The shelled pteropods of the northeast Pacific Ocean (Mollusca: Heterobranchia, Pteropoda)

ARIE W. JANSSEN1*, STEPHANIE L. BUSH2 & NINA BEDNARŠEK3

1Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands. E-mail: ariewjanssen@gmail.com.
2Smithsonian Institution National Museum of Natural History, Department of Invertebrate Zoology, 10th St & Constitution Ave NW, Washington, DC, USA, 20560. E-mail: bushsl@si.edu
3Southern California Coastal Water Research Project, 3535 Harbor Blvd #110, Costa Mesa, CA, USA, 92626. E-mail: ninab@sccwrp.org

*corresponding author.

Abstract

An overview of shelled pteropod species of the northeast Pacific Ocean, roughly north of 25°N and east of 160°W is presented. For the 34 recognised species (Limacinidae 6, Creseidae 4, Creseidae ? 2, Cuvierinidae 3, Cliidae 6, Cavoliniidae 10, Peraclidae 2, Clionidae 1) a brief description is given enabling identification. Data are based on several museum collections and the existing literature. For all species the original description and most important synonyms are referenced. Locations of type specimens are recorded as far as is known. All species are illustrated, for many species images of living specimens are included. Cavolinia labiata (d’Orbigny, 1835) is designated type species of Orbignyia Adams, 1859.

Key words: Euthecosomata, Pseudothecosomata, taxonomy, systematics, Limacinoidea, Cavoliniioidea, Cymbulioidea, Gymnosomata

This paper is dedicated to the memory of James H. McLean

Introduction

Pteropods are heterobranch gastropods that have evolved a holoplanktic way of life. Rare during the Late Cretaceous, pteropods evolved rapidly during the early and middle Cenozoic (Janssen & Peijnenburg 2017). They occur in all ocean basins and most seas worldwide, where they predominantly inhabit the epipelagic, though a number of species occur in meso- and bathypelagic waters. Pteropod distributions follow climatic zones, with generally high species diversity but low abundance in warm waters, and low diversity with high abundance in cold-water areas. They form an important part of the ocean food chain especially in polar ecosystems. For example, they can comprise a significant portion of the diet for early life stages of some commercially important fishes (Russell 1960). There is substantial literature on their morphology, anatomy, systematics, and distribution, much of which was summarised by Lalli & Gilmer (1989). While they regularly appear in plankton tows, pteropods rarely wash ashore or are found in sediment samples taken in areas where upwelling water is undersaturated with aragonite (Ωar: Feely et al. 2008). Such water promotes rapid dissolution of the pteropods’ thin-walled, aragonitic shells.

Currently, shelled (euthhecosome) pteropods are the topic of research on ocean acidification (OA) because of their extreme sensitivity to low Ωar (Bednaršek et al. 2014 and references therein). Upon exposure to corrosive water, their thin aragonitic shell starts to dissolve, leading to physiological impairments, and ultimately death (Bednaršek et al. 2014, 2017a, b). They have become OA indicators used to project the future state of ecological integrity (Bednaršek et al. 2017a and references therein). In comparison, nothing is known
about the OA effects on the adult stages of shell-less Pseudothecosomata and Gymnosomata, despite the fact that their most sensitive early-developmental stages have shells.

OA assessment of species’ vulnerability or resilience across different pteropod groups requires an accurate systematic and taxonomic framework to allow for correct identification of investigated species. Current taxonomic work also paves the way for establishing linkages with molecular identification tools (barcoding, eDNA, etc.) needed for rapid monitoring and assessment of climate change effects on pteropods in the future.

The present interest in the Pteropoda as indicators of OA has stimulated renewed attention to their phylogenetic relationships. While molecular analyses have changed previous taxonomic evaluations by revealing unexpected biodiversity, available molecular information in most pteropod taxa is limited to the COI locus. Currently, family-level systematics are being investigated by integrative studies, including morphology and DNA sequencing (Burridge et al. 2017 and references therein).

Despite improved pteropod systematics summarized in Bouchet et al. (2017), there is still a lack of integration between taxonomic and molecular approaches for more accurate species identification, a baseline for OA vulnerability assessment can be conducted.

Particularity in the regions with high pteropod biodiversity, such as the northeast Pacific, a comprehensive synthesis of euthecosome taxonomic identification is still lacking. This is largely because there were no consistent sampling efforts focusing on pteropod community over large spatial scales across the North Pacific, as well as inconsistent net deployments that can easily miss pteropods in the water column. For this reason, an accurate and up-to-date synthesis of euthecosome pteropod taxa of the North Pacific is essential. In addition, taxonomic identifications are also assisted by the photographs to ensure accurate species identification.

In this work a summary and brief description of all shelled pteropods known from the northeast Pacific Ocean, roughly north of 25°N and east of 160°W, is presented. References for first descriptions are provided as are relevant synonyms and type localities.

Material and methods

Data for this paper are based on the collections housed in the Natural History Museum of Los Angeles County, Los Angeles, USA, the Santa Barbara Museum of Natural History, Santa Barbara, USA, the Naturalis Biodiversity Center, Leiden, The Netherlands, and the Smithsonian Institution National Museum of Natural History, Washington, DC, USA, as well as on specimens or data received from various researchers. Other data were compiled from the existing literature.

Illustrations are based on specimens in the collections mentioned above, other museum collections’ specimens, or copied (with permission) from internet sources. Specimens from the northeastern Pacific were not available for all species, but illustrations of specimens from other areas are only included if their identification is certain.

Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Institution/Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>LACM</td>
<td>Natural History Museum of Los Angeles County, USA.</td>
</tr>
<tr>
<td>MCZR</td>
<td>Museo Civico di Zoologia, Roma, Italy.</td>
</tr>
<tr>
<td>MNHN</td>
<td>Muséum national d’Histoire Naturelle, Paris, France.</td>
</tr>
<tr>
<td>NHMD</td>
<td>Natural History Museum of Denmark, Copenhagen, Denmark.</td>
</tr>
<tr>
<td>NHMUK</td>
<td>The Natural History Museum, London, United Kingdom.</td>
</tr>
<tr>
<td>NMNZ</td>
<td>Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.</td>
</tr>
<tr>
<td>NMR</td>
<td>Natuurhistorisch Museum, Rotterdam, The Netherlands.</td>
</tr>
<tr>
<td>RGM</td>
<td>Rijksmuseum van Geologie en Mineralogie, currently in Naturalis Biodiversity Center, Marine Biology (fossil Mollusca), Leiden, The Netherlands.</td>
</tr>
<tr>
<td>RMNH</td>
<td>Rijksmuseum van Natuurlijke Historie, currently in Naturalis Biodiversity Center, Marine Biology (recent Mollusca), Leiden, The Netherlands.</td>
</tr>
<tr>
<td>SBNMH</td>
<td>Santa Barbara Museum of Natural History, Santa Barbara, USA.</td>
</tr>
<tr>
<td>USNM</td>
<td>United States National Museum, Smithsonian Institution, Washington (DC), USA.</td>
</tr>
</tbody>
</table>
ZMA Zoölogisch Museum, Amsterdam, The Netherlands, currently in RMNH.
ZMH Zoologisches Museum, Hamburg, Germany.

Systematics

Order Pteropoda Cuvier, 1804
Ptéropodes Cuvier, 1804: 232.

Description. Shelled or, in the adult stage, shell-less holoplanktic heterobranch gastropods have a modified foot that is a pair of parapodia (‘wings’) used for locomotion. For additional information on their habitat, soft part anatomy, etc. see Lalli & Gilmer (1989) and references therein.

Remarks. For a long time the name ‘Pteropoda’ has been used as an unofficial name for the orders Thecosomata and Gymnosomata. The molecular work of Klussmann-Kolb & Dinapoli (2006) revealed a close relationship between these two groups, which led to the re-establishment of the order Pteropoda as a sistergroup of the order Anaspidea P. Fischer, 1883 (= Aplysiida Pelseneer, 1906 emend. Bouchet et al. 2017).

Suborder Euthecosomata Meisenheimer, 1905
Thecosomata de Blainville, 1824: 271 (pars).

Description. Pteropods with fragile (thin-walled) aragonitic shells in the adult stage, sinistrally coiled or bilaterally symmetrical. Epi- to bathypelagic, with diel vertical migration.

Limacinoidea Gray, 1840
Limacinidae Gray, 1840: 155 (Principle of Coordination).

Description. Shell of higher or lower conical or planorboid spiral, seemingly sinistral, but anatomically ultra-dextral. Protoconch not clearly separated from teleoconch. Columella straight (rarely twisted), not ending in rostrum, umbilicus present but almost completely closed in some species. Apertural margin simple or reinforced. Periostracum insignificant. Operculum present but frequently lost in adults.

