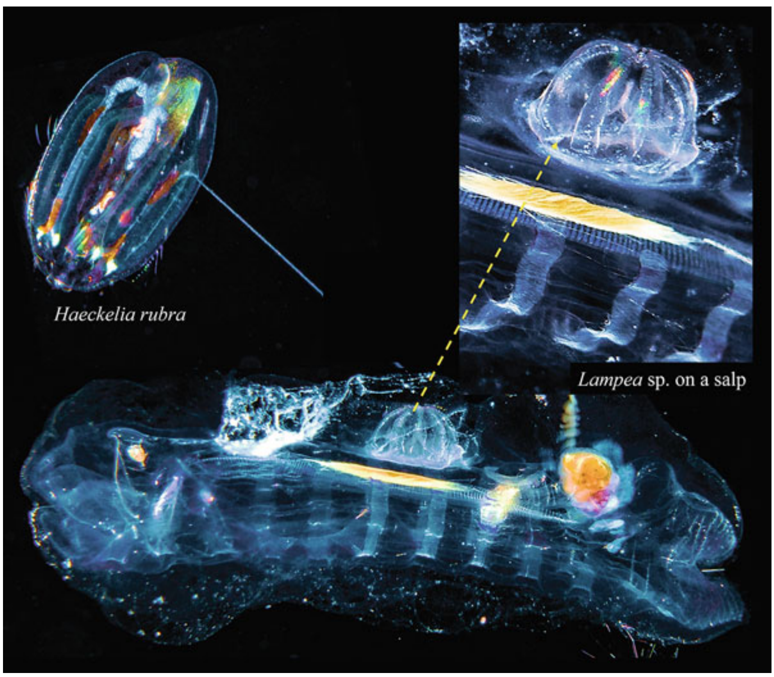


Fig. 28 Ctenophores with unusual feeding adaptations: *Haeckelia rubra* feeds on narcomedusae and is able to sequester their nematocysts for defense [102], and *Lampea* feeds on salps as a predator on small prey or as a parasite on larger individuals

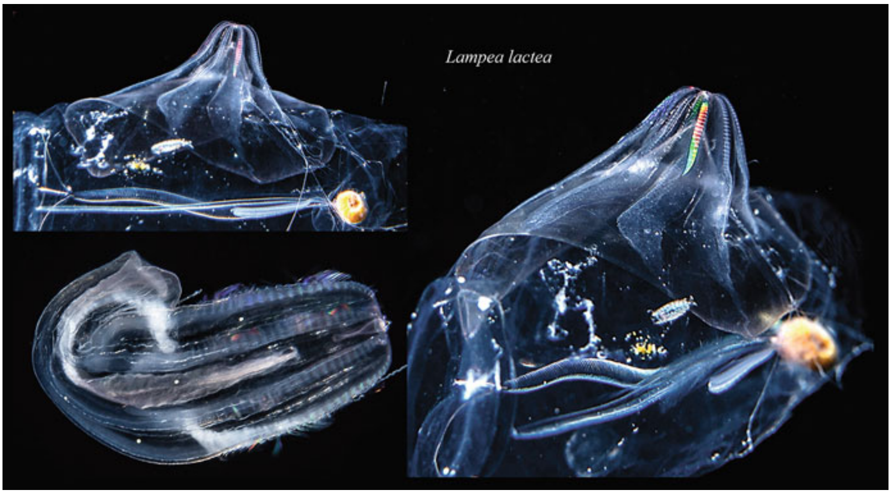


Fig. 29 *Lampea lactea*, Florida, USA

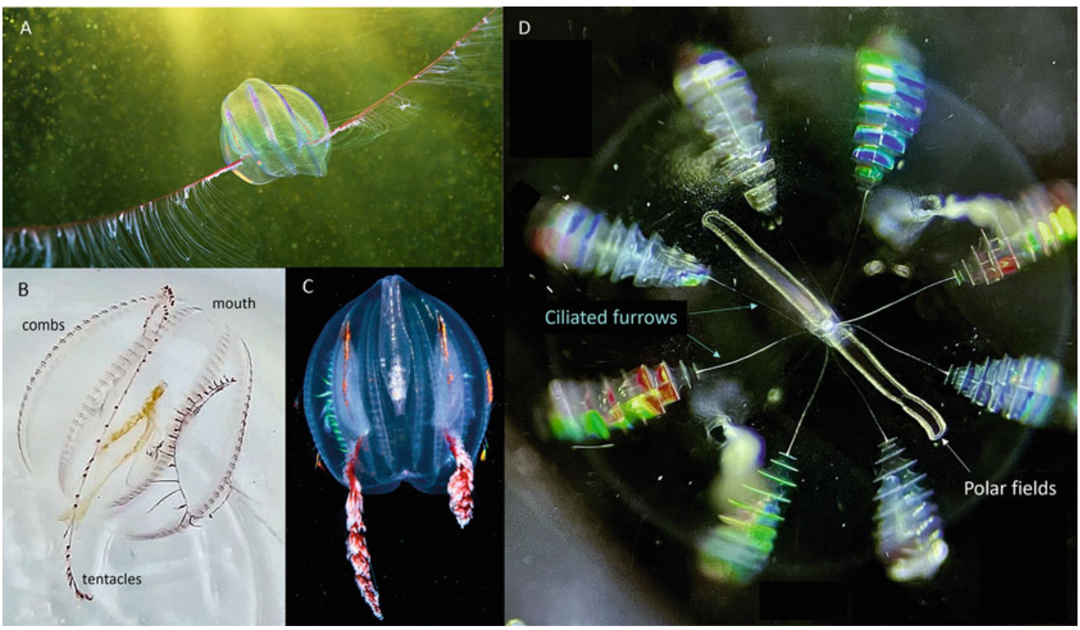


Fig. 30 Cydippid: *Mertensia ovum*. (**a**) This cydippid has dark magenta pigmentation in combs (**b**) and tentacles (**c**) [24]. (**a**) From the White Sea (Photo: Alexander Semenov©); (**b**–**d**) From Maine, USA

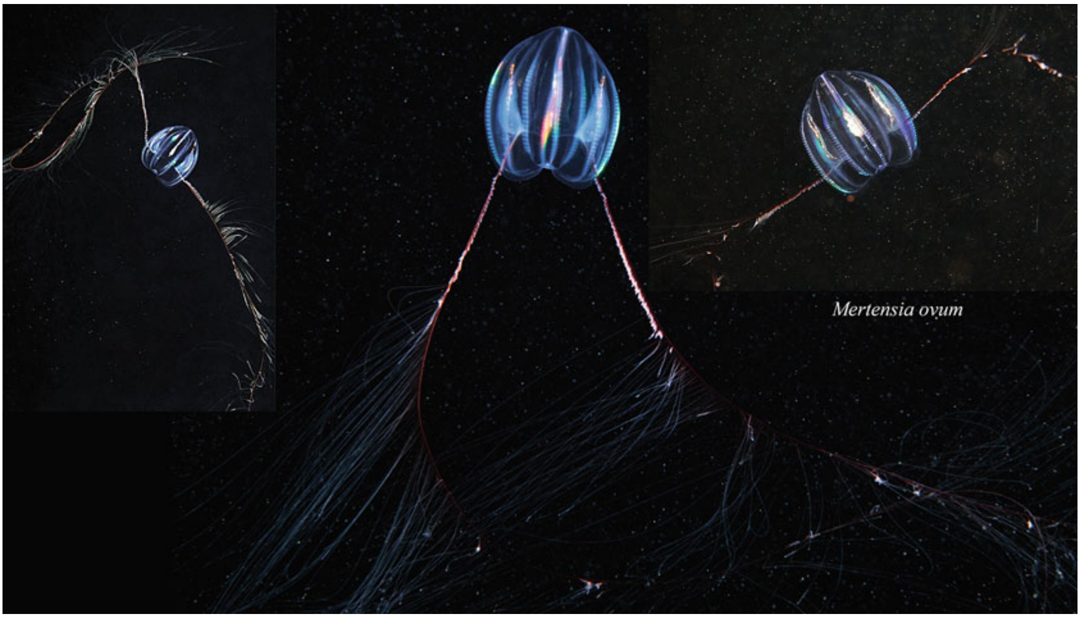


Fig. 31 Cydippid: *Mertensia ovum* from the White Sea. (Photo: Alexander Semenov©)

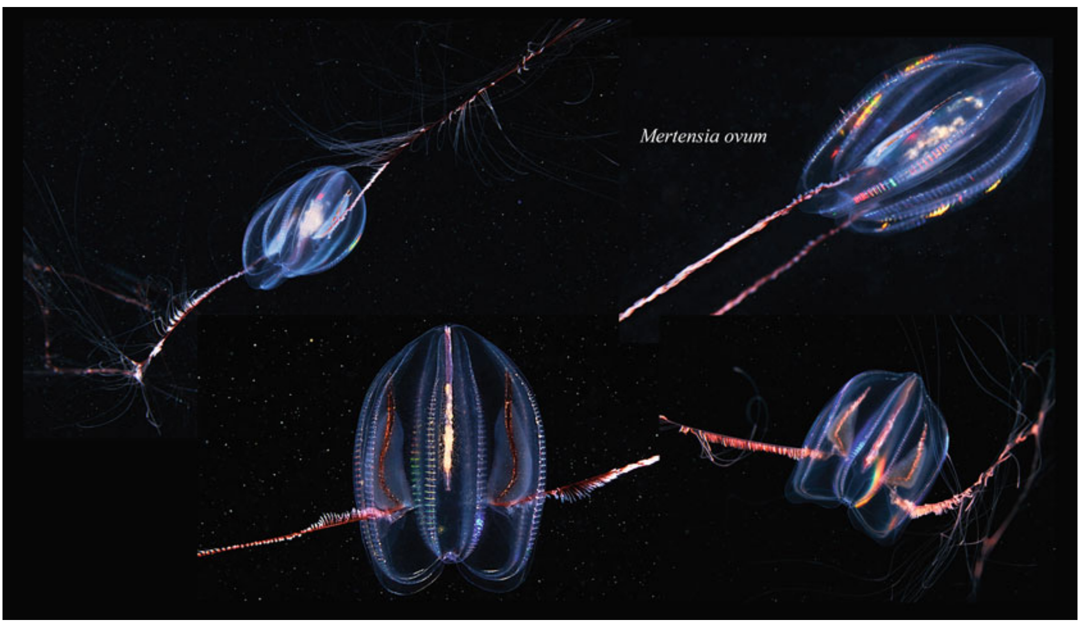


Fig. 32 Cydippid: *Mertensia ovum* from the White Sea. (Photo: Alexander Semenov©)

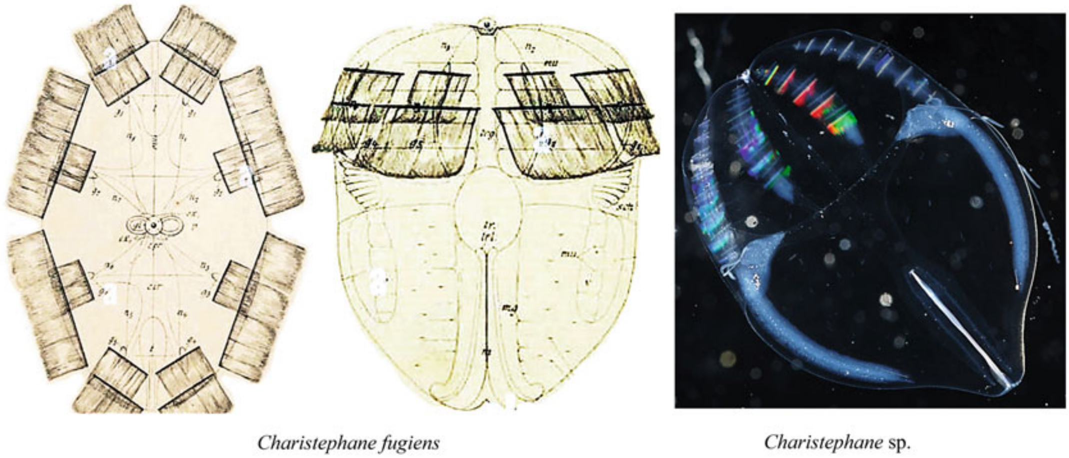


Fig. 33 *Charistephane fugiens* Chun, 1879. (from [74]. *Charistephane* sp. – https://imgur.com/gallery/BL8gS/comment/297275655). The right image: Photo: Steven Haddock© MBARI 2006. The specimen was collected from 300 meters near Davidson Seamount, 100 km off the coast of California

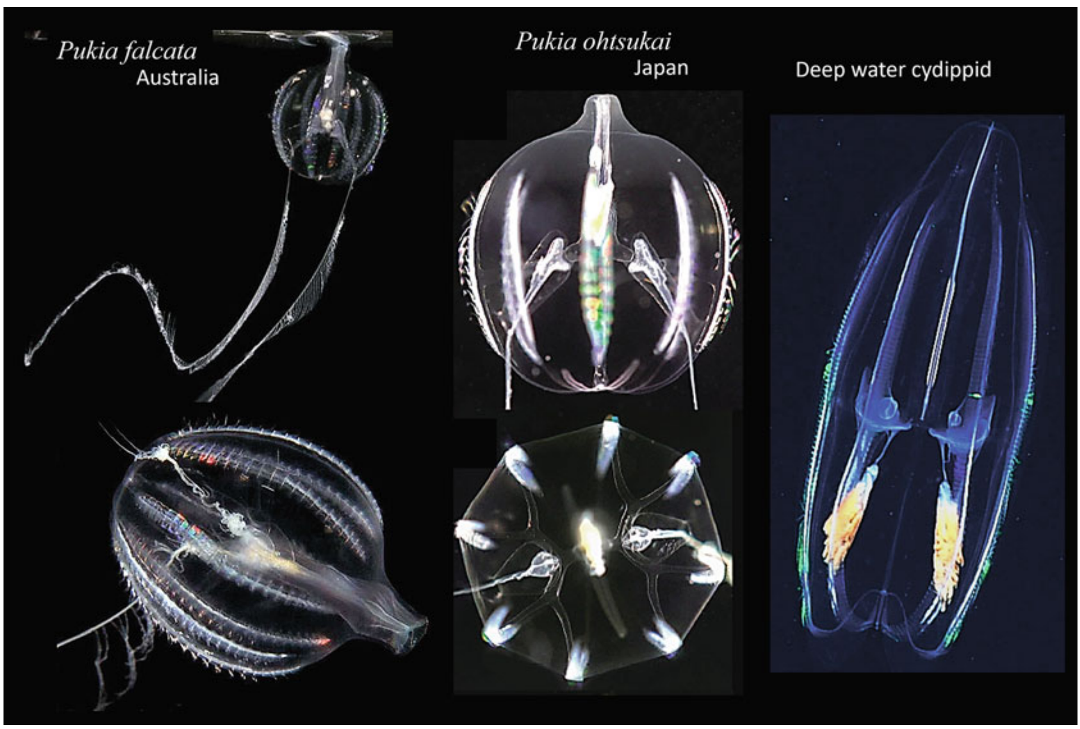


Fig. 34 *Pukia falcata*. (Photo: Denis Riek©; http://www.roboastra.com/Cnidaria3/brac178.html; *Pukia ohtsukai* Lindsay, 2017; from [68], Okinawa, Japan. The right image is a deepwater cydippid at the Blake Escarpment, Atlantic Ocean, courtesy NOAA Ocean Exploration, Windows to the Deep 2019, https://www.flickr.com/photos/oceanexplorergov/51816911735/in/photostream/)

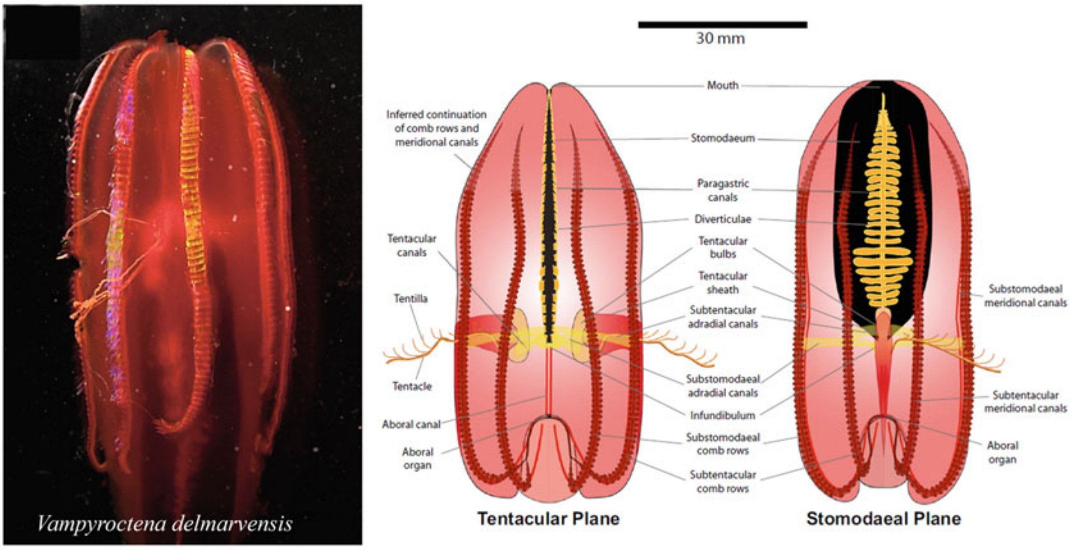


Fig. 35 Cydippida: *Vampyroctena delmarvensis*, from [109] (© Senckenberg Gesellschaft für Naturforschung 2020)