Limacinidae Gray, 1840
Spiralidae Chenu, 1859: 113.
Spiratellidae Dall, 1921: 58.

Description. As for superfamily. Epi- to mesopelagic, rarely bathypelagic.

Heliconoides d’Orbigny, 1836
Heliconoides d’Orbigny, 1836: 159, 174. Type species (SD Herrmannsen 1846: 514) Atlanta inflata d’Orbigny, 1835 = Heliconoides inflatus (d’Orbigny, 1835). Tropical and subtropical, worldwide.
Protomeda Costa, 1861: 73. Type species (SD Fischer 1883: 430) Protomeda elata Costa, 1861 = Heliconoides inflatus (d’Orbigny, 1835). Mediterranean.
Embolus Jeffreys, 1869: 114. Type species (OD) Spiralis rostralis Eydoux & Souleyet, 1840 = Heliconoides inflatus (d’Orbigny, 1835).
Skaptotion Curry, 1965: 368. Type species (M) Skaptotion bartonense Curry, 1965. Eocene, United Kingdom.

Description. Last whorl and apertural margin reinforced by subperipheral belt on internal wall, usually
projecting as a rostrum on the aperture margin because of damaged, extremely thin apertural margin above and below the belt.

Remarks. Genus monotypic with a single Recent species, but many fossil species. Possibly polyphyletic because the phylogenetic lineage of numerous extinct species is difficult to determine. Cretaceous (Campanian) to Recent (Janssen & Goedert 2016).

**Heliconoides inflatus** (d’Orbigny, 1835)

(Figure 1a–c)

*Allanta [sic] inflata* d’Orbigny, 1835: pl. 12, figs 16–19.


Atlantic and Indo-Pacific oceans, 36°N–36°S.

*Spirialis rostralis* Eydoux & Souleyet, 1840: 236. No types available. No type locality mentioned.


Equatorial Atlantic.

*Protomedeia elata* O.G. Costa, 1861: 74, pl. 11, fig. 5a–c. No types available. Mediterranean.

**Description.** Very fragile, planorboid shell, 1.5× wider than high, flattened to slightly sunken apical plane. Shell height to 1.6 mm. Initial whorl occasionally slightly raised. Three convex whorls, last one inflated, base perfectly rounded, umbilicus present, 1/6 of shell diameter. Aperture wide, as high as entire shell. Last whorl, apertural margin internally reinforced by narrow internal, subperipheral belt. Operculum present, transparent.

**Distribution.** Tropical to subtropical. In northeast Pacific to about 40°N. Epipelagic. Abundant, but more rare to the North.

Remarks. Two forms can be distinguished (Janssen 2004: 109) with a subperipheral belt starting on earlier whors, continuing to apertural margin, or a subperipheral belt only present in second half of last adult whorl and whorl from there on more or less swollen. It is unknown if these two morphological forms represent two taxa, as transitional forms also occur. It is possible that the forms have different geographical distributions.

**Genus Limacina Bosc, 1817**

*Limacina* Bosc, 1817: 42. Type species (OD) *Clio helicina* Phipps, 1774. Northern (subarctic) area of Atlantic and Pacific oceans.

*Spiratella* de Blainville, 1817: 407. Type species (OD) *Clio helicina* Phipps, 1774. Northern (subarctic) area of Atlantic and Pacific oceans.

*Heterofusus* Fleming, 1823: 498, pl. 15, fig. 2. Type species (SD Gray 1847) *Fusus retroversus* Fleming, 1823. Northern Atlantic Ocean.

*Spirialis* Eydoux & Souleyet, 1840: 235. Type species (SD Herrmannsen 1847: 489) *Atlanta trochiformis* d’Orbigny, 1835. Tropical and subtropical worldwide.


*Crino* Gistel, 1848: 166. Type species (OD) *Crino arctica* Fabricius, 1780 = *Limacina helicina* (Phipps, 1774). Northern (subarctic) area of Atlantic and Pacific oceans.

*Valvatina* Bornemann, 1855: 318. Type species (M) *Valvatina umbilicata* Bornemann, 1855. Oligocene, Germany.


**Description.** Apical plane not flattened but in higher or lower spiral. Apertural margin simple.

Remarks. The genera *Limacina* Bosc, 1817 and *Spiratella* de Blainville, 1817 were both introduced in December 1817 and are based on the same type species. Over time the name *Limacina* was predominantly used by biologists, whereas paleontologists usually applied the name *Spiratella*. Janssen & Zorn (2001) concluded that priority should be given to *Limacina*. 
FIGURES 1–3. Heliconoides, Limacina. 1a–c. Heliconoides inflatus (d’Orbigny, 1835). California. Shell diameter 1.5 mm (from McGowan, 1968). Note thickening of apertural margin in middle figure, showing presence of internal belt. 2. Limacina bulimoides (d’Orbigny, 1835), California. Shell height 3.0 mm (from McGowan 1968). 3a–b. Limacina bulimoides (d’Orbigny, 1835), microornamentation on nucleus (left) and early whorls (right); specimen from the eastern Mediterranean, core T87/2/20G; RGM 569378b (from Janssen 2012a: fig. 46D–E).
**Limacina bulimoides** (d’Orbigny, 1835)
(Figures 2, 3a–b)


**Description.** Shell high spired, to 3 mm high, ~1.5–1.7× higher than wide; up to six moderately convex whorls separated by incised suture. Aperture higher than wide, pointed below, above. Apertural margin simple. Umbilicus very small to almost absent. Surface of shell with faint growth lines, very fine microgranulations, especially on nucleus, first whorls. Fresh specimens with brownish color along suture and at aperture.

**Distribution.** Tropical to subtropical, in the northeast Pacific south of 40°N, epipelagic, uncommon.

**Limacina helicina helicina** (Phipps, 1774)
(Figures 4, 5a–b)


**Description.** Shell of brownish color when fresh, wider than high to almost as wide as high, with up to six whorls in low conical spire, separated by distinct suture. Last whorl large, swollen. Shell surface from 4th whorl onward with regular ornament of fine radial riblets. Aperture large, with straight columellar side, rounded outer lip. Umbilicus present, 1/6–1/4 shell diameter. Operculum present. Shell height to about 6 mm, H/W-ratio 0.70–1.10.

**Distribution.** Epipelagic species (to ~300 m). North Atlantic and North Pacific oceans, in the Pacific Ocean roughly between 45 and 65°N, more to the south, to c. 30°N in the eastern part of the North Pacific. Predominantly between 40 and 60°, with the greatest abundances in the northern part of that area (McGowan 1963: as *L. helicina* A). This species has been collected from under polar ice and may occur locally in large populations.

**Remarks.** A form with a somewhat elevated spire (H/W-ratio c. 0.9 to over 1.1 (McGowan 1963: fig. 2 left), described as *f. acuta* van der Spoel (1967: 40, fig. 5e; unavailable name: infrasubspecific), co-occurs with the typical form.

Juvenile specimens of *Limacina helicina helicina* less than four whorls do not have radial ornament and cannot be distinguished from *L. helicina pacifica*. Molecular analyses (Bednaršek unpubl. data) do not differentiate between these two taxa, thus herein they are interpreted as subspecies on the basis of different distributions, as indicated by McGowan (1963).

Two forms or subspecies, *Limacina helicina* (f.) *antarctica* Woodward, 1854 and *L. helicina* (f.) *rangi* d’Orbigny, 1835, are recorded from the Antarctic region. Hunt *et al.* (2010), however, restricted the species *L. helicina* on the basis of molecular work to the northern oceans, which makes *L. rangi* the valid name for the southern seas. Two subspecies are found in the northeast Pacific (McGowan 1963).

**Limacina helicina pacifica** Dall, 1871
(Figures 6, 7a–c)


**Description.** Subspecies *L. helicina pacifica* differs by the absence of radial ornament. Shell surface with faint growth lines only; spire relatively low conical (e.g. H 2.99, W 4.14 mm).

Remarks. According to McGowan (1963) and van der Spoel (1967: fig. 336) the subspecies is found in the northern Pacific Ocean, predominantly between 30 and 60°N, present from the Bering Sea to the Gulf of California (Angulo-Campillo et al. 2011). Both subspecies also occur in the estuarine regime of the Salish Sea. Limacina helicina is the best studied and characterized pteropod species used in OA research (Bednaršek et al. 2017).