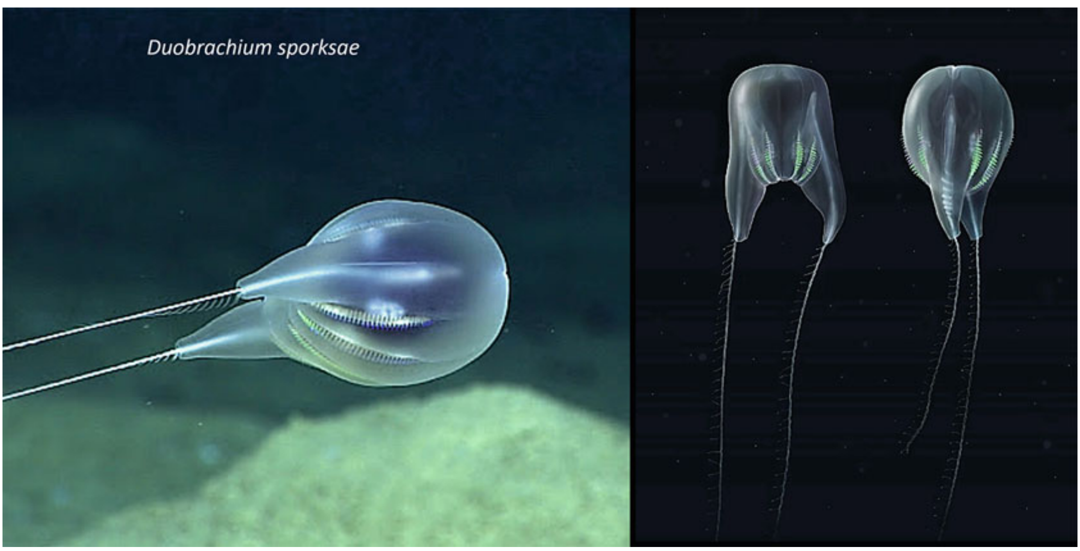


Fig. 36 The deepwater cydippid *Duobrachium sparksae* [56]. The species was found at a depth of approximately 3900 m, within meters of the seafloor in Guajataca Canyon, north-northwest of Puerto Rico (http:/novataxa.blogspot.com/2020/11/duobrachium.html)

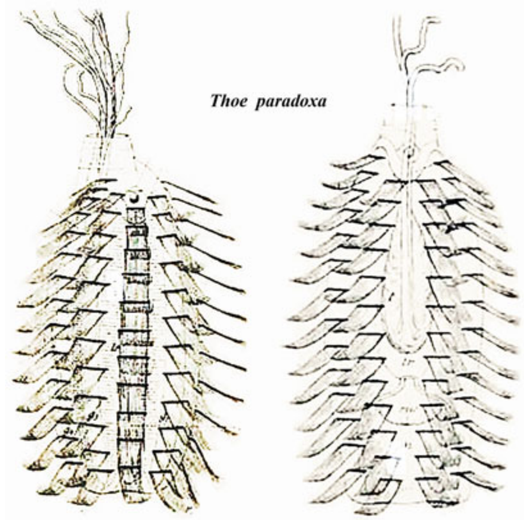


Fig. 37 *Thoe paradoxa* Chun, 1879. (from [74])

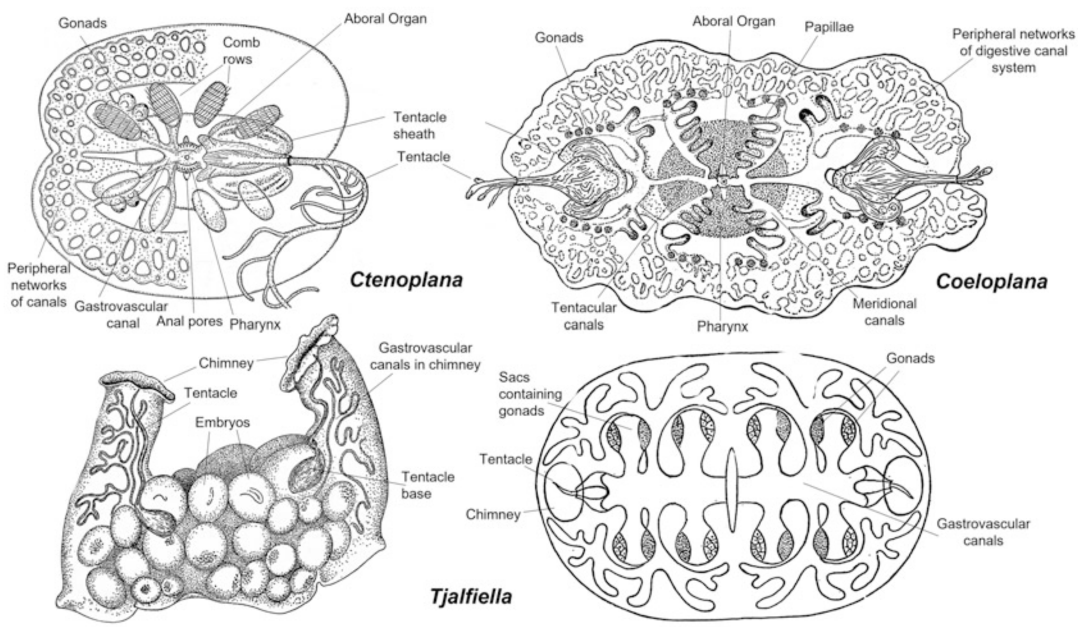


Fig. 38 General anatomy of Platyctenida with major organs and structures indicated (from [11]). See also images on the sea slug forum [210], and subsequent figures 26–47

Fig. 39 *Coeloplana astericola*, on the sea star *Echinaster luzonicus* from the Philippines (**a**) and Okinawa (**b**)

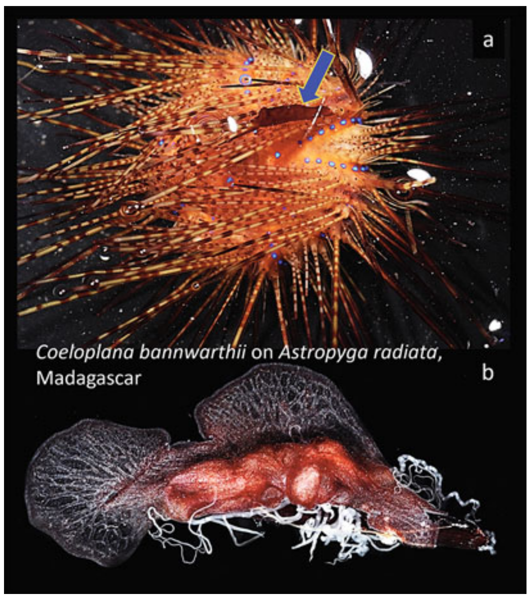


Fig. 40 *Coeloplana bannwarthii* on the sea urchin *Astropyga radiata*, Madagascar

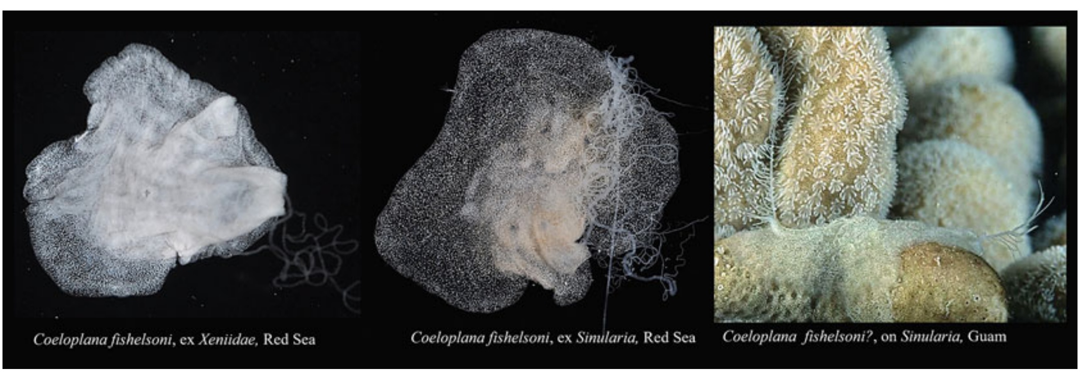


Fig. 41 *Coeloplana fishelsoni*, extracted from different species (soft corals *Xeniidae* and *Sinularia*, Red Sea), and in natural habitats, Guam (right image)

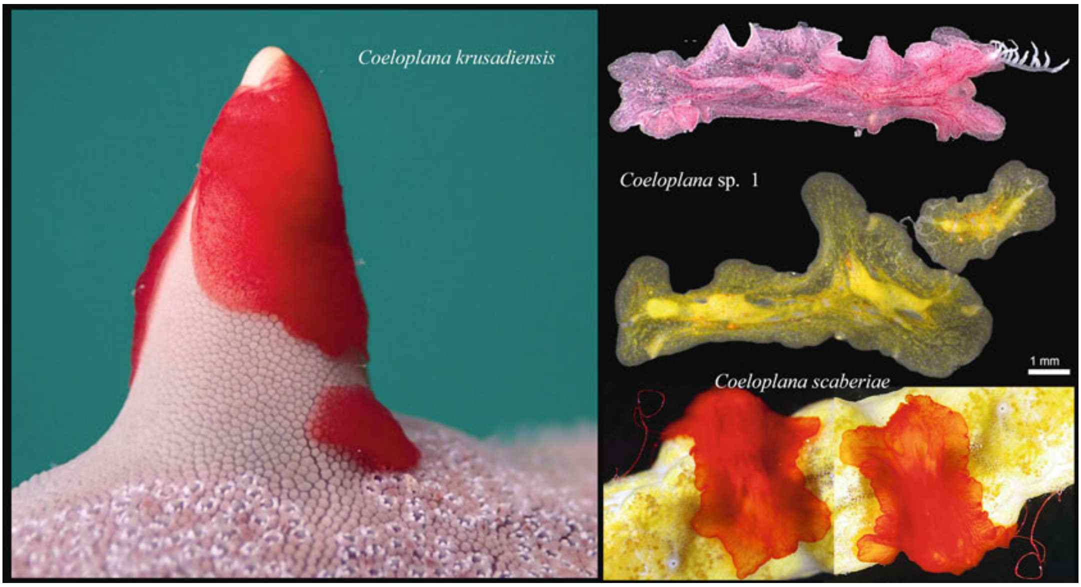


Fig. 42 *Coeloplana krusadiensis* from New Caledonia. (Photo: Claire Goiran© https:/guatemala.inaturalist.org/photos/249575709). Two color morphs of *Coeloplana* sp. 1 (undescribed species 1) from Oman [211]. *Coeloplana scaberiae* Matsumoto & Gowlett-Holmes, 1996 [127]. (Photo: Leon Altoff© – Barker Rocks, South Australia, https:/biocache.ala.org.au/occurrences/9428c840-bf78-4850-aa1c-4b6340c998bc)

Fig. 43 *Coeloplana loyai*, on the on the mushroom coral *Ctenactis echinata*, Red Sea. Bottom images are the same species collected from *Trachyphyllia geoffroyi* in New Caledonia

Fig. 44 *Coeloplana* cf. *loyai* from New Caledonia

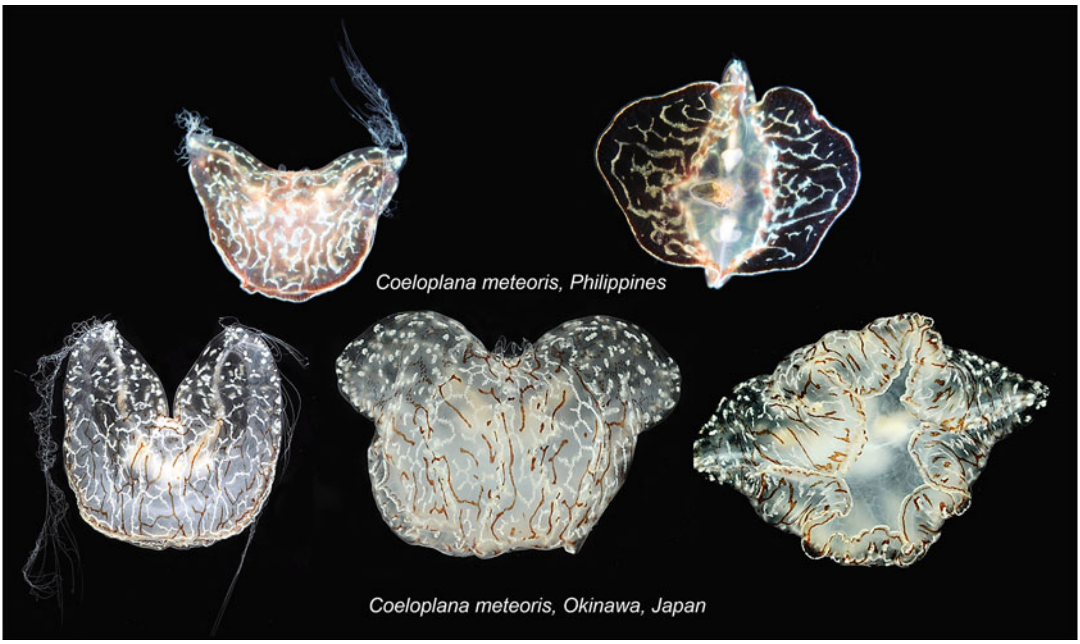


Fig. 45 *Coeloplana meteoris* from different locations

Fig. 46 The sea slug *Philinopsis ctenophoraphaga* feeding on the benthic ctenophore *Coenoplana meteoris*. (Images from [212]; http:/www.seaslugforum.net/find/15543) photos and description of event by Brian Francisco

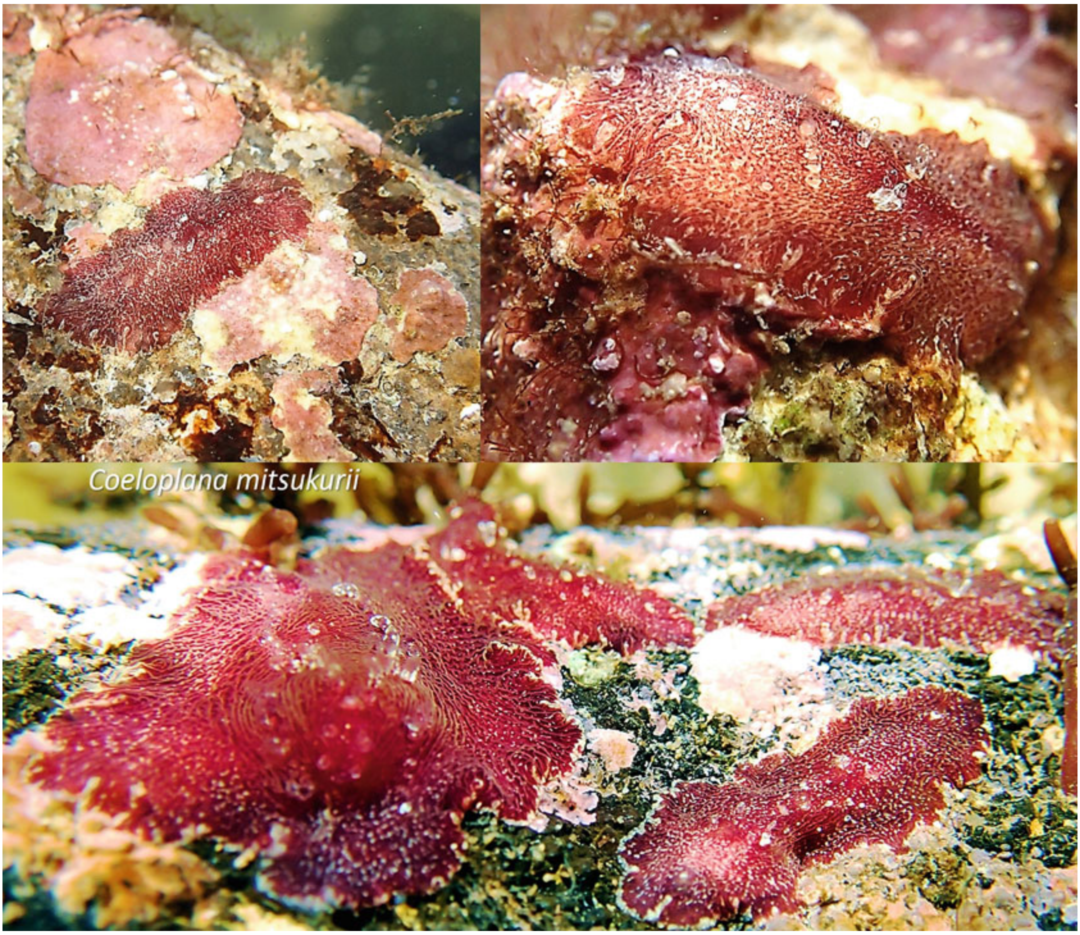


Fig. 47 *Coenoplana mitsukurii*, Oki Islands, Japan; photo: Masa-aki Yoshida. Photo by Masa-aki Yoshida, used with permission

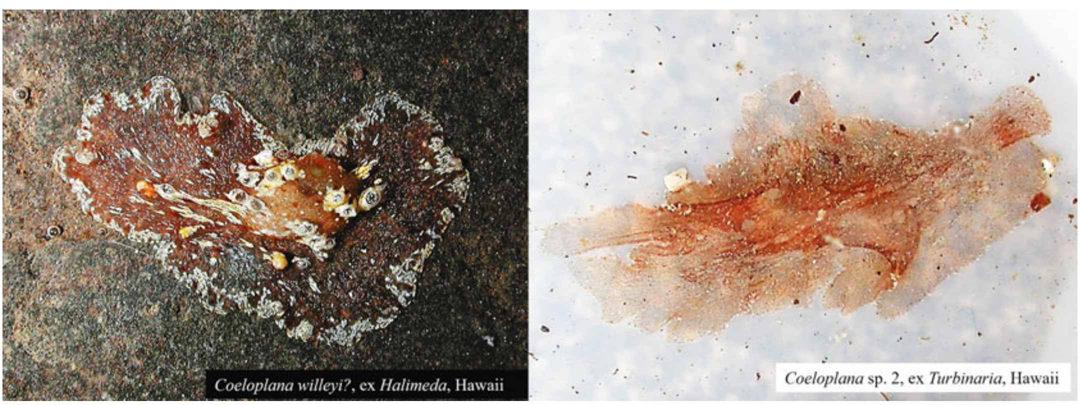


Fig. 48 *Coeloplana willeyi*? extracted from the green alga *Halimeda*, Hawaii (left); *Coeloplana* sp. 2, extracted from the brown alga *Turbinaria*, Hawaii (right). Cory Pittman photos with permission

Fig. 49 *Coeloplana* cf. *wuennenbergi* on the soft coral *Sarcophyton*, New Caledonia

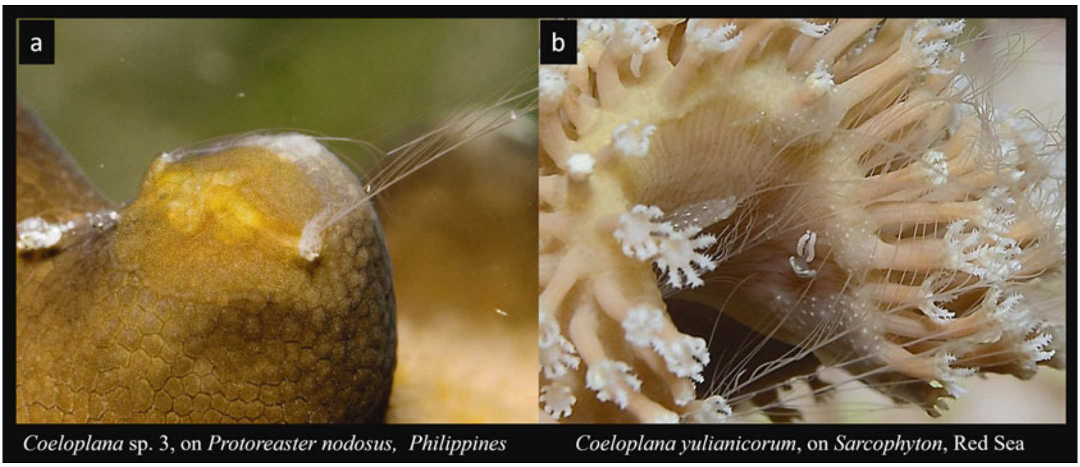


Fig. 50 (**a**) *Coeloplana* sp. 3, on the horned sea star *Protoreaster nodosus*, Philippines; (**b**) *Coeloplana yulianicorum*, on the soft coral *Sarcophyton*, Red Sea

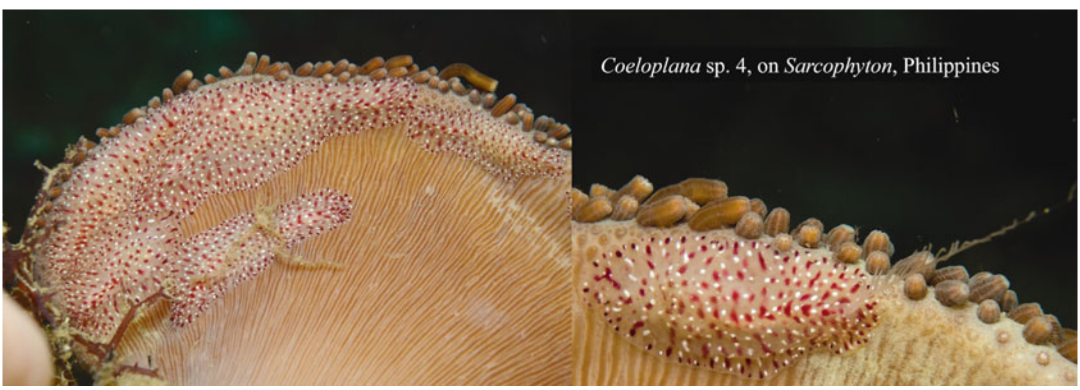


Fig. 51 *Coeloplana* sp. 4, on the soft coral *Sarcophyton*, Philippines

Fig. 52 *Coeloplana* sp. 5, on the soft coral *Sarcophyton*, Philippines (left); *Coeloplana* sp. 6, on *Sarcophyton*, Philippines (right)

Fig. 53 *Coeloplana* sp. 5 and 6, on the soft coral *Sarcophyton*, Philippines (left); *Coeloplana* sp. 6, extracted from *Sarcophyton*

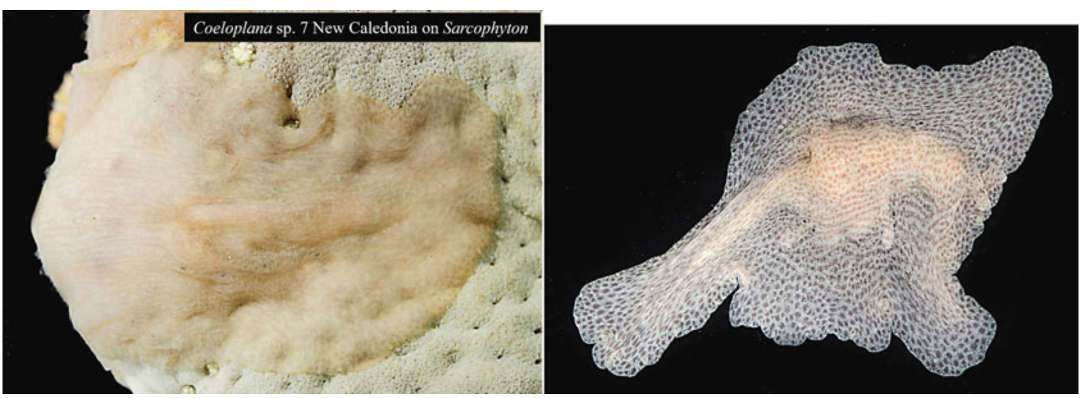


Fig. 54 *Coeloplana* sp. 7, New Caledonia, on the soft coral *Sarcophyton* (left), and the same species extracted (right)

Fig. 55 *Coeloplana* sp. 8, on the soft coral *Lobophytum*, Mascarene Islands

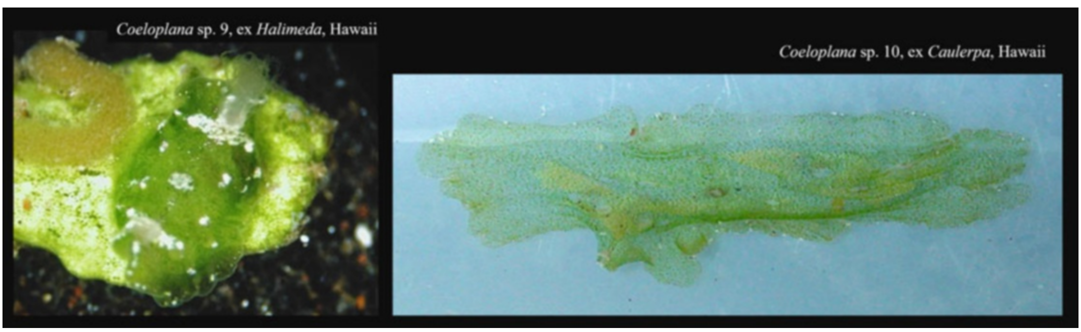


Fig. 56 *Coeloplana* sp. 9, extracted from the green alga *Halimeda*, Hawaii. *Coeloplana* sp. 10/9, extracted from the seaweed *Caulerpa*, Hawaii; Cory Pittman photos

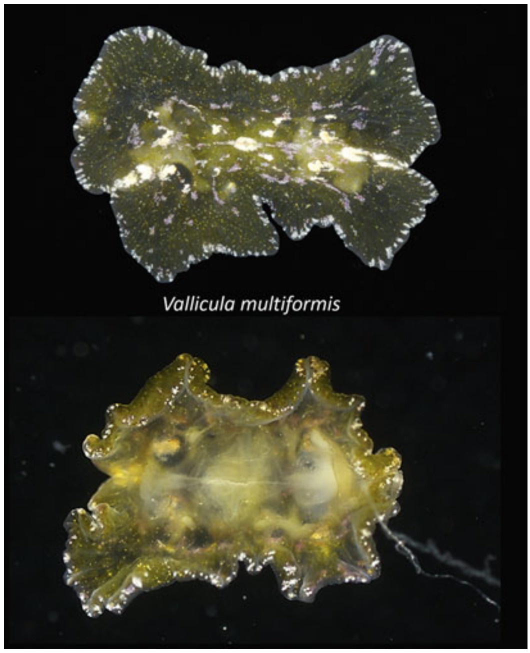


Fig. 57 *Vallicula multiformis* (dorsal [top] and ventral [bottom] views) from Oman

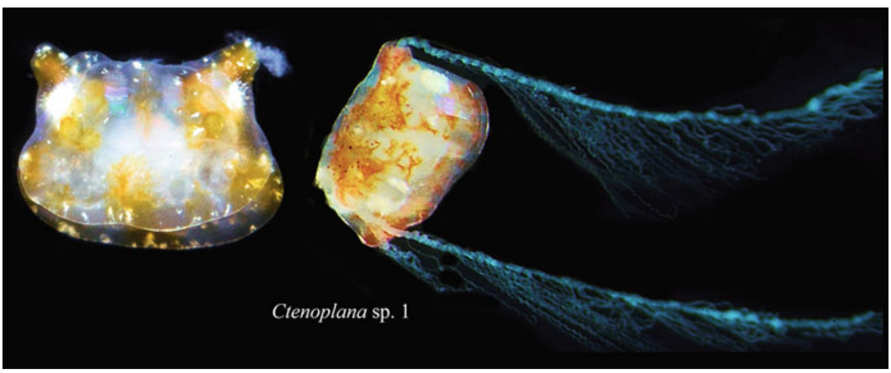


Fig. 58 *Ctenoplana* sp. 1 from New Caledonia

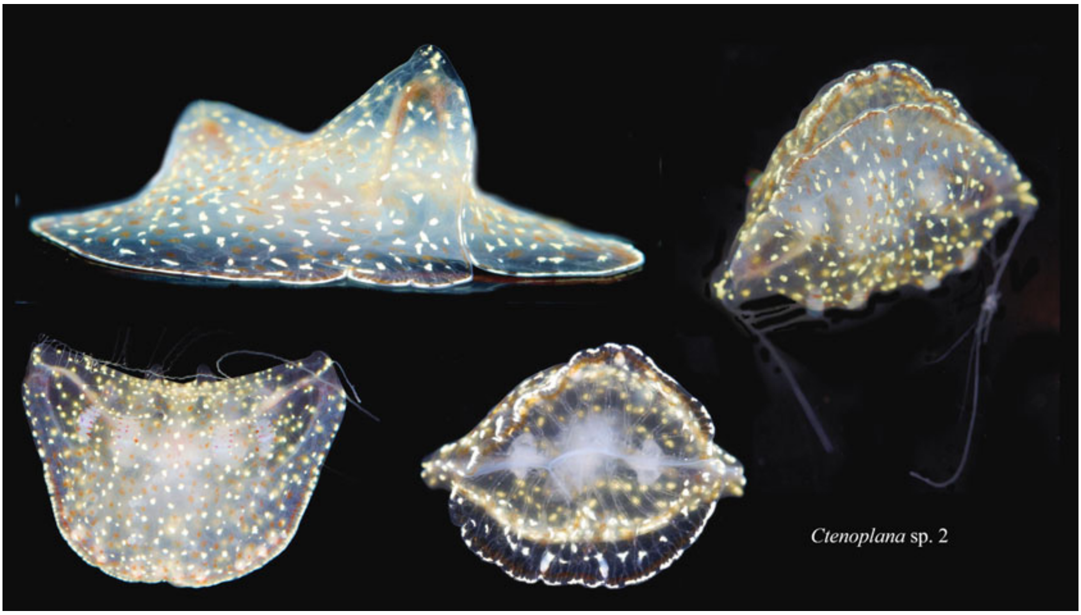


Fig. 59 *Ctenoplana* sp. 2 from New Caledonia

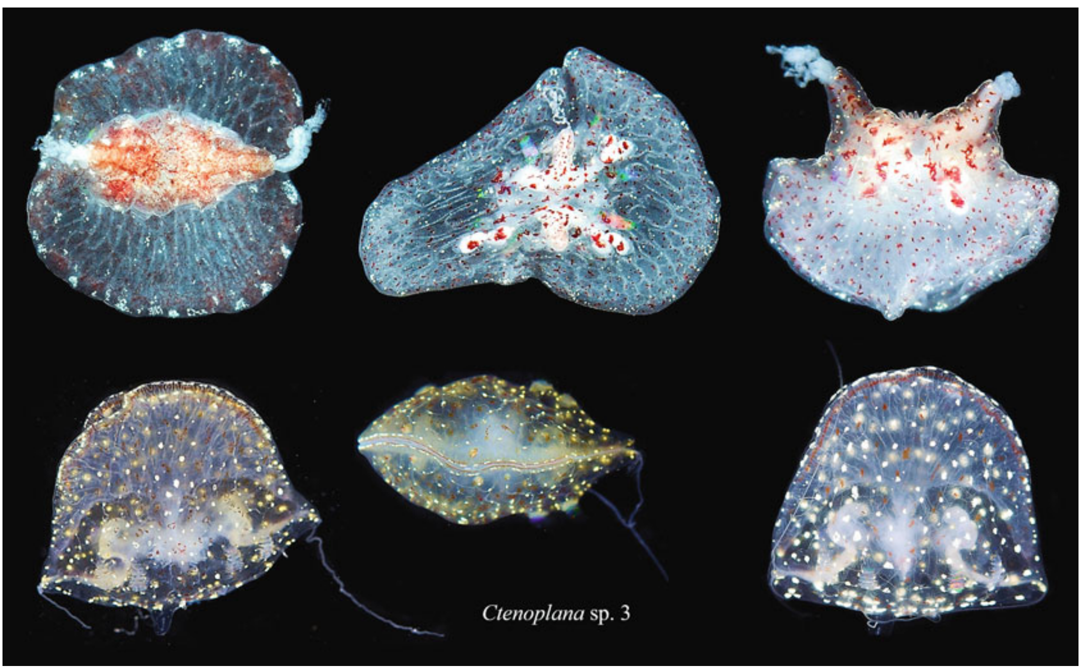


Fig. 60 *Ctenoplana* sp. 3 from New Caledonia

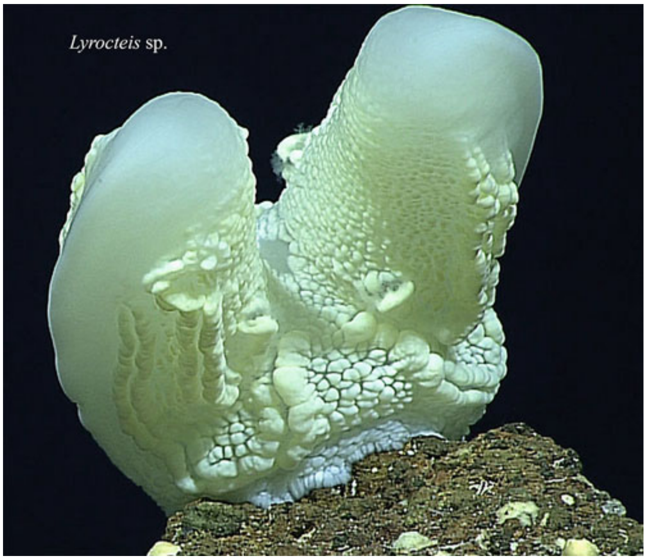


Fig. 61 The sessile platyctenid: *Lyrocteis* sp. (Image courtesy of the NOAA Office of Ocean Exploration and Research, 2016 Deepwater Exploration of the Marianas (https:/www.flickr.com/photos/oceanexplorergov/50218989191/in/photostream/))

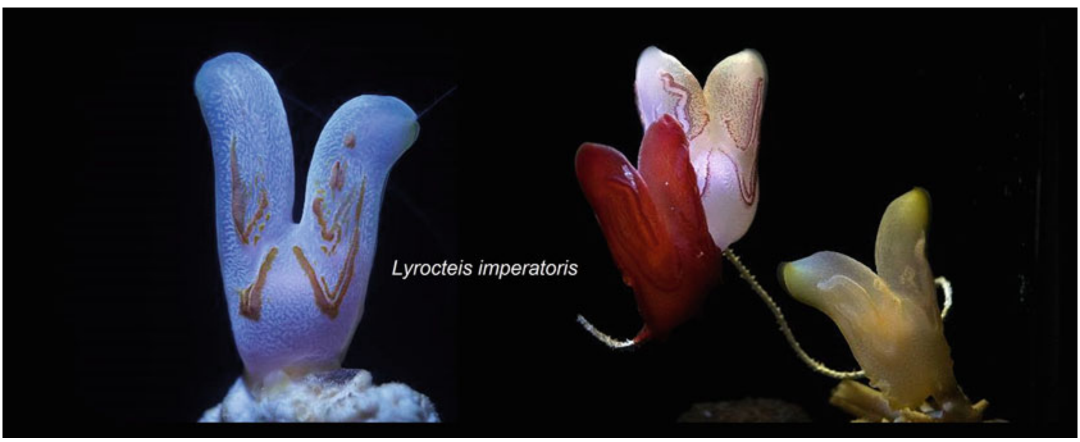
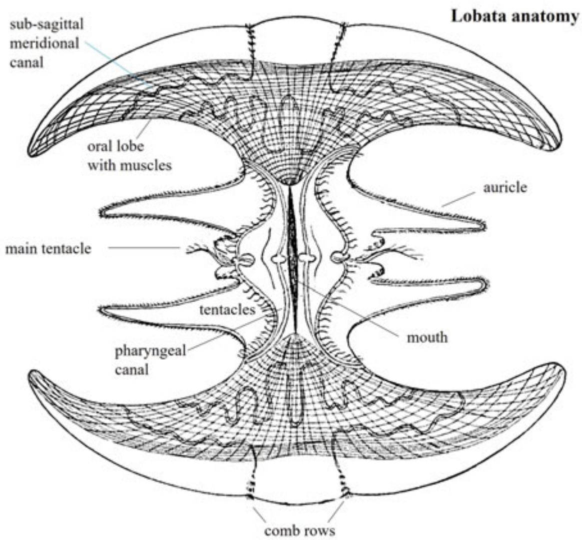