A related subspecies was described from the Sea of Okhotsk, west of Kamchatka and the Kurilian Islands, as Limacina helicina ochotensis Shkoldina (1999: 331, figs 2–5). In this subspecies the spire is depressed as in the typical form of L. helicina helicina, with the same radial ornament, but the last whorl is comparatively large and the shell is almost as high as it is wide.
**Limacina lesueurii** (d’Orbigny, 1836)
(Figure 8a–b)


**Description.** Shell wider than high, low conical spiral of ~4–5 rather convex whorls. Last whorl large, occupying more than 3/4 of total shell height. Base regularly rounded, with one or two incised spirals around very narrow umbilicus. Aperture large, obliquely elliptical, with straight columellar part and regularly rounded, simple margin. Maximum diameter ~1.5 mm.

**Distribution.** Bisubtropical in all oceans. In the northeast Pacific to ~40°N. Epipelagic. Uncommon, especially to the North.

**Remarks.** Morphologically similar to juveniles of *Limacina helicina sensu lato*. That species, however, has no spirals on its base, has a wider umbilicus, reaches far larger dimensions, and has a more northern distribution.

**Limacina trochiformis** (d’Orbigny, 1835)
(Figures 9–11)

*Al[llanta] [sic] trochiformis* d’Orbigny, 1835: pl. 12, figs 29–31.


*Limacina contorta* Sykes, 1905: 327, 1 fig. Types are not in National Museum of Wales, Cardiff (H. Wood pers. comm. 8/2017), they might be in NHMUK. Mediterranean.

**Description.** Shell very small, height to ~1 mm, with conical spire, slightly higher than wide, apical angle slightly less than 90°, about five rather convex whorls, separated by incised suture. Aperture occupying half shell height or slightly more, with somewhat concave columellar side, regularly curved margin. Umbilicus very small. Shell transparent, sometimes brownish in color on thickest parts. Shell smaller and less conical and with deeper suture than in *L. bulimoides*.


**Cavolinioidea** Gray, 1850 (1815)

Hyalinea Rafinesque, 1815: 140 [ICZN Art 40(2)].

Cavolinidae Gray, 1850: 3 (emended Fischer, 1883: 434, Principle of Coordination).

**Description.** Shell conical or bilaterally symmetrical. Protoconch usually clearly separated. Operculum absent.

**Remarks.** Molecular work of Burridge *et al.* (2017) has acknowledged the monophyly of uncoiled Euthecosomata, validating the superfamily Cavolinioidea. The currently applied subdivision in families (Janssen 2003, Bouchet & Rocroi 2005) based on shell-morphological characteristics, however, was not supported. Burridge *et al.* (2017: 13) found only one supported subdivision within Cavolinioidea based on maximum likelihood-produced phylogenies, with *Creseis* as a monophyletic group and a sister clade to *Cavolina, Clio, Cuvierina, Diacavolinia, Diacria, Hyalocylinis* and *Styliola*. This led Bouchet *et al.* (2017) to recognise just two families, Cavoliniidae and Creseidae within the Recent superfamily Cavolinioidea, considering Cuvierinidae and Clidiidae synonyms of Cavoliniidae.

However, the general morphology of species previously included in Cuvierinidae and Clidiidae is so analogous and so strongly different from more typical Cavoliniidae that further detailed, integrative research is expected to result in a more robust subdivision validating these families.

For the genera *Hyalocylinis* and *Styliola* one or even two new families may be desirable (compare Corse *et al.* 2013: fig. 2; Burridge *et al.* 2017: fig. 2) and it is expected that ongoing molecular work will shed more light on this. In anticipation, these genera are here still included in Creseidae as has been customary so far (but with a query).
Creseidae Rampal, 1973

Description. Shell elongated, conical, straight or curved; dorsal and ventral parts not separated by lateral carinae, transverse section circular or elliptical, lacking lateral slits. Shell surface only with growth lines or transverse annulation. Epi- to mesopelagic.

Remarks. Creseidae seems to be polyphyletic (Klussmann-Kolb & Dinapoli 2006, Corse et al. 2013, Burridge et al. 2017). Current (Corse et al. 2013: fig. 2, Burridge et al. 2017: fig. 2) molecular work indicates that the genera Styliola and Hyaloctis take a separate position, apart from Creseidae. The complicated history of Creseis nomenclature was discussed in Gasca & Janssen (2014) and Janssen (2018).

Genus Creseis Rang, 1828

Cleodora (Creseis) Rang, 1828: 305. Type species (SD Fischer 1883) Cleodora acicula Rang, 1828. Tropics and subtropics worldwide.

Cresis (Boasia) Dall, 1889: 80. Type species (M) Cresis (Boasia) chierchiae Boas, 1886.

Description. Shell elongated, conical, transverse section circular, surface smooth or with transverse annulation, apical angle variable 3–15°. Shell height of adult specimens <2 to >30 mm.

Remarks. The names Cresis, Crisia and Criseis, sometimes found in older literature, are erroneous spellings of Creseis.

Creseis acicula (Rang, 1828)
(Figures 12–13)


Creseis acus Eschscholtz, 1829: 17, pl. 15, fig. 2. Type material unknown. Coast of Brazil.

Styliola recta Gray, 1850: 18. Syntypes should be in NHMUK. Sicily.


Description. Shell very elongately conical, needle-shaped, apical angle ~3°, straight or slightly irregular, with circular transverse section. Shell height to >30 mm, width to ~1.4 mm. Protoconch not clearly separated, with rounded tip.


Remarks. The distinction of Creseis species for a long time has been difficult and subject to many discussions and speculations, because of a rather ambiguous first description (Frontier 1965, Rampal 1985, 2002, 2017, Janssen 2007, 2012a, Gasca & Janssen 2014). Especially the interpretations of Creseis acicula (Rang, 1828) and C. clava (Rang, 1828) have been confusing for a long time, and only clarified when illustrations of the lectotypes of both became available, acknowledging the synonymy of these names. The choice of C. clava as the valid name for the type species of Creseis instead of C. acicula, as done by Janssen (2007) and Gasca & Janssen (2014), cannot be substantiated: d’Orbigny (1836: 123), acting as First Reviser (ICZN 1999: Art. 24.2.1) had already established the name C. acicula (although misspelled as aciculata) as valid (Janssen, 2018).
**Creseis chierchiae** (Boas, 1886)
(Figure 18)

*Cleodora chierchiae* Boas, 1886: 62, 202, figs 39ter, 43bis-ter. About 60 probable syntypes, partly decalcified, NHMD-91145. Panama, 110°E, 10°N.

*Creseis virgula constrixta* Chen & Bé, 1964: 194, figs 3d, 4d. Holotype ?. Surface water 44°N, 41°W.

*Creseis bulgia* Sakhkivel, 1974: 619, figs 1–2. Holotype Biological Centre, Cochin 10 BC-0239-06-36, Indian Ocean, off Kalpeni Island, Laccaradives Sea, 10°04′N, 73°36′E.

**Description.** Shell very small (height 2.5 mm), conical, straight or very slightly curved, especially in lower part, apical angle ~15°, transverse section circular. Larval shell 0.42–0.58 mm high, with rounded tip, initial part tubiform, followed by swelling, separated from teleoconch by clear, gradual constriction. Surface of adult shell, or only part of it, transversely annulated in typical form, smooth, apart from vague growth lines in some (= *C. virgula constrixta* Chen & Bé, 1964, currently considered a forma of *C. chierchiae*, see Janssen, 2007: 65).

**Distribution.** In the northeast Pacific recorded from 36°04.0′N, 162°13.5′E (McGowan 1960: 161). Patchy distribution, Uncommon.


**Creseis conica** Eschscholtz, 1829
(Figures 14–15)

*Creseis conica* Eschscholtz, 1829: 17, fig. 3. Syntypes ? Coast of Brazil.

*Creseis conica* A. Costa, 1869: 45, pl. 1, fig. 2).

*Cleodora conoidea* A. Costa, 1873: 17, pl. 4, fig. 6. Nom. nov. for *Creseis conica* A. Costa, 1869 *non* Eschscholtz, 1829.

*Styliola vitrea* Verrill, 1872: 211, pl. 6, fig. 7. Syntypes should be in the Museum of Yale College. Off Gay Head, Martha's Vineyard.


*Creseis rotunda* G.B. Sowerby II, 1878: pl. 5, fig. 28a–b. Syntypes in MNHUK? Type locality unknown.


**Description.** Elongated conical shell, straight or slightly curved lengthwise, surface smooth, shell height to ~8 mm, width at aperture 1 mm. Apical angle > 3–11°.

**Distribution.** In northeast Pacific south of ~40°N. Epipelagic, abundant to the south. Common.

**Creseis virgula** (Rang, 1828)
(Figures 16, 17a–b)

*Cleodora* (*Creseis*) *virgula* Rang, 1828: 316, pl. 17, fig. 2. Syntypes? Atlantic Ocean and Antilles.