Fig. 62 The rare and beautiful sessile platyctenid: *Lyrocteis imperatoris* [141], Japan. (Image from https:/churaumi.okinawa/sp/en/fishbook/1459390728/). It attaches itself to rocks and gorgonian octocorals horny corals. This species varies in color, and there are many colorful individuals (© Okinawa Churaumi Aquarium)



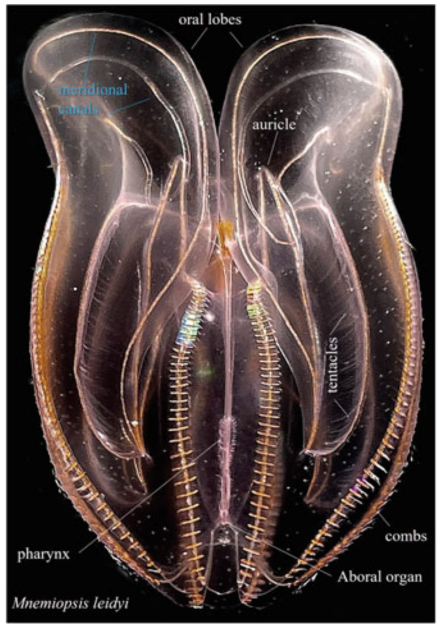


Fig. 63 General anatomy of Lobata with major organs and structures indicated (from [11]). The right image - *Mnemiopsis* from St. Augustine, Florida,. USA

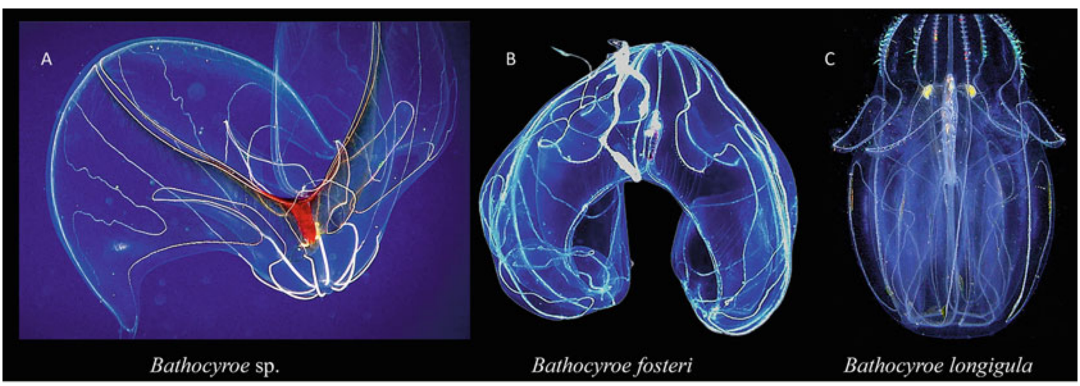


Fig. 64 (**a**) *Bathocyroe* sp. (https:/www.flickr.com/photos/oceanexplorergov/50091043518). (**b**) *Bathocyroe fosteri*. (Photo courtesy of Marsh Youngbluth; This image is in the public domain because it contains materials that originally came from the US National Oceanic and Atmospheric Administration, taken or made as part of an employee's official duties). (**c**) *Bathocyroe longigula*. (https:/www.facebook.com/blackwaterdive/posts/2854790224767581/)

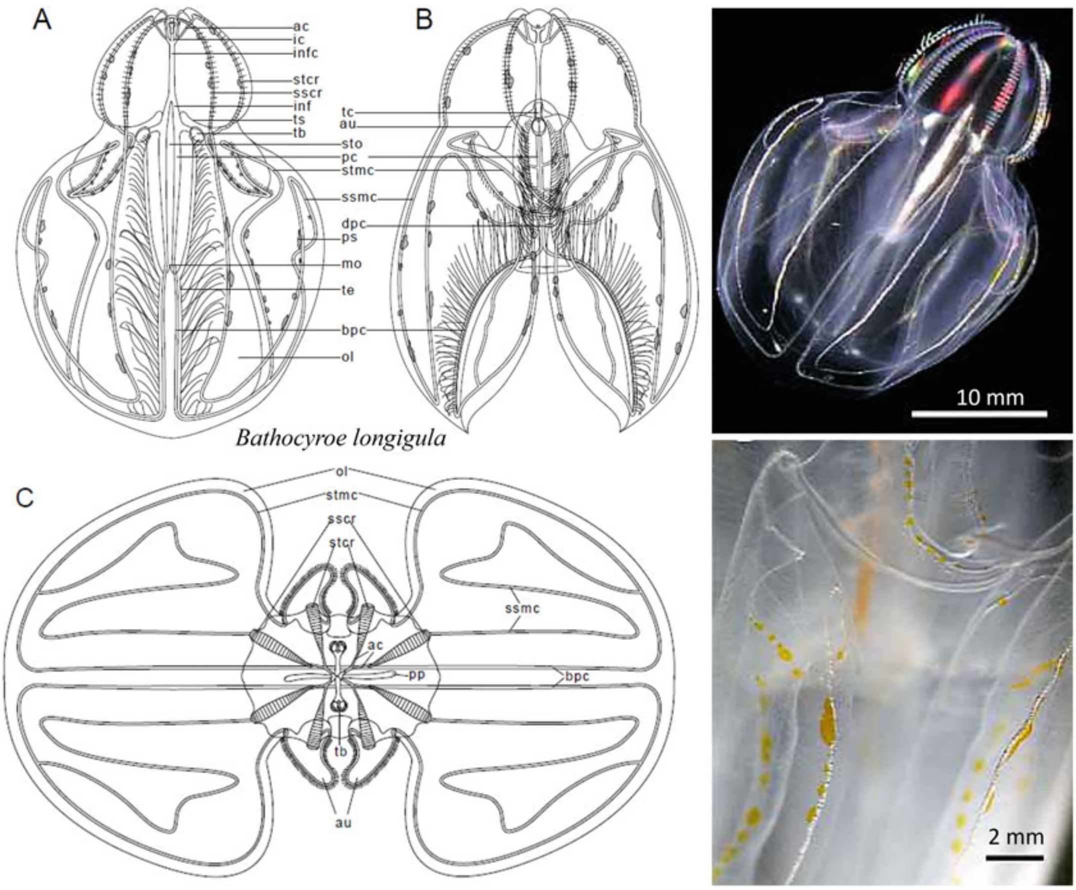


Fig. 65 *Bathocyroe longigula*, from [146], Japan. (**a**) The tentacular plane, (**b**) the stomodaeal plane, and (**c**) the aboral pole view. Abbreviations: ac, adradial canal; au, auricle; bpc, branch of paragastric canal; dpc, diverticulum of paragastric canal; ic, interradial canal; inf, infundibulum; infc, infundibular canal; mo, mouth opening; ol, oral lobe; pc, paragastric canal; ps, pigment spot; pp, pole plate; sscr, substomodaeal comb row; ssmc, substomodaeal meridional canal; stcr, subtentacular cmb row; stmc, subtentacular meridional canal; sto, stomodaeum; tb, tentacle bulb; tc, tentacular canal; te, tentacle; ts, tentacle sheath. Scale bar: 10 mm. (The right photos are the holotype image and the distribution of pigment spots (as in fig. 2 from [146]). Permission from the publisher)

Fig. 66 *Bolinopsis ashleyi*. The left image: Cairns Australia. (Photo: © djwitherall; (https:/guatemala.inaturalist.org/observations/183142120)). The central image: Sydney, Australia. (Photo: © Niki Hubbard, https:/guatemala.inaturalist.org/observations/142985877). The right image: Heron Island, Australia

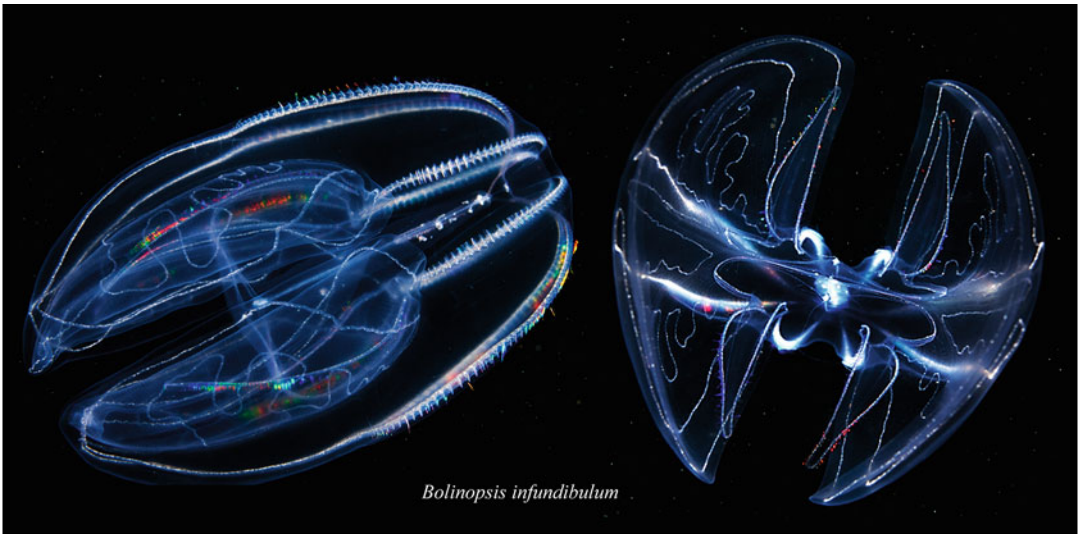


Fig. 67 Lobata: *Bolinopsis infundibulum* from White Sea. (Photo: Alexander Semenov©)

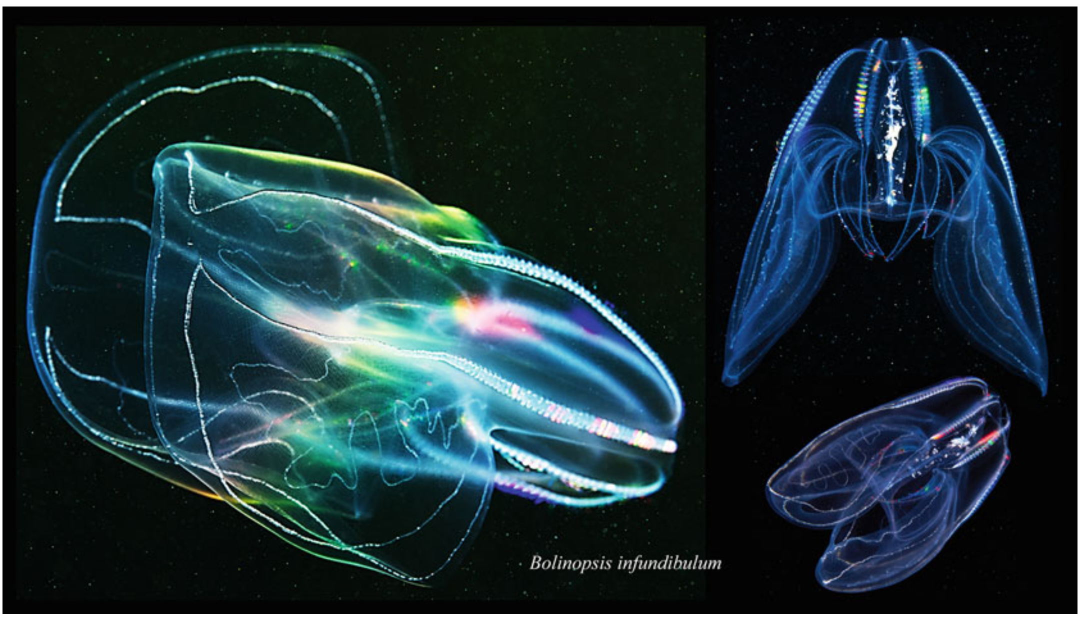


Fig. 68 Lobata: *Bolinopsis infundibulum*; different views (White Sea). (Photo: Alexander Semenov©)

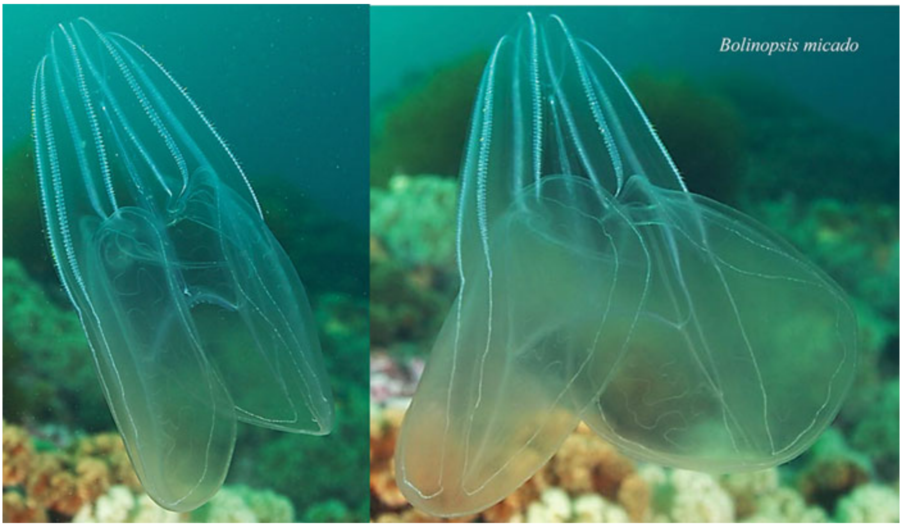


Fig. 69 Lobata: *Bolinopsis mikado* from Vityaz bay, Japan Sea. (Photo: Alexander Semenov©)

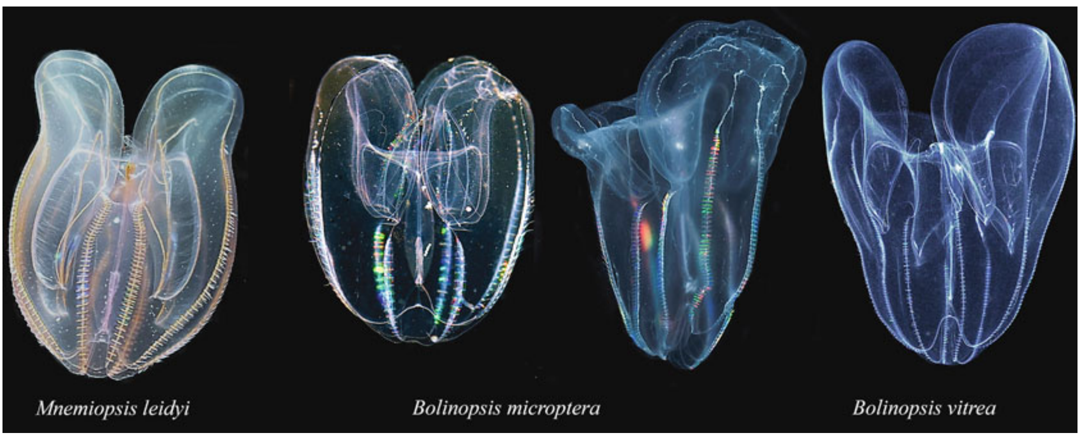


Fig. 70 Lobata: *Mnemiopsis leidyi* (Central Florida), *Bolinopsis microptera* (Friday Harbor, WA, USA), and *Bolinopsis vitrea* (South Florida)

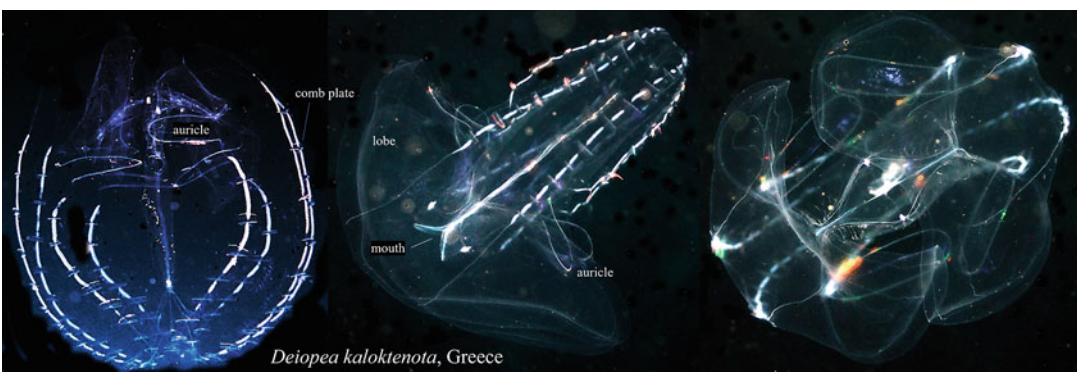


Fig. 71 *Deiopea kaloktenota*, Lobata, from Saronida, Attica, Greece. (Photos: iNaturalist Canada by Stergios Vasilis (https:/inaturalist.ca/taxa/949340-Deiopea-kaloktenota)). The left photo was taken by Stergios Vasilis. The original source is https:/www.inaturalist.org/observations/69830733. The other two shots are from https:/www.inaturalist.org/taxa/949340-Deiopea-kaloktenota