*Creseis unguis* Eschscholtz, 1829: 17, pl. 15, fig. 4. No syntypes available. North Atlantic near Canary Islands.

*Creseis cornucopiae* Eschscholtz, 1829: 17, fig. 5. No syntypes available. In der Südsee, in der Nähe der niedern Inseln [Southern sea, near the lower islands].

*Creseis caligula* Eschscholtz, 1829: 18, pl. 15, fig. 6. No syntypes available. South Sea, near the Equator.

*Hyalea corniformis* d'Orbigny, 1836: 120. No type specimens available. All warm seas N and S of the equator.


*Cleodora virgulata* Locard, 1886: 24 [incorrect spelling of *virgula*].

*Styliola africana* Bartsch, 1915: 3, pl. 34, fig. 4. Holotype USNM 249794. Port Alfred.

**Description.** Shell strongly curved dorsally in posterior part only, straight or slightly curved ventrally in anterior parts of larger specimens, apical angle 10°–15°, transverse section circular. Shell height to ~12 mm.
**Distribution.** In northeast Pacific to ~42°N. Common, less frequent to the north.

**Creseidae Rampal, 1973?**

**Remark.** The genera *Hyalocylis* and *Styliola* are currently included in Creseidae, but ongoing molecular work (see above) suggests that for these genera a separate family might be desirable. Awaiting further results we retain them in Creseidae, but with a query.

**Hyalocylis Fol, 1875**

*Hyalocylis Fol, 1875: 177. Type species (M) *Hyalocylis striata*. Tropics and subtropics.*

**Description.** Shell to 9 mm, conical, slightly curved in apical part, distinctly annulated, slightly oval in transverse section, aperture simple, protoconch usually absent, opening covered with tissue.

**Hyalocylis striata** (Rang, 1828)

(Figures 19–20)


**Description.** Same as for genus.

**Distribution.** In northeast Pacific, to ~40°N. Uncommon.

**Remarks.** Current molecular work (e.g. Burridge *et al.* 2017: fig. 2) indicates a more remote relationship with Creseidae than is currently accepted. The larval shell of this species remained unknown for a long time or was interpreted erroneously by presuming that *Creseis chierchiae* in fact represents its larval shell. Richter (1976), van der Spoel & Newman (1990) and Janssen (2012a: 37ff) clarified the morphology of that shell part. It is evident, however, that living specimens are usually found without a protoconch, the apical opening of the shell presumably closed with organic tissue.

**Styliola Gray, 1847**

*Styliola Gray, 1847: 203. Type species (M) *Styliola recta* Gray, 1850 = *Styliola subula* (Quoy & Gaimard, 1827). Tropical and subtropical seas worldwide*

**Description.** Shell conical, straight or somewhat curved apically, transverse section circular, apart from groove running in weak spiral towards aperture, forming dorsal spine on apertural margin. Protoconch pointed, with weak inflation between two constrictions.

**Styliola subula** (Quoy & Gaimard, 1827)

(Figure 21)

*Cleodora subula* Quoy & Gaimard, 1827: 233, pl. 8D, figs 1–3. Neotype RMNH 57267 (Janssen 1999: 19, fig. 3). South of Palma, Canary Islands.

*Creseis spinifera* Rang, 1828: 313, pl. 17, fig. 1. Syntypes not in MNHN; Ocean (Atlantic ?) between 30°N and 26°S; Indian Ocean; Antilles.

**Description.** Same as for genus.

**Distribution.** In northeast Pacific to ~40°N. Epipelagic. Uncommon.
Cuvierinidae van der Spoel, 1967 (1840)

Cuvieridae Gray, 1840: 148 [invalid because based on junior homonym Cuvieria Rang, 1827 (non Cuvier ex Peron, 1817, nec Lesueur & Petit, 1807, nec Leach, 1814, nec Jaeger 1833)].
Tripteridae Gray, 1850: 23 [declared nomen oblitum ICZN Art. 23.9 by Bouchet & Rocroi (2005: 175)].

**Description.** Bottle shaped to almost cylindrical, somewhat flattened ventrally near aperture. Protoconch conical pointed with slight inflation, usually shed, opening closed by convex calcareous septum. Aperture reniform to rounded triangular. Shell surface smooth or with radial microornamentation.

**Remarks.** See note on the validity of this taxon under Cavolinioidea above.

*Cuvierina* Boas, 1886

? *Triptera* Quoy & Gaimard, 1825: 76, pl. 2, fig. 5. Type species (M) *Triptera rosea* Quoy & Gaimard, 1825 (= ? *Cuvierina* sp. indet.). Type specimen lost. Port Jackson, Australia.
*Tripter* Rang, 1829: 116. Incorrect spelling of *Triptera*.
*Triptera* Menke, 1830: 9. Unnecessary replacement name for *Triptera* Quoy & Gaimard, 1825.
*Herse* Gistel, 1848: 174 (replacement name for *Cuvieria* Rang, 1827. Homonym of *Herse* Oken, 1815: 762 (Lepidoptera; rejected ICZN Opinion 417) and *Herse* Hawle & Corda, 1847: 19 (Trilobita).
*Hyperia* Gistel, 1848: VIII. Replacement name for *Cuvieria* Rang, 1827 (junior homonym of *Hyperia* Desmarest (ex Latreille MS), 1823: 347 (Crustacea).
*Cuvierina* Boas, 1886: 131, 214 (replacement name for *Cuvieria* Rang, 1827 non Lesueur & Petit, 1807).
*Rangistela* Pruvot-Fol, 1948: 278. Unnecessary replacement name for ‘*Cuvierina*’ (lapsus for *Cuvieria*) Rang, 1827.

**Description.** Same as for family.

**Distribution.** Epi- to mesopelagic. Three species are represented in the North Pacific.

**Remarks.** Ever since Boas (1886) this genus was considered monotypic with only some formae or subspecies distinguished. Morphometric and molecular work, however, led to the distinction of six recent species (Janssen, 2005, Burridge *et al.* 2016). Two subgenera (Janssen 2005, 2006) based on differences in development interpreted as lineages of fossil species were rejected based on DNA data by Burridge *et al.* (2016).

*Cuvierina columnella* (Rang, 1827)
(Figures 22, 23a–d)

*Cuvieria columnella* Rang, 1827: 323, pl. 45, figs B1-8. Neotype MNHN-IM-2000-33856 (Janssen 2005: 45, fig. 10). Marion Dufresne Expedition, MD32, SW Indian Ocean, 21°08.7'S 55°11.8' E.
*Triptera rosea* Quoy & Gaimard, 1825: 416, pl. 66, fig. 6 (soft parts only). No types available. Australia, near Port Jackson.
*Cuvierina spoeli* Rampal, 2002: 214, fig. 1A–Cs. Holotype MNHN-IM-2000-33848. Indian Ocean, 21°08'S, 55°11'E.

**Description.** Shell 7.1–11.1 mm, moderately inflated, longitudinal microornament present, aperture rounded triangular.

**Distribution.** In the eastern Pacific to ~20°N. In the northeastern Pacific only known from two specimens from 29°34'N 128°9’W (Fig. 20) in the Santa Barbara Museum of Natural History (SBMNH 133302, shell height 7.9 mm, width 2.7 mm, aperture height 1.25 mm, width 2.1 mm (Fig. 20) and shell height 8.1 mm, width 2.7 mm, aperture height 1.25 mm, width 2.1 mm). Rare.

**Remarks.** *Cuvierina spoeli* Rampal, 2002 was considered a synonym of *C. columnella* by Janssen (2007), which was rejected by Rampal (2017). The synonymy was again demonstrated by Janssen (2018a).
**Cuvierina tsudai** Burridge, Janssen & Peijnenburg, 2016
(Figure 24)

*Cuvierina tsudai* Burridge, Janssen & Peijnenburg, 2016: 5, fig. 1A–I. Holotype RMNH.5004167. Pacific Ocean, 8°47'N, 158°49'W.

**Description.** Shell 7.2–8.8 mm, moderately inflated, no microornamentation, aperture triangular.

**Distribution.** In the northeastern Pacific to 37°N. Rare.

**Cuvierina urceolaris** (Mörch, 1850)
(Figure 25a–b)


**Description.** Shell 5.1–6.7 mm high, strongly inflated, microornament present, aperture reniform.

**Distribution.** Indian and Pacific Oceans, warm water species. From the northeastern Pacific recorded from off San Francisco (Rampal 2002: 212). Rare.

**Clidae Jeffreys, 1869**

Clionae van der Spoel, 1967: 31, 57 (partim).
Clionidae auct. (incorrect subsequent spelling: Bouchet & Rocroi 2005).
Non Clionidae Menke, 1828: 5 (as Cliodinae), nowadays Clionidae (Gymnosomata).