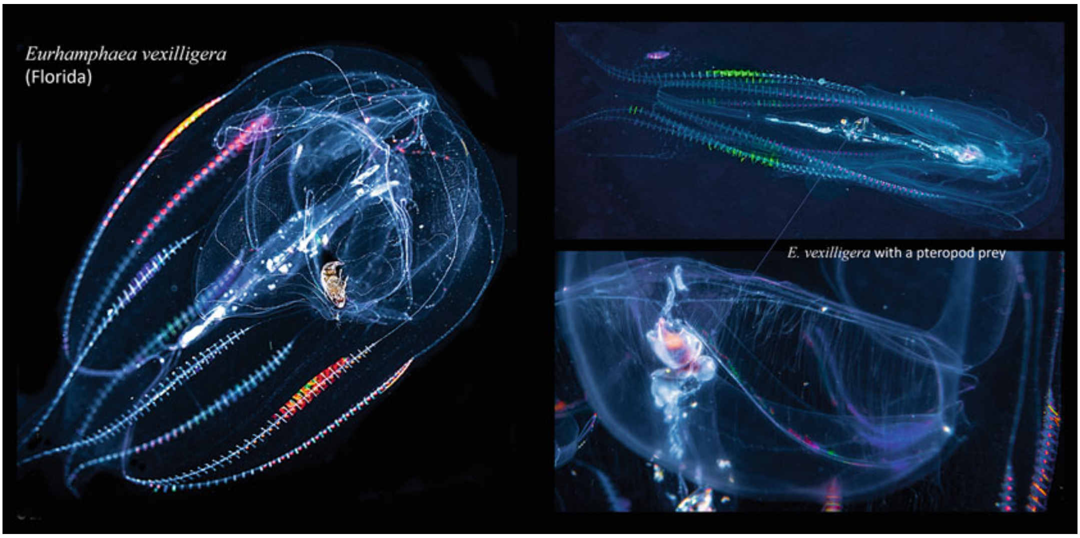


Fig. 72 *Eurhamphaea vexilligera* with crustacean and pteropod prey, Florida

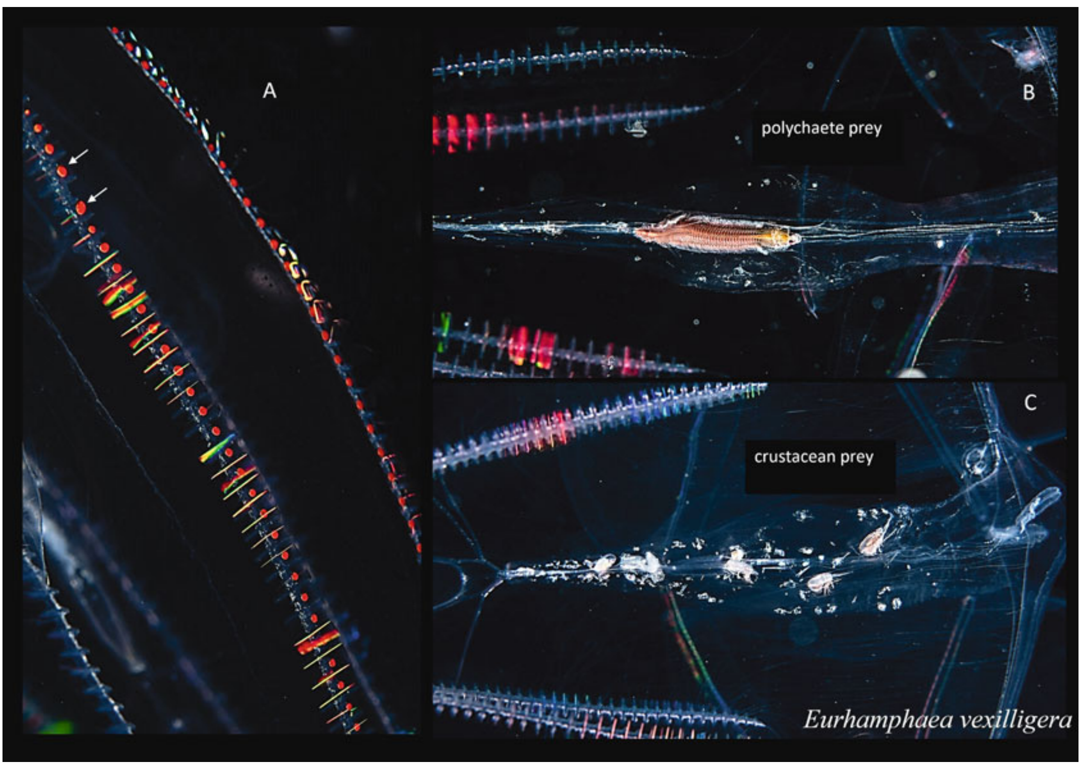


Fig. 73 *Eurhamphaea vexilligera* – ink release sites (arrows – (**a**), see also [153]) and with polychaete prey (**b**), crustacean prey (**c**)

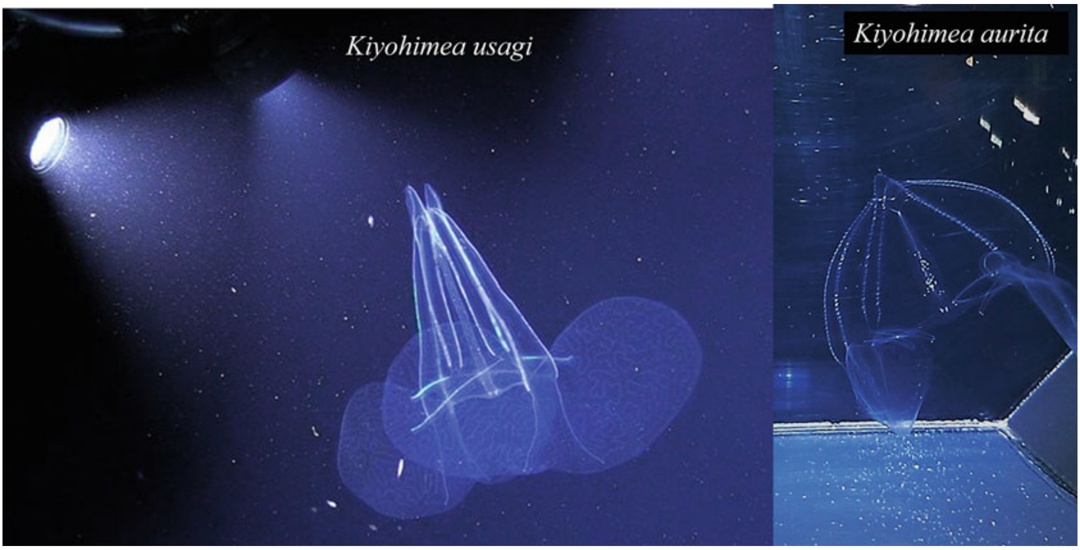


Fig. 74 *Kiyohimea usagi*. (Photo: Henk Jan T. Howing/GEOMAR, Cape Verde https:/twitter.com/GEOMAR_en/status/1140616744110874625/photo/2); *Kiyohimea aurita* Nagasaki Aquarium, Japan (https:/photozou.jp/photo/show/1143978/127124448; see also https:/www.umikirara.jp/en/creature/)

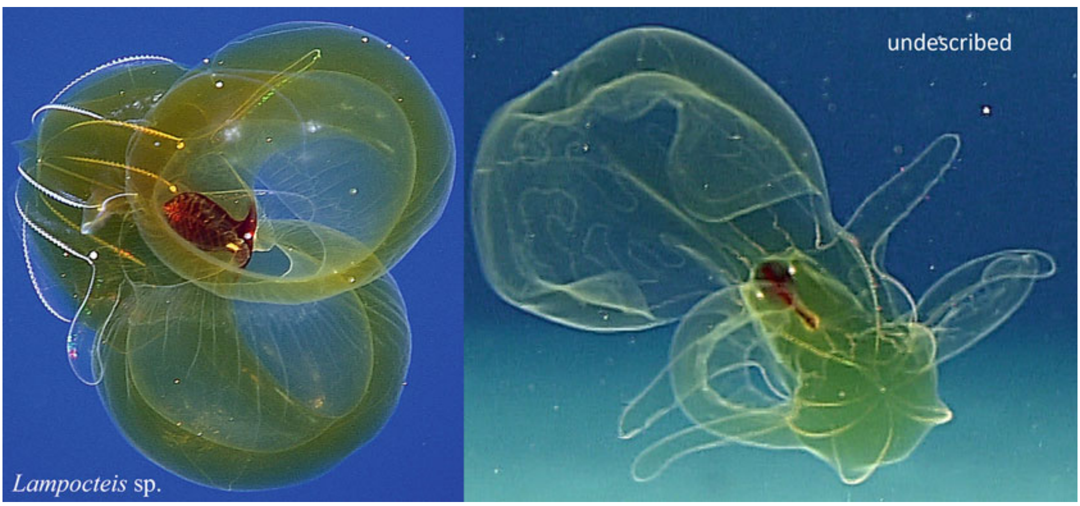


Fig. 75 *Lampocteis* sp. (Image courtesy of NOAA Ocean Exploration, Voyage to the Ridge 2022; https:/www.flickr.com/photos/oceanexplorergov/52648188412/in/photostream/) and undescribed deepwater lobate. (Image courtesy of the NOAA Office of Ocean Exploration and Research, Western Gulf of Mexico 2018; https:/www.flickr.com/photos/oceanexplorergov/51236540164/in/photostream/)

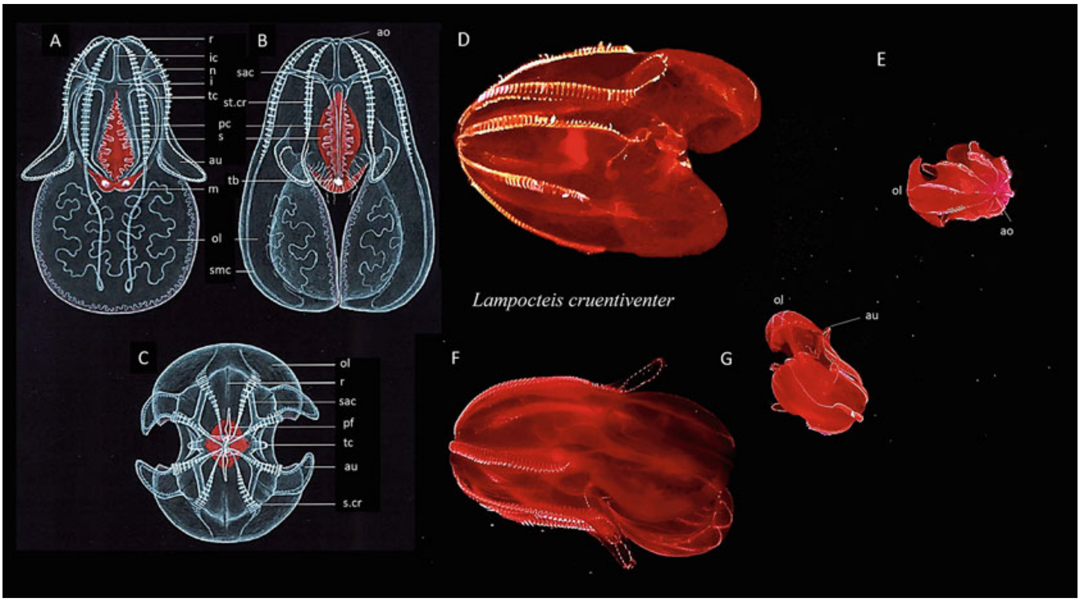


Fig. 76 Schematic anatomy of the bloodybelly comb jelly *Lampocteis cruentiventer*, (**a**–**c**) from [157]. This deepwater lobate (up to 15 cm) can be found at ~250–1500 m. The red pigmentation makes the ctenophore practically invisible to predators. It is also suggested such red color mask bioluminescence. The rest are the general views of living *Lampocteis*, from San Francisco area. Abbreviations: ao, aboral organ; au, auricles; i, infundibulum; ic, infundibular canal; m, mouth; n, notch; pc, paragastric canal; s, stomodaeum; sac, substomodaeal adradial canal; s.cr, substomodaeal comb row; smc, substomodaeal meridional canal; st.cr, subtentacular comb row; tb, tentacle bulb; tc, tentacular canal. (Credits: (**a**) [157] © Rosenstiel School of Marine, Atmospheric & Earth Science (see also images from Vincenzoxvivolo, CC BY-SA 4.0 https:/creativecommons.org/licenses/by-sa/4.0, via Wikimedia Commons); from https:/www.mbari.org/animal/bloody-belly-comb-jelly/. Additional images and videos of *L. cruentiventer* can be found at https:/www.mbari.org/animal/bloody-belly-comb-jelly/, see also [60])

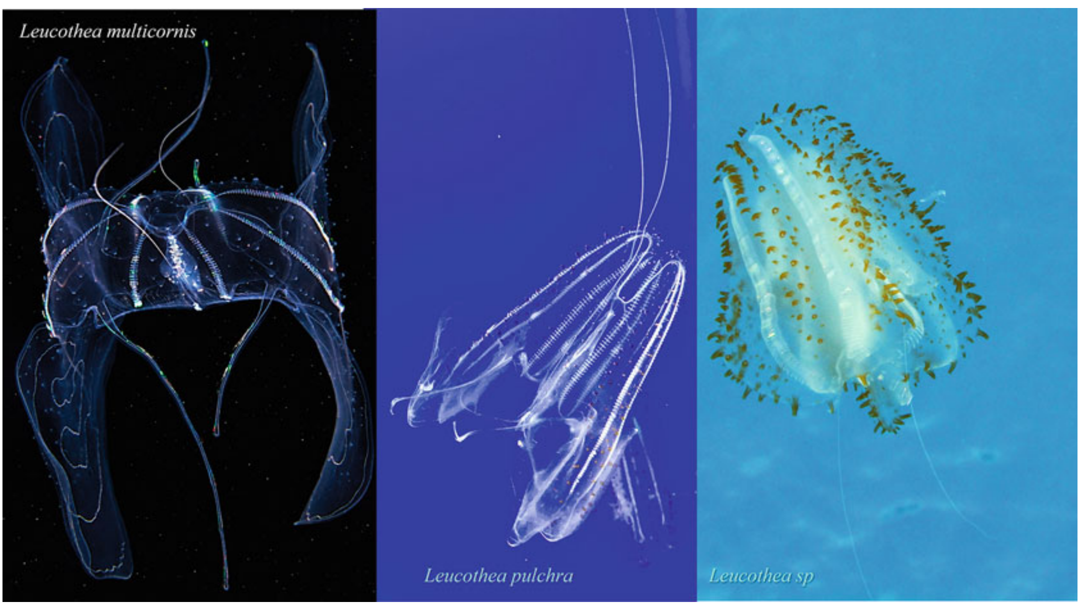


Fig. 77 *Leucothea multicornis*, Mediterranean Sea (Photo: Alexander Semenov©) and *Leucothea pulchra* (California), and *Leucothea* sp. The right image: Photo: Emily Hale©

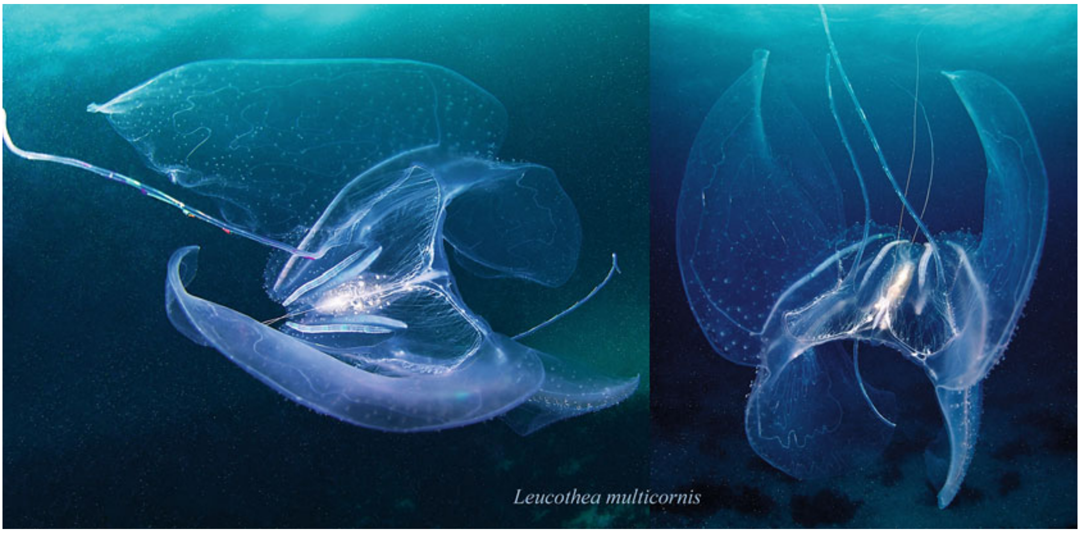


Fig. 78 *Leucothea multicornis*, Ponza Island, Italy, Tyrrhenian Sea. (Photo: Alexander Semenov©; https:/www.flickr.com/photos/a_semenov/15342819150/in/photostream/)

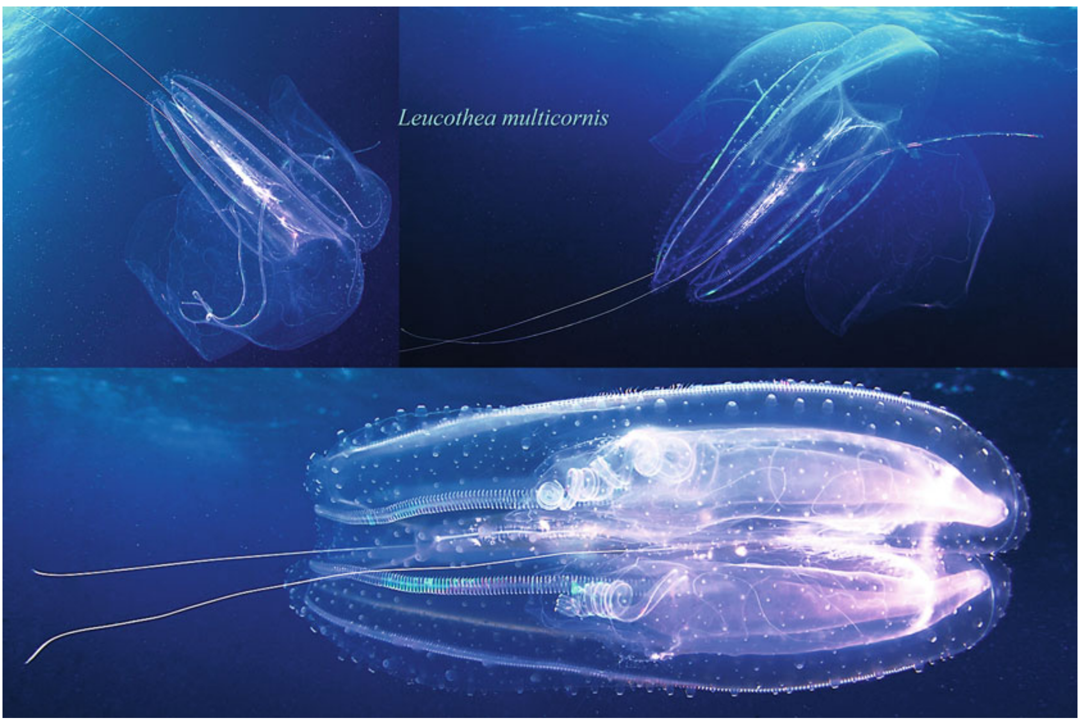


Fig. 79 *Leucothea multicornis*, Red Sea. (Photo: Alexander Semenov©)