**Description.** Shell conical to triangular, bilaterally symmetrical, straight or dorso-ventrally curved; ventral and dorsal shell parts separated by carinae, protoconch inflated, with or without apical spine; radial, transverse ornamentation present or absent.

**Remarks.** See note on the validity of this taxon under Cavolinioidea above.

**Clio** Linnaeus, 1767

*Cleodora* Péron & Lesueur, 1810: 66. Type species (M) ‘Cléodore Pyramidale’ = *Clio pyramidata* Linnaeus, 1767. Type locality not given.
*Euclio* Bonnevie, 1913: 20 (objective junior synonym of *Clio*; van der Spoel 1967: 66).
*Proclio* Hubendick, 1951. Type species (M) *Proclio subteres* Hubendick, 1951 = *Clio antarctica* (Dall, 1908). South Atlantic, 48°27’S 42°36’W.

**Description.** Same as for the family.

**Remarks.** Since its introduction in 1810, the name *Cleodora* was generally used, as the name *Clio* was frequently utilized for shell-less pteropod species (Gymnosomata) that are today included in the genus *Clione* Pallas, 1774. Several other names introduced as (sub)genera in the Clidae, such as *Balantium* Children, 1823 or *Bellardiclio* Janssen, 2004 as well as a number of names based on fossil species by Bellardi (1873) are currently not used in the WoRMS database.

**Clio andreae** (Boas, 1886)
(Figures 26a–b, 27a–b, 28a–b)

*Cleodora Andreae* [sic] Boas, 1886: 80, 203, pl. 1, fig. 1; pl. 2, fig. 12; pl. 4, fig. 49; pl. 5, fig. 92. Holotype (nearly dissolved, shell fragments and soft parts) in NHMD-91479. Atlantic Ocean, 33°30’S, 11°E.
FIGURES 23–28. Cuvierina, Clio. 23a–d: Cuvierina columnella (Rang, 1827). W of Guadelupe Island, California State, Fisheries Laboratory 65.S.3#2; 29°34′N 128°9′W; shell height 7.89 mm; 1 June 1965. SBMNH 133302. Photo by Ronald Pouwer. 24. Cuvierina tsudai, Burridge, Janssen & Peijnenburg, 2016; holotype, Pacific Ocean, 8°47′N, 158°49′W; shell height 7.3 mm. RMNH 5004167 (courtesy of Alice K. Burridge). 25a–b. Cuvierina urceolaris (Mörch, 1850). South China Sea, north of Philippines, DANA expedition, sta 3729(v), 20°3.5′N 120°50′E. Shell height 6.4 mm, NHMD collection (courtesy of Alice K. Burridge). 26a–b. Clio andreae (Boas, 1886), holotype; South Atlantic Ocean, 33°30′S, 11°E (from Boas 1886) (left, shell height 20 mm) and what remains of it (from van der Spoel 1976) (right; sizes/magnification not given); NHMD-91479. 27a–b. Clio andreae (Boas, 1886), holotype; South Atlantic Ocean, 33°30′S, 11°E (from Boas 1886) (left, shell height 20 mm) and what remains of it (from van der Spoel 1976) (right; sizes/magnification not given); NHMD-91479. 28a–b. Clio andreae (Boas, 1886), Monterey Bay, California, collection depth 2556 m; shell height 40.6 mm. Photos by Stephanie L. Bush.
Description. Shell height to 20 mm, elongated triangular, apical angle ~25°, apical part curved dorsally; dorsal and ventral shell parts equally convex, dorsal shell part with three weakly developed longitudinal riblets; dorsal and ventral parts with transverse ribbing. Protoconch clearly separated, spherical, no apical spine.

Remarks. *Clio andreae* (Boas, 1886) was considered a senior synonym of *C. polita* Pelseneer, 1888 by van der Spoel (1976: 49, 191) based on fragments of the *C. andreae* holotype. However, Janssen (2012a: 49) preferred to consider both species as valid. Although very similar in shell shape, *C. andreae* has weak but distinct longitudinal and transversal ornament, whereas in *C. polita* both dorsal and ventral shell parts are unornamented.

*Clio chaptalii* Gray, 1850
(Figures 29a–d, 30a–c)


Description. Shell to 17 mm, triangular with straight sidelines, apical angle to almost 60°, curved dorsally in apical part. Dorsal shell part with three radial ribs; dorsal and ventral sides both with transverse ornament of numerous narrow riblets, curved in apertural direction.

Distribution. In northeast Pacific 53–59°N and 139–164°W. Epi- to bathypelagic species (100–1200 m). Rare.

*Clio cuspidata* (Bosc, 1802)
(Figures 31a–d, 32)

*Hyalaea cuspidata* Bosc, 1802: 241, pl. 9, figs 5–7. Syntypes probably present in MNHN, Paris, but unrecognizable as such by incomplete labeling (van der Spoel 1976: 191). ‘In ocean’.

*Cleo dora Lessonii* Rang & de Férussac, 1830: 261 (*nomen nudum*).

*Cleo dora quadr里斯pinosa* Lesson, 1831: 248, pl. 10, figs 1–1”, 2. Type material not available. Moluccas, 26°S 92°E.

Description. Shell to 20 mm high, lateral carinae strongly diverging, transverse section triangular, ventrally flattened with wide central swelling, dorsal shell part convex with sometimes strong central longitudinal rib; weaker ribs between central rib and lateral carinae; transverse ornament variably strong on both sides, following adaperturally curved growth lines. Lateral carinae, frequently also central dorsal rib elongated to apertural spines; protoconch spherical with distinct apical spine.

Distribution. In northeast Pacific to ~45°N. Epipelagic. Rare.

*Clio polita* Pelseneer, 1888
(Figures 33a–c, 34a–b, 35a–b)


Description. Shell height to ~22 mm, elongated triangular, apical angle ~25°, apical part curved dorsally; dorsal, and ventral shell parts convex, ventrally slightly more so, no ornamentation present. Carinae simple. Protoconch separated by distinct ring, globular, no apical spine.

Distribution. Bathypelagic species (> 1000 m). Predominantly Atlantic, only rarely reported from the north Pacific (McGowan 1960) between 150°W and 170°E, 40–53°N. McGowan’s specimens, however, consisted of the soft parts only, no shells, so it is unclear if they belonged to *C. polita* or *C. andreae*. Bé & Gilmer (1977) recorded *C. polita* from the Pacific (Gulf of Panama) and included McGowan’s records in their distribution map. They did not recognize *C. andreae*, but their illustration (pl. 6, fig. 16a–c) clearly represents that species. New material from the north Pacific is needed to clarify this situation. Three lots (USNM 857720, 857745, 857764) from the North Pacific (54–57°N, 141°W) are identified as *C. andreae*, but their shells are dissolved.
FIGURES 29–32. Clio. 29a–d. *Clio chaptalii* Gray, 1850. Shell height c. 13 mm, locality not indicated (from Tesch 1946: pl. 3, fig. 13 [inverted]). 30a–c. *Clio chaptalii* Gray, 1850. Shell height c. 17 mm, equatorial Atlantic (from Bé & Gilmer 1977). 31a–d. *Clio cuspidata* (Bosc, 1802); Northern Atlantic Ocean, shell height 14.5 mm, protoconch (upper right) diameter 0.2 mm (from Bé & Gilmer 1977). 32. *Clio cuspidata* (Bosc, 1802), colonized by the hydroid *Pandea* sp. Monterey Bay, California; shell height 7 mm. Photo by Stephanie L. Bush.
**Clio pyramidata** Linnaeus, 1767  
(Figures 36a–d, 37, 38a–b)

? **Clio caudata** Linnaeus, 1767: 1094. No syntypes available. Type locality ‘in oceano’.
**Clio retusa** Linnaeus, 1767: 1094. No syntypes available. Type locality ‘in oceano’.


? **Cleodora brownii** de Blainville, 1825: 481, pl. 46bis, figs 1, 1a–b). Types unknown. Type locality not mentioned.

**Clio exacuta** Gould, 1852: 488; 1856: pl. 51, fig. 605a–b. Syntypes were not located by Johnson (1964: 73). Pacific Ocean, 44°N, 154°W.

**Clio occidentalis** Dall, 1871: 140. Types unknown. Pacific Ocean, off California coast, 33°N, 130°W.

**Cleodora sulcata** Pfeffer, 1879: 240, figs 11–12. Syntypes probably in Museum für Naturkunde, Berlin, Germany, not in the Zoologisches Museum, Hamburg, Germany (as stated by van der Spoel, 1976: 190). South Atlantic Ocean; 45°53.9'S 122°1.1'W; 50°34.6'S 83°44.5'W; Kerguelen.

**Cleodora martensii** Pfeffer, 1880: 95, figs 16, 16a–c. Lectotype and paralectotype (van der Spoel 1976: 190) ZMH 3013-3014. Atlantic Ocean.

**Clio antarctica** Dall, 1908: 501 (replacement name for *Hyalaea australis* d'Orbigny, 1836: 117, pl. 8, figs 9–11 non *Clio australis* Bruguère, 1792: 507, pl. 75, figs 1–2 = *Clione limacina* (Phipps, 1774) nec *Hyalaea australis* Péron & Lesueur, 1807: pl. 31, fig. 5 = *Cavolinia tridentata* (Forskål in Niebuhr, 1775). Syntypes not in MNHN. ‘Du cap Horn, par 57 degrés 10 minutes de latitude sud, et 70 degrés de longitude ouest de Paris’.

? **Proclio subteres** Hubendick, 1951 = *Clio antarctica* (Dall, 1908). Holotype in ZMS. South Atlantic, 48°27'S 42°36'W.

**Description.** Shell straight, lateral carinae diverging, apical angle strongly increasing towards aperture, carinae simple, transverse section initially circular, becoming triangular towards aperture, dorsal shell part with strong central longitudinal rib, lateral ribs weaker, ventral shell part slightly concave laterally with weak, wide central swelling, apertural margin simple, dorsally triangularly protruding, ventrally lower, rounded, protoconch pear-shaped, separated by constriction, sharply pointed.

**Distribution.** In the northeast Pacific to 60°N. Eurythermal, meso- to epipelagic. Common to ~40°N, uncommon but present to 60°N.

**Clio recurva** (Children, 1823)  
(Figures 39a–b, 40a–d, 41a–d, 42)

*Balantium recurvum* Children, 1823: 220, pl. 7, fig. 107. Syntypes in NHMUK? ‘Congo expedition ‘(Gulf of Guinee?).

**Cleodora balantium** Rang, 1834: Class V, pl. 44. Type material unknown. Golfe du Guinée, near Cap de Palame.

**Description.** Largest species in the genus (shell height to 30 mm), straight longitudinally, but apical shell part curved dorsally, lateral carinae double-lined, somewhat flexuous in apical part, very slightly convex adaperturally. Both sides of shell convex, dorsal side with three radial ribs, middle one stronger, ventral side with single, wide swelling. Transverse ornament of numerous curved riblets on both sides. Protoconch clearly separated, spherical, with distinct (but easily worn) apical spine.

**Distribution.** In northeast Pacific 30–45°N. Meso- to bathypelagic (300–2500 m), rare, but occasionally collected from the sea surface.

**Remarks.** Shells of living specimens are frequently encrusted with hydroids.

**Cavoliniidae** Gray, 1850 (1815)

*Hyalinea* Rafinesque, 1815: 140 [ICZN Art. 40(2)].

*Cavoliniidae* Gray, 1850: 3.

*Cavoliniidae* Official List of Family Group Names in Zoology, nr 438.
Description. Ventral and dorsal shell parts convex, separated by lateral slits (Cavolina, Diacavolinia) or carinae (Diacria), dorsal side with radial ornament, higher than more convex ventral side with only fine transverse ornamentation, dorsal lip with thickened margin (Diacria) or overhanging aperture (Cavolina, Diacavolinia), ventral apertural margin curved outward, apical spine with protoconch either straight or curved dorsally, pointed, with transverse microornament (Cavolina), or straight and with apical bulb; shed in some species, then opening subsequently closed by septum, or apical shell parts always missing (Diacavolinia).

Remarks. The authority of some species in Cavoliniidae originally described in the genus Hyalaea in the work of de Blainville (1821a, b) (e.g., Diacavolinia longirostris and Diacria trispinosa) has also been given erroneously as Lesueur, 1821 (e.g. WoRMS). De Blainville (1821a: 79) wrote “On doit la connoissance et la distinction de la plupart des espèces de ce genre, à MM. Péron et Lesueur, et surtout à ce dernier, qui en a fait une monographie avec figures, dont le manuscrit m’a été confié” [One owes the knowledge and the distinction of the majority of the species of this genus to MM. Péron and Lesueur, and certainly to the latter, who has made of it a monograph with figures, of which the manuscript was entrusted to me.] Accordingly, the description is based on a Lesueur manuscript, which makes the authority of those taxa de Blainville, ex Lesueur MS. As Lesueur’s text was not copied verbatim, the authority is not Lesueur in de Blainville (ICZN Art. 50.1 Example).

Cavolina Abildgaard, 1791

Cavolina Abildgaard, 1791: 175 (emended ICZN 1969 Opinion 883; Official List name nr 1841). Type species (M) Cavolina natans Abildgaard, 1791 = Cavolina tridentata Forsskål in Niebuhr, 1775. Hyalaea Lamarck, 1801: 139. Type species (M) Hyalaea cornea Lamarck = Cavolina tridentata (Forsskål in Niebuhr, 1775). Tropics and subtropics worldwide.

Pleuropus Eschscholtz, 1825: 735, pl. 5, fig. 2. Type species (M) Pleuropus pellucidus: Eschscholtz, 1825 = Cavolina inflexa (Lesueur, 1813).’Südsee’ [southern ocean].

Orbignyia Adams, 1859: 45. Type species (here designated) Cavolina (Orbignyia) labiata d’Orbigny. Atlantic and Indian oceans.

Warning. Although the generic name Orbignyia is not currently used, the group of taxa related to Cavolina inflexa (Lesueur, 1813) as distinguished by Rampal (2002) is so homogeneous and different from Cavolina, sensu stricto that ongoing integrative morphological and molecular work is expected to result in a separate status of this group. Therefore, it is thought useful to designate a type species. Adams (1859) included two species in Orbignyia, ‘C. inflexa, Lesueur’ and ‘C. labiata D’Orb.’. Designation of C. inflexa as type species would make it a junior synonym of Pleuropus Eschscholtz, 1825. Therefore, C. labiata is here chosen as the type species of Orbignyia.

Cavolina gibbosa flava (d’Orbigny, 1835)

(Figure 43a–c)

Hyalaea flava d’Orbigny, 1835: 97, pl. 5, figs 21–25. Holotype NHMUK 1854.12.4.13. Pacific Ocean 30°S, 92°E.

Pleuropus hargeri Verrill, 1882: 555. No syntypes known. West Atlantic Ocean, George’s Bank, 41°25’N, 65°5’ to 65°30’W.

Description. Shell height to 11 mm, dorsal shell part with five, sometimes rather weakly developed radial ribs, dorsal apertural lip overhanging aperture at angle of ~45° respective to shell vertical axis; ventral shell part not regularly convex as in most Cavolina species, but with clear, rounded angularity above mid shell height, fine transverse lirae on most convex part.
FIGURES 41–45. *Clio, Cavolinia*. 41a–d. *Clio recurva* (Children, 1823). Off Central California, 0 m, 36°30′N 130°30′W, shell height 21.2 mm (SBMNH 116445). The brown patches are hydroid remnants (compare Fig. 42); shell height 21 mm. Photo by Ronald Pouwer. 42. *Clio recurva* (Children, 1823), shell height 11 mm, colonized by the hydroid *Pandea* sp. Monterey Bay. Photo by Stephanie L. Bush. 43a–c. *Cavolinia gibbsa flava* (d’Orbigny, 1834). Between California and Hawaii, from stomach of *Alepisaurus*, 27°41′N 135°3′W, shell height 10.79 mm (SBMNH 124733). Photo by Ronald Pouwer. 44a–c. *Cavolinia globulosa* (Gray, 1850), shell height 5 mm. Hawaii, south west of Kaula Rock; Vanderbilt Pacific Equatorial Expedition; 1951 from website: http://seaslugsflohawaii.com/species/Cavolinia-globulosa-a.html; photographed at CAS (courtesy of Cory Pittman). 45a–c. *Cavolinia inflexa imitans* (Pfeffer, 1880). Off La Jolla, San Diego County, California, USA, 32°49′59.995″N, 117°16′0.013″; shell height 6.2 mm (SBMNH 457570). Photo by Ronald Pouwer.
Remarks. Typical *C. gibbosa* is smaller (to c. 7.5 mm shell height), with a more sharply vaulted ventral shell part, and dorsal apertural lip and apical spine with protoconch more strongly curved. These two taxa, and two additional ones, *C. plana* Meisenheimer, 1905, described from the eastern Indian Ocean, and *C. gibboides* Rampal, 2002, from the eastern Mediterranean, are usually interpreted as forms or subspecies, but Rampal (2002) considered them to be distinct species (see Janssen 2012a, Rampal, 2014).