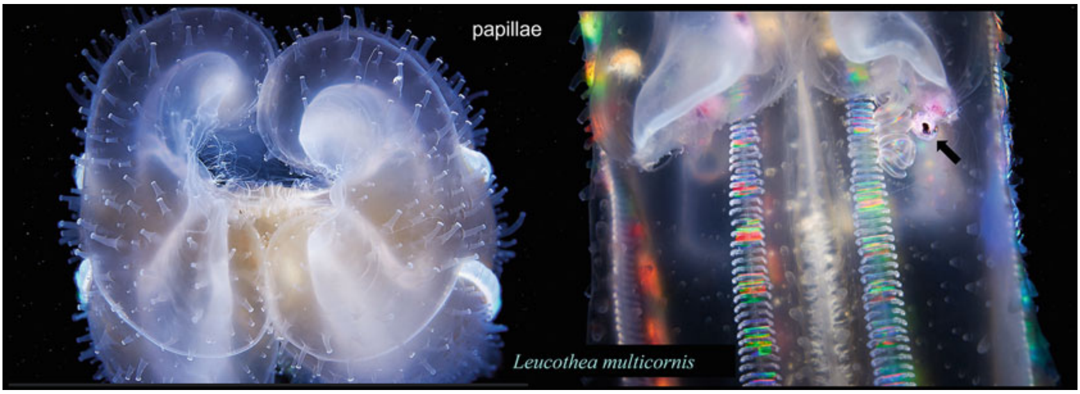


Fig. 80 *Leucothea multicornis*. (Photo: Alexander Semenov©)

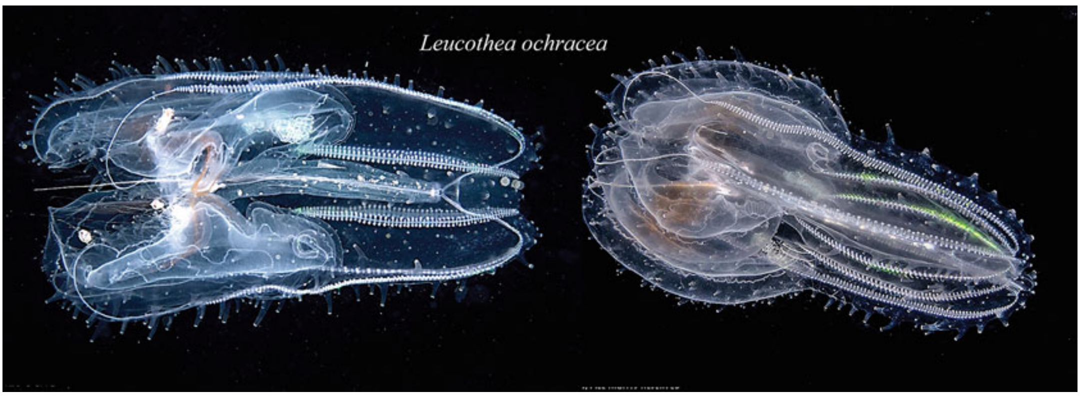


Fig. 81 *Leucothea ochracea*. (Photo: Susan Mears©)

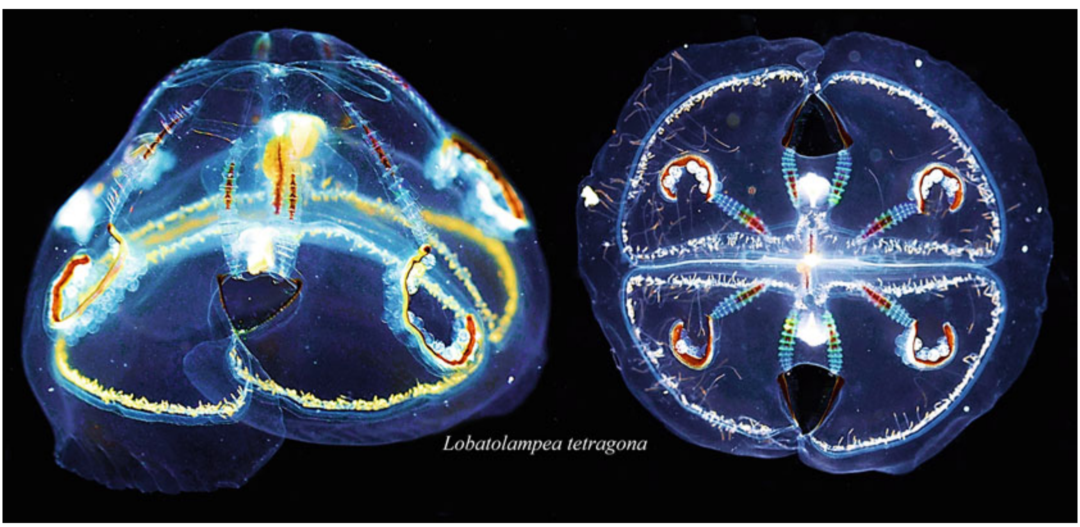


Fig. 82 Benthic *Lobatolampea tetragona*, Philippines

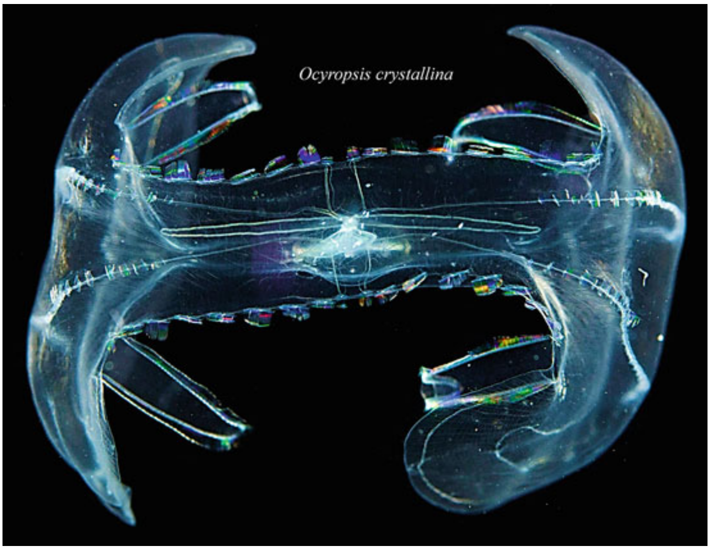


Fig. 83 *Ocyropsis crystallina*, New Caledonia

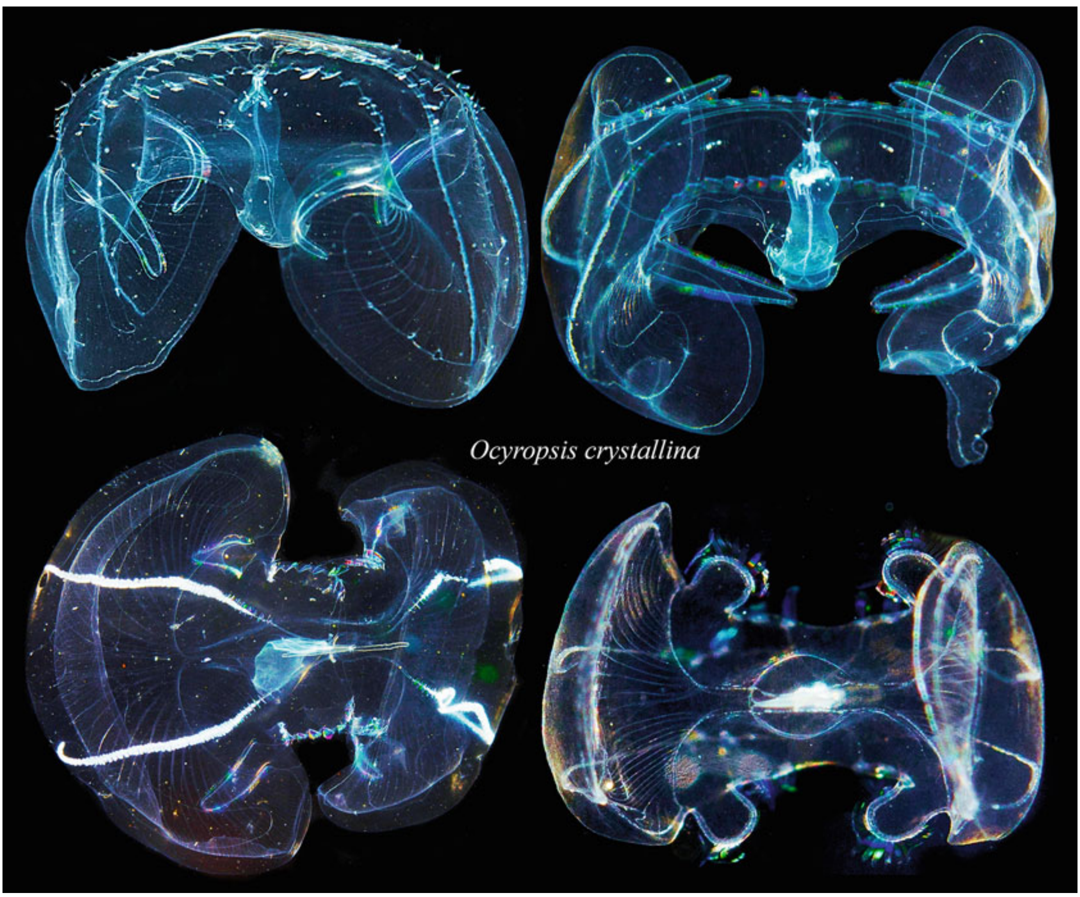


Fig. 84 *Ocyropsis crystallina*, New Caledonia

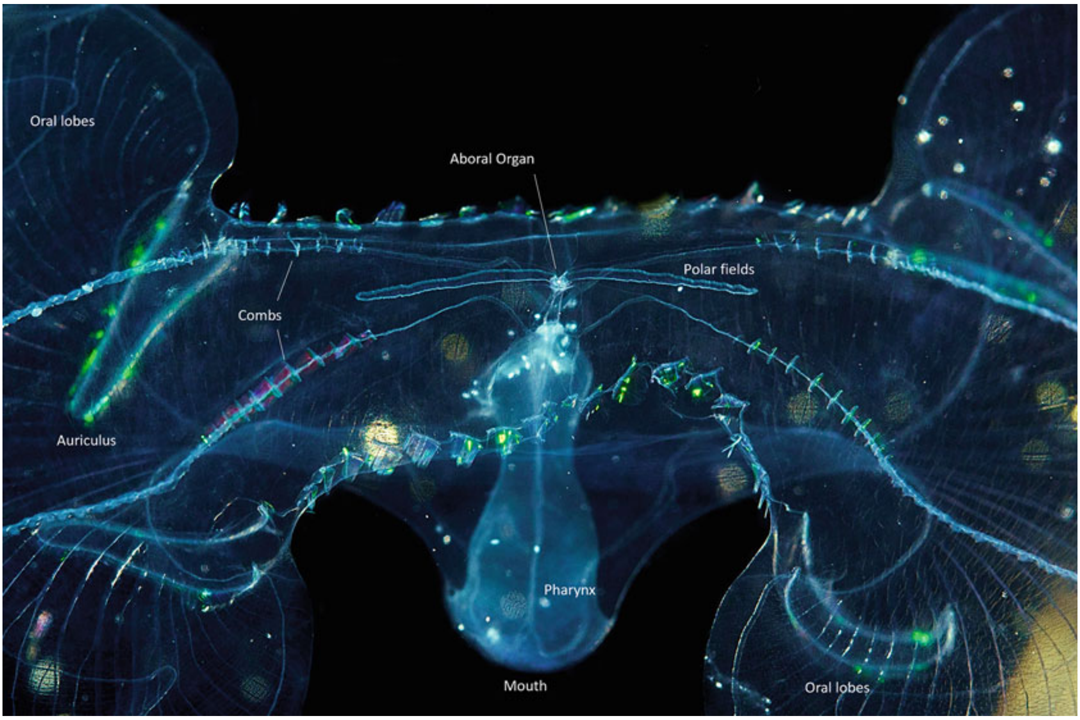


Fig. 85 *Ocyropsis crystallina*, New Caledonia

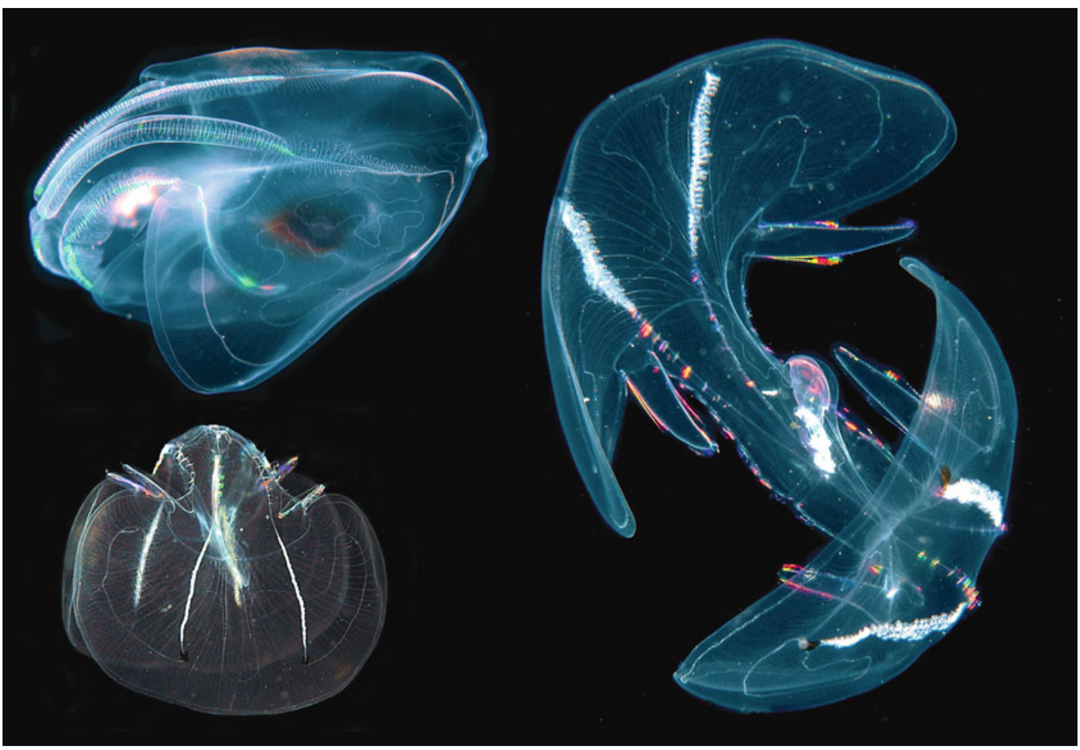


Fig. 86 The upper right photo is *Ocyropsis maculata maculata*, Florida. The images on the right and lower left are *Ocyropsis cristalina guttata*

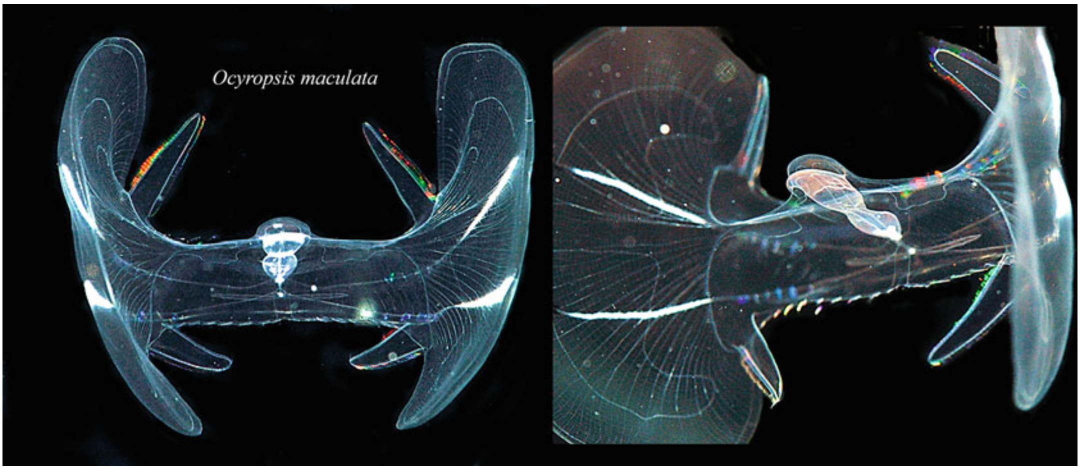


Fig. 87 *Ocyropsis maculata*, Florida

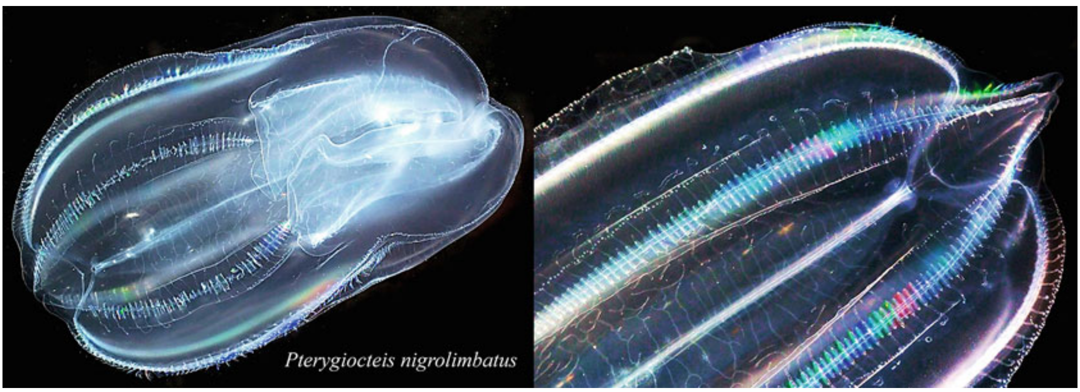


Fig. 88 Subantarctic Lobata (*Pterygiocteis nigrolimbatus*, Punta Arenas, Chile)