Distribution. Epipelagic, mainly bisubtropical, warm water species with a patchy distribution. Known in the northeast Pacific Ocean from c. 45°N and east of 175°W. Rare.

*Cavolinia globulosa* (Gray, 1850)
(Figure 44a-c)


Description. Shell height to approximately 6 mm, spherical with largest shell width at mid height, above small lateral spines; dorsal shell part with five, rather weak radial ribs, dorsal apertural lip strongly curved ventrally, overhanging aperture; ventral shell part very convex, regularly rounded to sometimes very slightly angular, with clear transverse lirae on most convex part.

Distribution. In northeast Pacific to about 40°N. Epi- to mesopelagic (~ 600 m). Rare.

*Cavolinia inflexa* imitans (Pfeffer, 1880)
(Figures 45a–c, 46)


Description. Less spherical, more elongate than other species of genus; apical shell part below lateral spines relatively large, reaching half shell height or slightly less, dorsal shell part with three weakly developed radial ribs only central one of which sometimes well-visible, dorsal lip rounded, not deviating from long axis; ventral side gradually convex, smooth; ventral apertural lip clearly separated by transverse groove; apical spine curved dorsally.

Remarks. The *C. inflexa* species complex has been the subject of several taxonomic interpretations (Boas 1886, van der Spoel, 1967, Rampal, 2002). Various related forms (or subspecies?) were described, of which three seem to be accepted presently: *inflexa*, *imitans* (Pfeffer, 1880) and *labiata* (d’Orbigny, 1835), each of these being treated as independent species, subspecies, or forma in the literature.

Distribution. In the northeast Pacific the species is found between 20 and 40°N. All specimens seem to belong to the form *C. inflexa* imitans. Meso- to epipelagic (200–800 m). Common.

*Cavolinia tridentata* (Forskål in Niebuhr, 1775)
(Figures 47a–c, 48a–c)


*Cavolinia natans* Abildgaard, 1791: 175. Type material not available. Mediterranean.

*Hyalaea cornea* Lamarck, 1801: 140. Type material not available. Mediterranean.

*Hyalaea papilionacea* Bory de St. Vincent, 1804: 138, pl. 5, fig. 1A –F. Type material unknown. West Africa.

*Hyalaea australis* Péron & Lesueur, *in* Péron, 1807: 46, pl. 31, fig. 5. Type material not available. Type locality. ‘Océan Austral’.

*Hyalaea chemnitziana* Lesueur, 1813: 284. Name based on *Anomia alata* et *aurita* scarabaeiformis Martini & Chemnitz, 1785: 72, vignette 13, figs G–F. No locality indicated.

*Hyalaea peronii* Lesueur, 1813: 284. Type material not available. Mediterranean.

*Hyalaea teniobranchea* Lamarck, 1816: 13, pl. 464, fig. 7. Type material not available. Location not indicated.

*Hyalaea forskahlii* de Blainville, 1821a: 79 (*nomen nudum*); 1821b: 95. Type material not available. Mediterranean.
Hyalea rangii Deshayes, 1832: 310. Type material not available. ‘des mers d’Afrique’.


Hyalea melly Benoit, 1843: 4. Type material not available. Forte del Salvador, Sicily (Italy).

Pleuropus longifilis Troschel, 1854: 202, pl. 8, figs 1–3. Type material not available. Near Messina, Sicily (Italy).

Cleodora trifilis Troschel, 1854: 205, pl. 8, fig. 4. Type material not available. Sicily (Italy).

Hyalea [sic] complanata Gegenbaur, 1855: 40, pl. 1, figs 1–4. Type material not available. Near Messina, Sicily (Italy).

Hyalea cumingii G.B. Sowerby II, 1878: caption of Pteropoda pl. 1, fig. 5a–b. Syntypes in NHMUK. Origin not mentioned.

Cavolina occidentalis Dall, 1908: 233, pl. 12, fig. 1, 1b. Holotype USNM 110591, paratypes USNM 110590. North Pacific Ocean, 38°4′N, 137°W.

**Description.** Shell large (in the northern Pacific height up to 14 mm), spherical, brownish, lateral spines short, somewhat curved downward, dorsal apertural lip well separated, rounded, ventral shell part swollen, with clear transverse striae close to curved apertural margin; apical spine with protoconch pointed, straight, not curved dorsally.

**Distribution.** In northeast Pacific disjunct distribution to ~50°N, but occasionally occurring to 67°N. Epipelagic. The northeast Pacific population is usually referred to as forma *affinis* (d’Orbigny, 1835). Common.

**Cavolina uncinata** (d’Orbigny, 1835)
(Figures 49a–c, 50)


**Description.** Shell resembling *C. tridentata* in shape, but relatively wider, height less than 10 mm, only faintly colored brownish, usually colorless (clear). Dorsal shell part with five radial ribs, stronger than in *C. tridentata*. Dorsal apertural lip more strongly overhanging aperture. Lateral spines well-developed, pointing downward, apical spine with protoconch strongly curved backward, its initial part perpendicular to shell’s vertical axis.


**Remarks.** Although frequently cited with the authorship of Rang (1829) that author did not describe the species, but merely mentioned the name as an example for the genus *Hyalea*. Rang illustrated the species (1829: pl. 2, fig. 2) but without a name (Gofas 2018). D’Orbigny (1835) validly introduced the taxon. As d’Orbigny referred to Rang’s paper we consider Rang’s material to be syntypes and the lectotype designation of van der Spoel (1976) as valid.

Van der Spoel (1969, 1971) introduced several formae in *C. uncinata*, based on small shell characteristics or color pattern. These names are nomenclaturally invalid, being published after 1961 (ICZN Art. 10.2). The form represented in the northeast Pacific agrees with f. *pulsata* van der Spoel, 1969.

**Diacavolinia van der Spoel, 1987**

*Diacavolinia* van der Spoel, 1987: 78. Type species (OD) *Diacavolinia longirostris* (de Blainville, ex Lesueur MS 1821b). Atlantic Ocean.

**Description.** Differing from *Cavolinia* by second interlock system on both sides of aperture (only one in *Cavolinia*), apical spine with protoconch shed in adult specimens, opening closed with septum or fusion of ventral and dorsal shell parts.

**Remarks.** The taxonomy of *Diacavolinia* is unresolved. Numerous taxa have been introduced (van der Spoel 1970, 1971, 1973, van der Spoel *et al.* 1993) that are considered either forms or species, but are difficult to distinguish genetically (Maas *et al.* 2013).
Diacavolinia aff. longirostris (Blainville, ex Lesueur MS, 1821)  
(Figures 51a–c, 52)

Hyalaea longirostris de Blainville, ex Lesueur MS, 1821b: 81. Type material not available in MNHN (van der Spoel 1976: 193). ‘Océan atlantique par 22°9′ de latitude, a trois lignes de long sur deux de large’. Van der Spoel et al. (1993: fig. 38) interpreted this as western central Atlantic Ocean.

**Description.** Same as for genus.

**Distribution.** In northeast Pacific from 29°N (SBMNH 127831). Epipelagic. Rare.

**Remarks.** Using van der Spoel et al.’s (1993: 149) identification key did not lead to a confident identification of the Diacavolinia specimens recorded here (Figs 48, 49) from the northeast Pacific. Therefore, herein they are indicated as Di. aff. longirostris. It should be noted, however, that they do not at all resemble the single Diacavolinia species recognized for this area by van der Spoel et al. (1993), which was Di. pacifica van der Spoel et al., 1993 (Figure 53a–b herein), a form distinguished by a distinct ‘dorsal hump’ (Fig. 53b), contrary to the available specimens, in which the lip is gradually connected to the dorsal shell part.

**Diacria Gray, 1840**

Diacria Gray, 1840: 155. Type species (SD Gray 1847: 203) Hyalaea trispinosa de Blainville, ex Lesueur MS, 1821. Tropical and subtropical seas worldwide.

**Description.** Shell of two main shapes: 1) rhombic, dorso-ventrally flattened with long but frequently broken apical spine, spherical protoconch, lateral spines well-developed (D. trispinosa-group); 2) shell rather spherical, cavoliniform, apical spine with elliptical protoconch shed during metamorphosis, opening closed by septum, lateral spines small (D. quadridentata-group).

**Remarks.** The various forms and species introduced in the genus Diacria based on shell morphology (mainly measurements or color patterns) require re-assessment. Here, the species classification accepted in the WoRMS database is used.