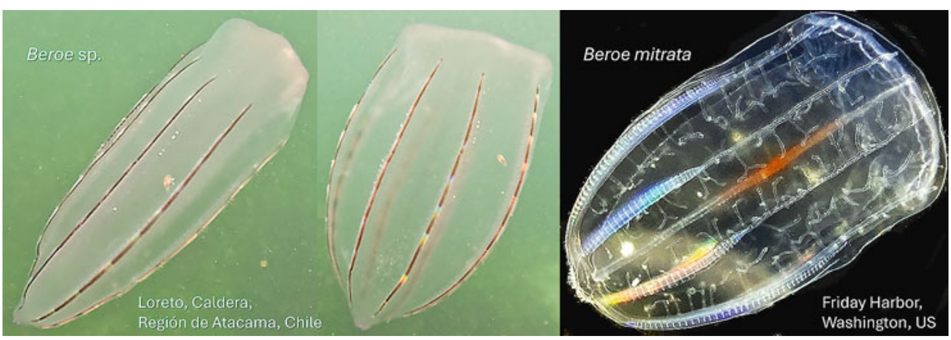


Fig. 89 Two species of *Beroe* from the Pacific Coasts of North (right) and South America (left). The left image shows *Beroe* from the northern part of the Humbolt Current (photo: Rigoberto Moreno Mendoza); the right photo shows *Beroe mitrata* with the orange gut from the San Juan Archipelago (Washington, USA)

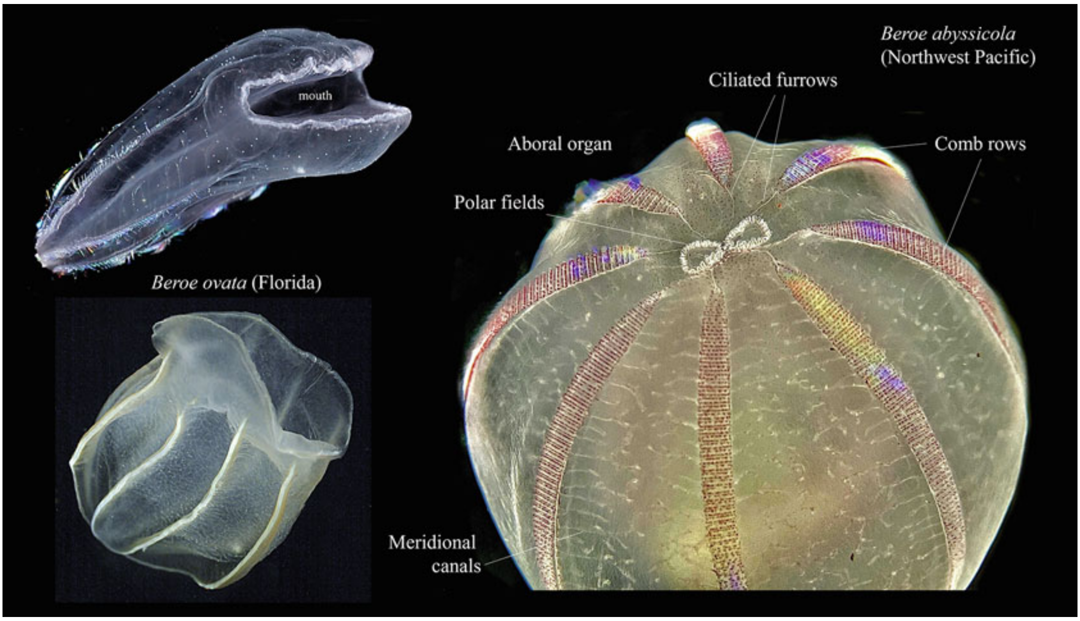


Fig. 90 *Beroe ovata* (Florida) and *Beroe abyssicola* (Friday Harbor, WA, USA)

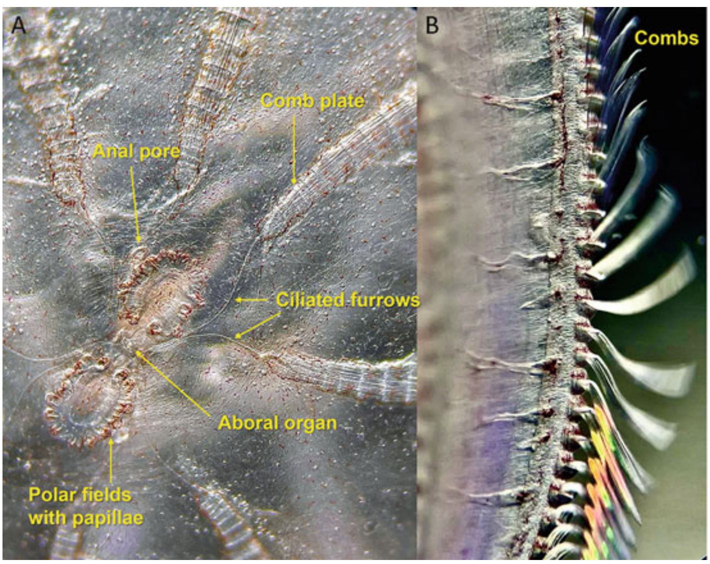


Fig. 91 (**a**) Aboral view of *Beroe abyssicola*. (**b**) Cilia of comb plates in *B. abyssicola*

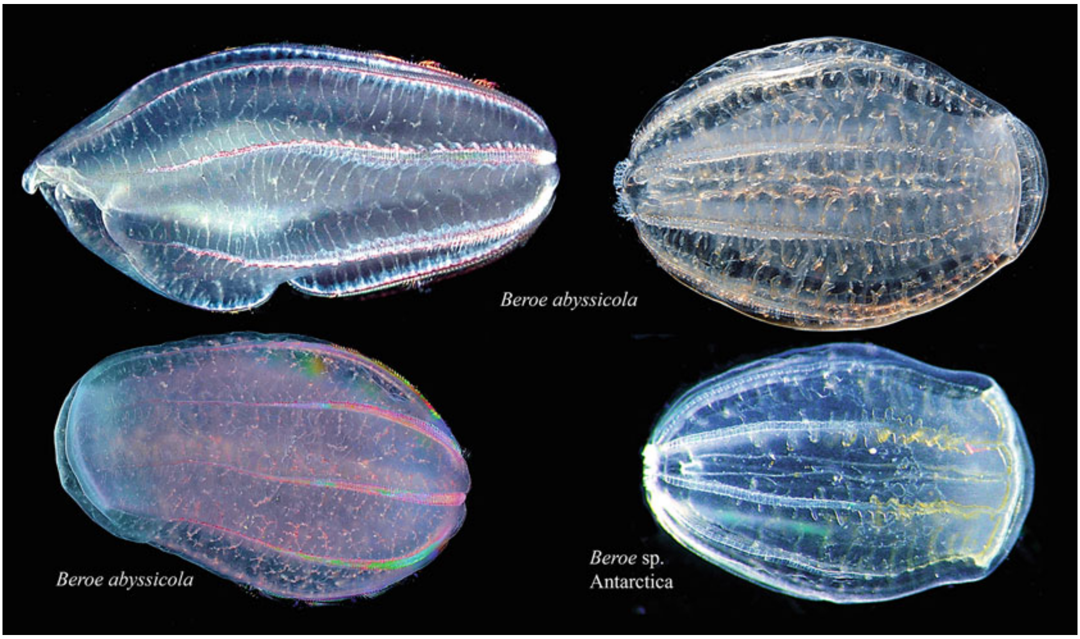


Fig. 92 *Beroe abyssicola* (Friday Harbor, WA, USA) and *Beroe* sp. (Weddell Sea, Antarctica)

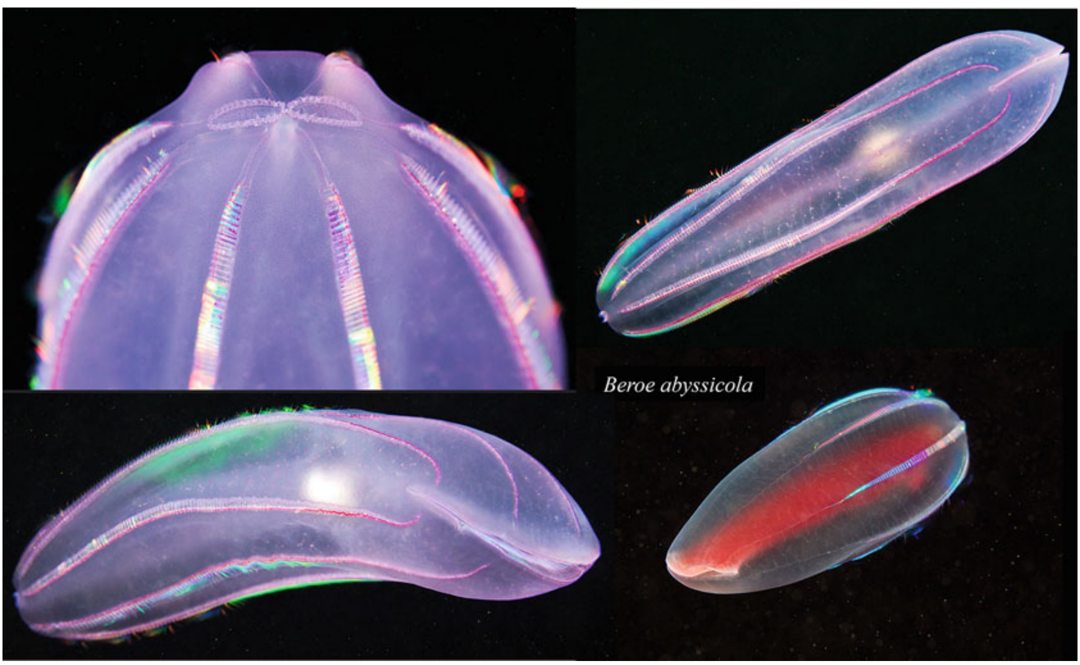


Fig. 93 *Beroe abyssicola*, White Sea. (Photo: Alexander Semenov©). Mortensen 1927, says among other things, that *B. abyssicola* is very similar to *Beroe cucumis*. the former is a deep sea speices and "claret" red but less colored when young, the latter is found near the surface and not intensely colored. Figure 93 shows images by A. Semenov,. I beleive he is a diver so these are near surface water images. If shot near the surface they may not be B abyssicola. The image in the lower right has very short ctene plates relative to the other specimen and is colored differently. The type photos have shorter plates

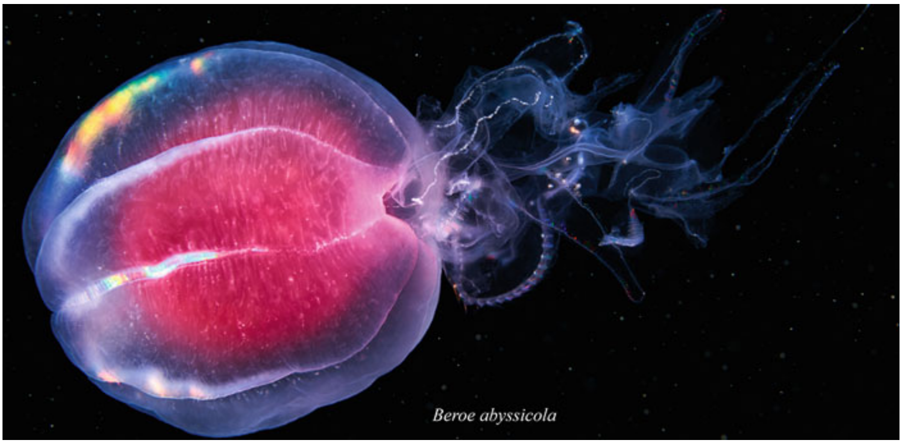


Fig. 94 *Beroe abyssicola* feeding on *Bolinopsis infundibulum*, White Sea. (Photo: Alexander Semenov©)

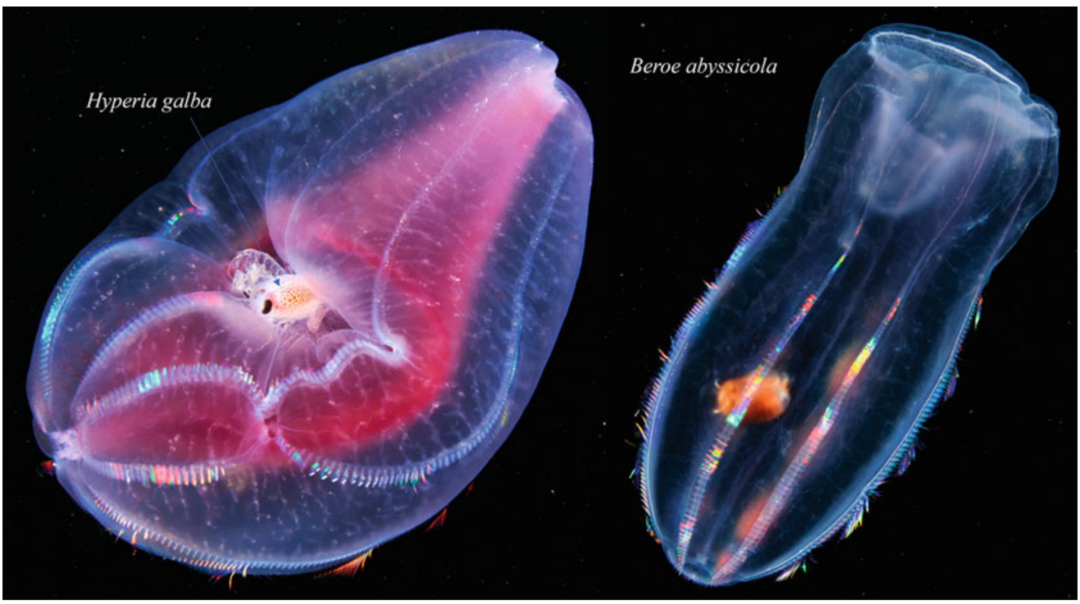


Fig. 95 *Beroe abyssicola* with the amphipod ectoparasite *Hyperia galba* (Montagu), White Sea. (Photo: Alexander Semenov©)

Fig. 96 *Beroe cucumis*, White Sea. (Photo: Alexander Semenov©)

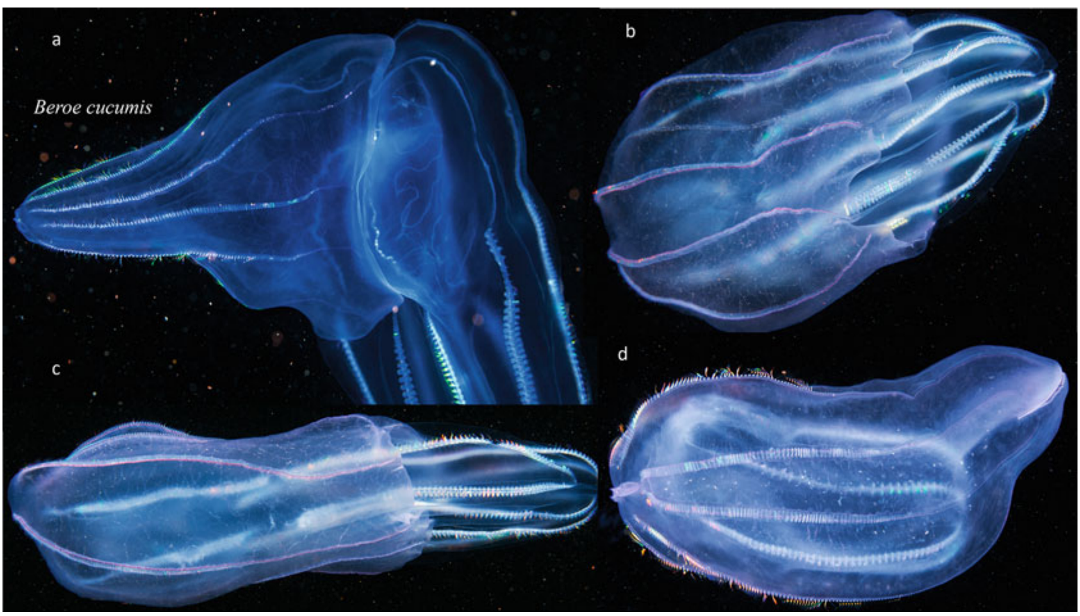


Fig. 97 *Beroe cucumis* feeding on *Bolinopsis infundibulum*, White Sea. (Photo: Alexander Semenov©)