**Species of the Diacria trispinosa (de Blainville, ex Lesueur MS, 1821)-group**

**Diacria major** (Boas, 1886)  
(Figures 54–55)


**Description.** Shell height to approximately 13 mm, lateral spines pointing downwards. Dorsal shell part above lateral spines as high as wide or higher; higher than in Di. trispinosa.

**Diacria trispinosa** (de Blainville, ex Lesueur MS, 1821)  
(Figure 56a–c)


Hyalaea mucronata Quoy & Gaimard, 1827: 231, pl. 8B, figs 1–2. Type material not available. Gibraltar, near Ceuta.


Cavolinia reeveana Dunker, 1853: 2. Type material not available. ‘Sinu Guineensi’ (= Gulf of Guinee, W. Africa).


Diacria rampali Dupont, 1979: 39, fig. 3. Holotype NHMD-91487. Caribbean Sea 16°06’N, 76°02’W (Dana expedition sta. 1215 IV).

Diacria piccola Bleeker & van der Spoel, 1988: 60, figs 2–4. Holotype USNM 276782, paratype USNM 859098. Philippines, off Magavao Island, Mindanao, 8°50’45″N, 126°26’52″E.


Diacria rampali Bleeker & van der Spoel, 1988: 39, fig. 3. Holotype NHMD-91487. Caribbean Sea 16°06’N, 76°02’W (Dana expedition sta. 1215 IV).

Diacria danae van Leyen & van der Spoel, 1982 (Figures 57a–c, 58a–b)

Diacria quadridentata (de Blainville, ex Lesueur MS, 1821) forma danae van der Spoel, 1968: 217, fig. 1A–C. [unavailable infrasubspecific name]


Diacria schmidti van Leyen & van der Spoel, 1982 (Figure 59a–c)


**Suborder Pseudothecosomata Meisenheimer, 1905**

Thecosomata de Blainville, 1824: 271 (pars).
Pseudothecosomata Meisenheimer, 1905: 37.

**Description.** Anatomically different from Euthecosomata in structure of nervous system, digestive organs, and presence of proboscis.
Cymbulioidea Gray, 1840

Cymbuliidae [sic] Gray, 1840: 156.

**Description.** Shelled adult specimens only in Peraclididae, in other families only a minuscule shell during larval (veliger) stages, or with gelatinous pseudoconch.

**Remarks.** Three families (Peraclididae, Cymbuliidae, Desmopteridae) are members of this superfamily.

Peraclididae Tesch, 1913

Peraclididae Tesch, 1913: 71.
Procymbuliidae Tesch, 1913: 77.

**Description.** Shell sinistral with higher or lower spire, no umbilicus, but columella twisted, forming basal rostrum with membrane in most species; last whorl relatively large; subsutural crests and/or spines on apertural margin present in some species, epidermis with reticulate pattern (cuticulum). Epipelagic to mesopelagic, some species bathypelagic.

**Peracle Forbes, 1844**

? *Campylonaus* Benson, 1835a: 176 (*nomen nudum*, introduced with no species included). Type species *Atlanta reticulata* d’Orbigny, 1836 (SD Gray 1847: 149). Southern Atlantic or Indian oceans.


*Procymbulia* Meisenheimer, 1905: 13. Type species (M) *P. valdiviae* Meisenheimer, 1905. South Pacific Ocean, 34°14′S, 80°31′E.

**Description.** Same as for family.

**Peracle diversa** (Monterosato, 1875)

(Figure 60)


*Peracle apicifulva* Meisenheimer, 1906: 122, pl. 5, fig. 9. Poorly preserved syntypes ZMB (van der Spoel 1976: 197). Four localities in Atlantic Ocean, 27°30′S to 21°N.


**Description.** Shell width ~75% of total height, apical angle more than 90°; columellar membrane well-developed; subsutural crests present.

**Distribution.** In northeast Pacific to 30°N–50°N. Epipelagic to mesopelagic. Rare.

**Peracle reticulata** (d’Orbigny, 1835)

(Figure 61)

*Atlanta (sic) reticulata* d’Orbigny, 1835: pl. 12, figs 32–35, 39;


**Description.** Shell about twice as high as wide, apical angle less than 90°; columellar membrane insignificant, no subsutural crests.

**Distribution.** Epipelagic, tropical and subtropical seas, worldwide. In northeast Pacific to c. 35°N. Uncommon.
FIGURES 60–63. Peracle, Clione. 60. Peracle diversa (Monterosato, 1875). Atlantic Ocean, 16°06′N, 76°02′W; shell height c. 4 mm (from van der Spoel 1976, as P. apiciflava). 61. Peracle reticulata (d’Orbigny, 1834), Atlantic Ocean, 07°22′N, 46°51′W; shell height c. 6 mm. (from van der Spoel 1976). 62. Clione limacina (Phipps, 1774), adult specimen; Monterey Bay, California, body length 12 mm. Photo by Stephanie L. Bush. 63. Clione limacina (Phipps, 1774), larval shell from plankton catch, Nova Scotia; shell height 0.36 mm (from Lalli & Conover 1973: fig. 7).

Suborder Gymnosomata de Blainville, 1824

Gymnosomata de Blainville, 1824: 273.

Remarks. Gymnosomata are pteropods without a shell in the adult stage. Larvae, however, have a minuscule calcareous (aragonitic) shell that is shed during metamorphosis. Although such larval shells were observed and described by Krohn (1860), it was the work of Lalli & Conover (1973) who succeeded in keeping gymnosomes under laboratory conditions, and observed them spawning. They described the larval shell of three identified species, including Clione limacina Phipps, 1774) (Figs 62–63 herein). Since then, various types of gymnosome larval shells have been recorded from sediment samples, but are usually unidentifiable to species. For an overview see Janssen (2012b: 451–455, pl. 26). As various other gymnosome species have been recorded from the northeastern Pacific (see van der Spoel 1976), larval shells may be collected in plankton tows or in sediment samples.

Several additional gymnosome pteropods occur in the northeast Pacific (van der Spoel 1976), but their larval shells are unknown: Thliptodon diaphanus (Meisenheimer, 1902), Thliptodon sp. nov., Notobranchaea cf. macdonaldi Pelseneer, 1886, Pneumodermopsis spp., and Cliopsis krohni Troschel, 1854.
Acknowledgements

The authors are grateful to the following colleagues for sharing data or making specimens or samples available from the collections in their care: Orso Angulo-Campillo (Centro Interdisciplinario de Ciencias Marinas-IPN, Departamento de Plancton y Ecología Marina, La Paz, México); Rebeca Gasca (ECOSUR-Chetumal, Chetumal, Mexico), Daniel Geiger (SBMNH), Lindsey Groves (LACM), Alexandra Hangsterfer ( Scripps Institution of Oceanography, La Jolla, California, USA), Bernard Hausdorf (ZMH), Virginie Héros (MNHN), Pete Kohnert (Bavarian State Collection of Zoology, München, Germany), Tom Schiøtte (NHMD), Michael Vecchione (NMFS National Systematics Laboratory, USNM), and Harriet Wood (National Museum of Wales, Cardiff, U.K).

We thank Alice K. Burridge (RMNH), Conquilologistas do Brasil, Russell R. Hopcroft (Institute of Marine Science, University of Alaska, USA), Kees Moeliker (NMR), Alexander Semenov (Moscow State University’s White Sea Biological Station, Russia) and Cory Pittman (Sea slugs of Hawaii) for permissions to include their photographs. New images were made by Ronald Pouwer (Naturalis Biodiversity Center, Leiden, The Netherlands).

References


Janssen, A.W. (2012a) Late Quaternary to Recent holoplanktonic Mollusca (Gastropoda) from bottom samples of the eastern Mediterranean Sea: systematics, morphology. Bollettino Malacologico, 48 supplemento 9, 1–104.


https://doi.org/10.11646/zootaxa.4459.2.9


https://doi.org/10.5479/si.03629236.239


https://doi.org/10.1111/j.1439-0469.2006.00351.x


https://doi.org/10.5962/bhl.title.4968


https://doi.org/10.1007/BF00355415


Pelseneer, P. (1906) *Biscayan plankton collected during a cruise of H.M.S. ‘Research’ 1900*, 7. Mollusca (excluding
https://doi.org/10.1111/j.1096-3642.1906.tb00188.x


https://doi.org/10.1111/j.1096-3642.1906.tb00188.x

https://doi.org/10.1111/j.1096-3642.1906.tb00188.x


344 – Zoosymposia 13 © 2019 Magnolia Press

JANSSEN ET AL.
Note: Gray (1855, preface) wrote in January 1855 that the zoological part of the ‘Voyage’ was not yet published. As we do not find another publication date for this volume, we maintain the year 1852.

SHELLED PTEROPODS

Zoo symposia 13 © 2019 Magnolia Press · 345