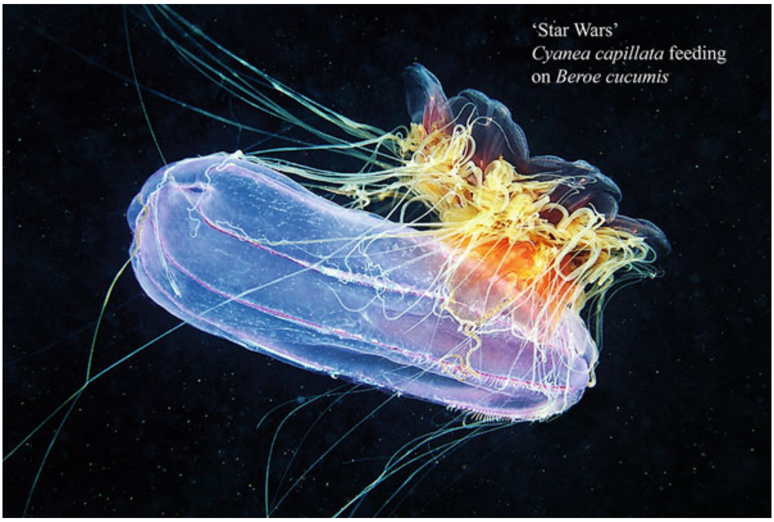


Fig. 98 The jellyfish *Cyanea capillata* feeds on *Beroe cucumis*. (Photo: Alexander Semenov©; https:/www.flickr.com/photos/a_semenov/9147073560/in/photostream/)

Fig. 99 *Beroe foskalii*, Mediterranean Sea. (Photo: Alexander Semenov©)

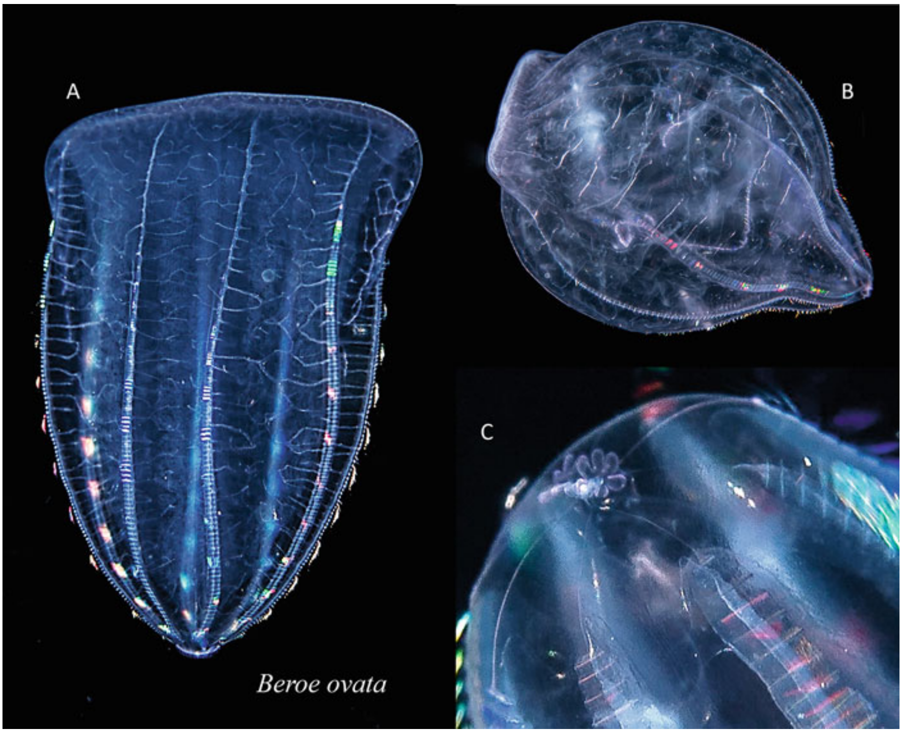


Fig. 100 *Beroe ovata* – general view (**a**); *Beroe* sp. with *Bolinopsis* inside (**b**); the aboral organ of *Hormiphora beehleri* (**c**); Florida, USA

Fig. 101 Beroida: *Neis cordigera*, Brunswick River (New South Wales, Australia). (Photo: Denis Riek© (http:/www.roboastra.com/Cnidaria3/brac195.html); see also https:/bie.ala.org.au/species/https:/biodiversity.org.au/afd/taxa/be04b5e5-a9ed-49a3-b726-03e69be5188c)

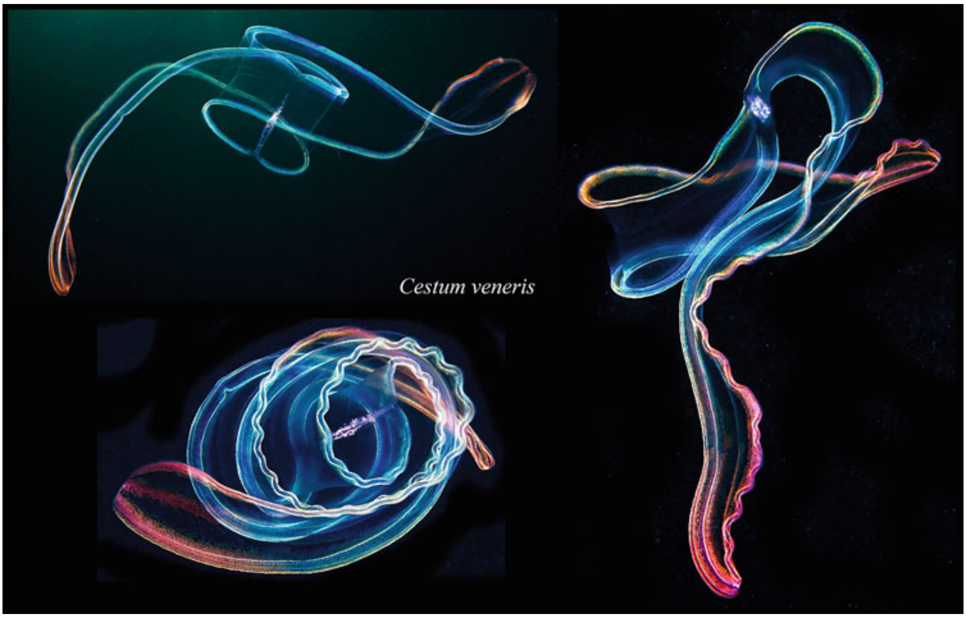


Fig. 102 Cestida: *Cestum veneris*, Ponza Island, Tyrrhenian Sea, Italy. (Photo: Alexander Semenov©. https:/www.flickr.com/photos/a_semenov/25886898121/in/photostream/, https:/www.flickr.com/photos/a_semenov/23003342862/in/photostream/, and https:/www.flickr.com/photos/a_semenov/22481800260/in/photostream/)

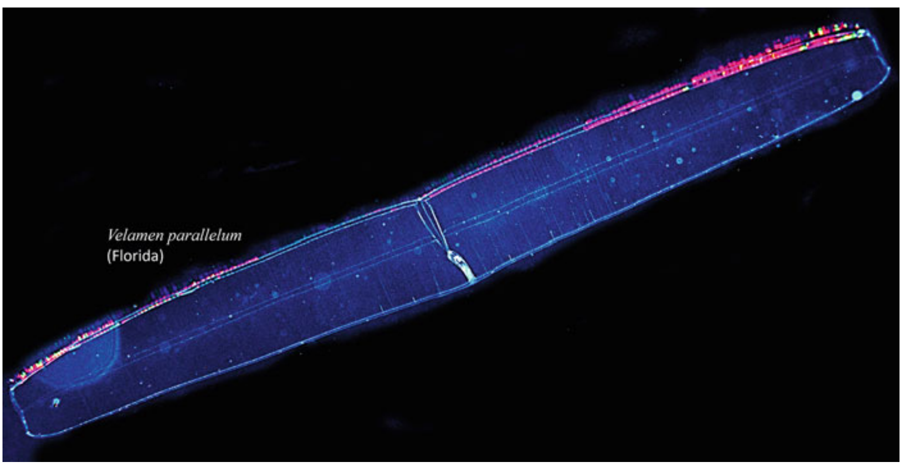


Fig. 103 Cestida: *Velamen parallelum* (Florida)

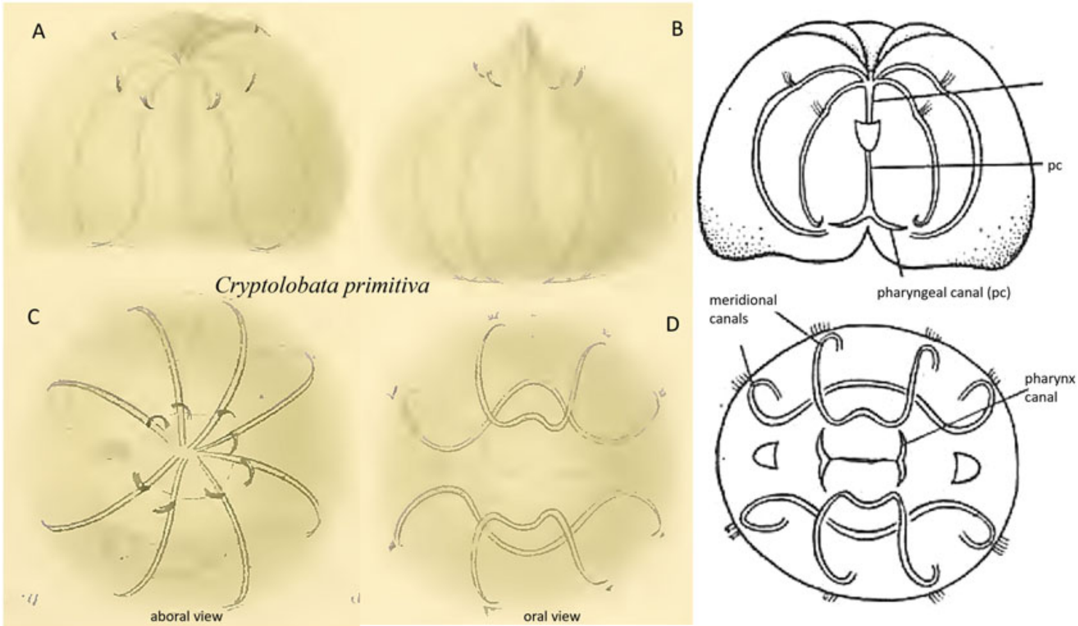


Fig. 104 *Cryptolobata primitiva* Moser, 1909. (from [71])

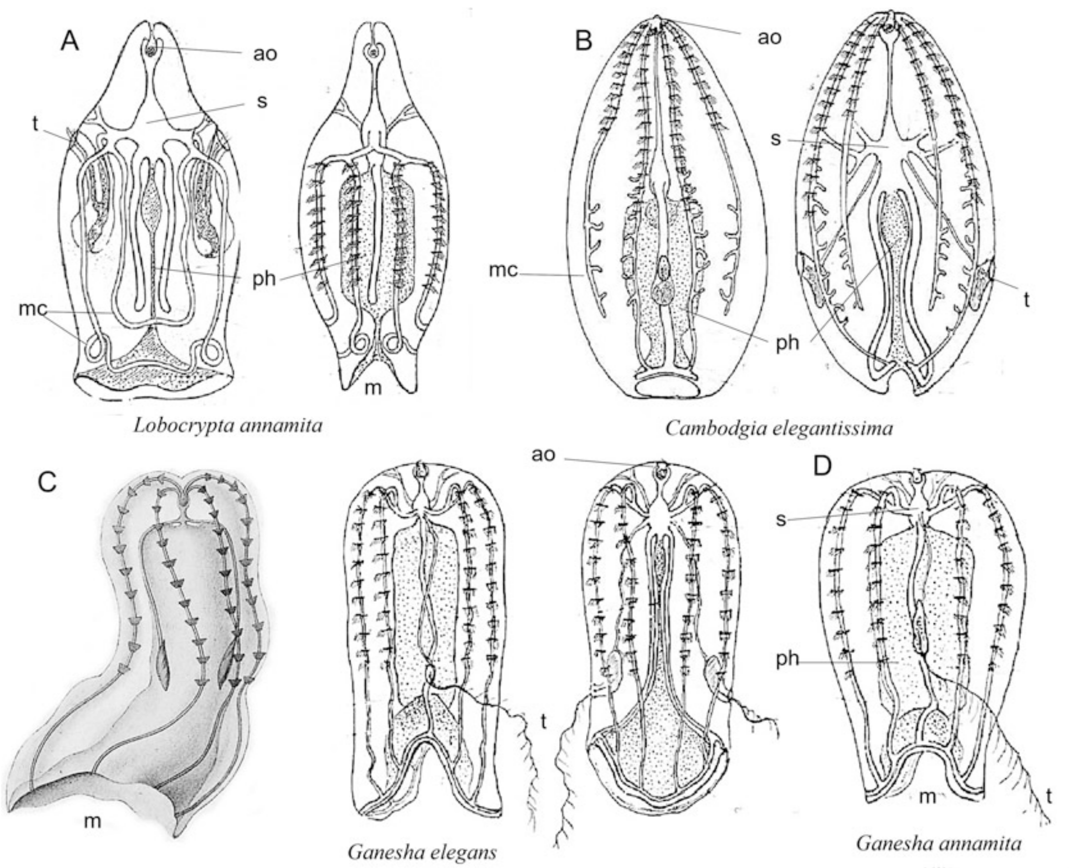


Fig. 105 Rare ctenophores of the orders Cryptolobiferida (**a** – *Lobocrypta annamita*), Cambojiida (**b** – *Cambodgia elegantissima*), Ganeshida (**c** – *Ganesha elegans*, **d** – *Ganesha annamita*). (from C. Dawydoff 1929–1946 [72], IndoPacific). Abbreviations: ao, aboral organ; m, mouth; mc, meridional canals; ph, pharynx; s, stomach; t, tentacles

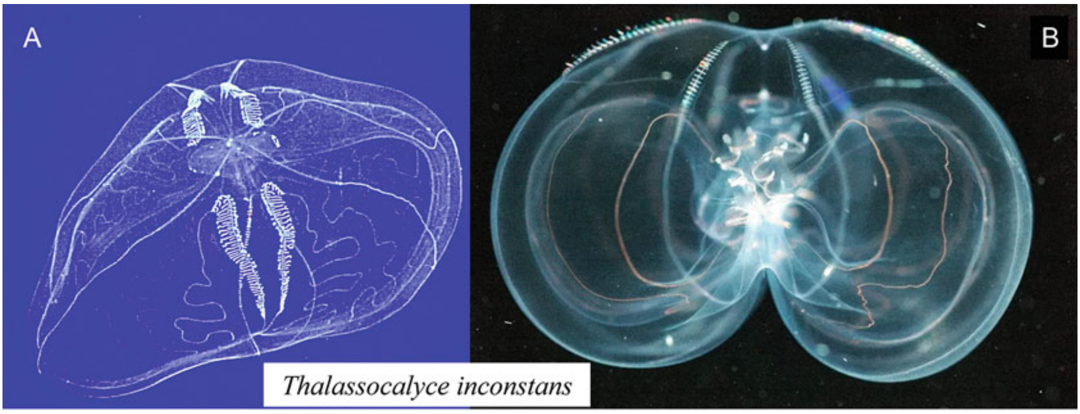


Fig. 106 Thalassocalycida: *Thalassocalyce inconstans*. ((**a**) Image courtesy of the NOAA Office of Ocean Exploration and Research, Laulima O Ka Moana. NOAA Ocean Exploration & Research from USA (https:/upload.wikimedia.org/wikipedia/commons/1/12/Ctneophore_-_Flickr_-_NOAA_Ocean_Exploration_%5E_Research.jpg); (**b**) Photo by L. Madin, Woods Hole Oceanographic Inst. (WHOI) (www.cmarz.org and https:/ocean.si.edu/ocean-life/plankton/ctenophore-feeds))

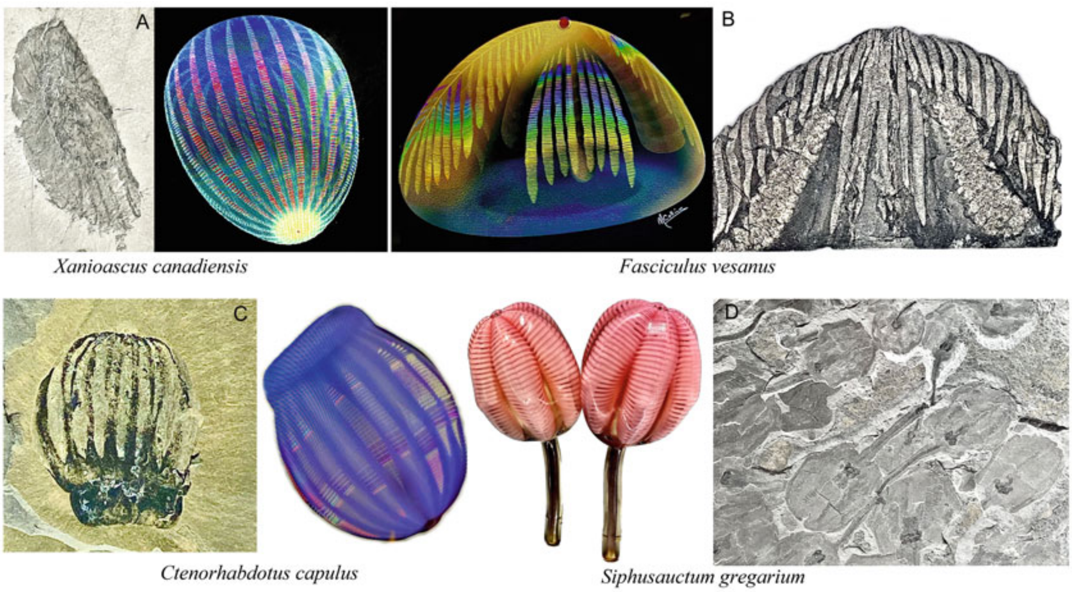


Fig. 107 Unusual fossils that have been attributed to the Ctenophora, Middle Cambrian (~506 million years ago), Burgess Shale, Canada. *Xanioascus canadiensis* (**a**, actual fossil and reconstruction), *Fasciculus vesanus* (**b**), *Ctenorhabdotus capulus* (**c**), and *Siphusauctum gregarium* (**d**). See text and [183] for details. These species and their reconstruction are at the exposition in the Royal Ontario Museum© in Toronto, Canada (see also https://burgess-shale.rom.on.ca/phylas/ctenophora/)

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