Euprymna hoylei Adam, 1986

Euprymna hoylei Adam, W. (1986). Contribution a la connaissance du genre Euprymna Steenstrup, 1887 (Mollusca Cephalopoda). Bulletin de l'Institut royal des Sciences naturelles de Belgique 56, 131–136 [133].
Type data: holotype WAM 465-65.
Type locality: Sulu Archipelago, 4°31'N, 119°22'E.

DISTINGUISHING CHARACTERS

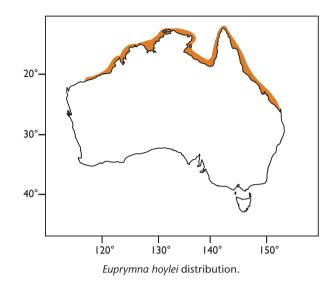
Similar to *E. hyllebergi* Nateewathana, 1997 but the suckers on arms 2-4 of *E. hyllebergi* do not are not



Preserved museum specimen, dorsal view (AM C.303915, L. Mott).



Preserved museum specimen, ventral view (AM C.303915, L. Mott).



significantly enlarged. *Euprymna hyllebergi* has a large number of stout papillae with slit-like apertures on the distal half of the hectocotylus; these papillae are crowded into rows of four to six suckers medially and in two series distally.

DIAGNOSTIC FEATURES

Males with three or four enlarged suckers in dorsal and ventral series of arm pair 4 and ventral series only of arm pair 3. No enlarged suckers on arms 2.

REMARKS

See Nateewathana (1997: 472).

DISTRIBUTION

Tropical Indo-Pacific: western tropical Pacific and northern Australia.

REFERENCE

Norman and Lu (1997).

Euprymna pardalota Reid, 2011

Euprymna pardalota Reid, A. (2011). Euprymna pardalota sp. nov. (Cephalopoda: Sepiolidae), a new dumpling squid from northern Australia. The Beagle, Records of the Museums and Art Galleries of the Northern Territory, 27, 135–142 [136, figs 1–9].

Type data: holotype NTM P.15796.

Type locality: Australia: Western Australia, Timor Sea, Cartier Reef, 12°32′S, 123°33′E.

COMMON NAME

Leopard-Spotted Dumpling Squid

DISTINGUISHING CHARACTERS

Differs from all other Australian *Euprymna* in having biserial arm suckers.

DIAGNOSTIC FEATURES

Small species, up to 9.5 mm ML. Funnel organ dorsal element spade-shaped. Arm suckers biserial. Left dorsal arm hectocotylised in males: basally, two pairs of normal suckers; third sucker pedicel in ventral row modified into distally directed, enlarged, fleshy papilla, without terminal sucker; following two or three rows suckers normal; distal end of arm bears 9–15 pairs of suckers on enlarged columnar sucker pedicels. Spermatophores with discrete cement body. Spermatophores 46–76% ML.

Colour. Preserved specimens cream with large, deep purple, irregularly shaped pigment spots on dorsal and ventral head and mantle. Fins with one to three large spots close to junction with mantle. Aboral surface of arms with mediolongitudinal series of large dark purplish blotches and smaller spots between base of each sucker and extending onto sucker pedicels. Aboral surface of club with series of large blotches close to keel and smaller blotches or bars and spots towards club margin.

HABITAT AND BIOLOGY

Coral reef.

SIZE

Up to 9.5 mm ML. Males and females similar in size.

REMARKS

Euprymna pardalota differs from other *Euprymna* occurring in the region and from the only other species definitely known to occur in Australian waters, *E. tasmanica* (Pfeffer, 1884), in having two series of suckers on the arms rather than four. This trait is known from only one other nominal species of *Euprymna: E. phenax* Voss, 1962, which is found in the Philippines.

DISTRIBUTION

Western Australia from 12°14′S, 122°56′E to Queensland 23°30′S, 152°28′E. Known depth range 0.2–20 m.

REFERENCE

Reid (2011).

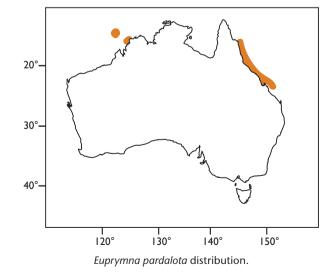


Dorsal view (A. Reid).

Ventral view (A. Reid).



Hectocotylus (A. Reid).



Euprymna tasmanica (Pfeffer, 1884)

Sepiola tasmanica Pfeffer, G. (1884). Die Cephalopoden des Hamburger Naturhistorischen Museums.
Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg 8(1), 1–30. [6, fig. 7].
Type data: holotype ZMH 3849.
Type locality: Australia: Bass Strait.

COMMON NAME

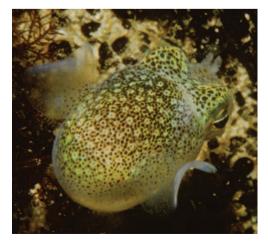
Southern Dumpling Squid

DIAGNOSTIC FEATURES

Dorsal mantle fused to head. Fins wide, rounded, semicircular; short, do not exceed length of mantle anteriorly or posteriorly. Non-hectocotylised arm sucker arrangement same in both sexes: arm suckers tetraserial. Dorsal and ventral series of suckers on arms 2–4 in males enlarged; ventral marginal series of arms 2 and 3 with one to three greatly enlarged suckers basally (8–11% ML); dorsal and ventral marginal series of arms 2–4 with > 10 enlarged suckers (diameter 4–7% ML). Hectocotylus

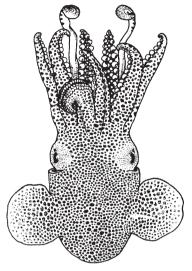


Live animals mating (P. Mercurio).

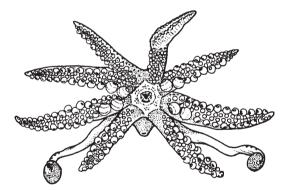


Live animal (C. Bryce).

present, distal half of left dorsal arm modified: third and/or fourth proximal suckers in ventral series elongated into long papilla(e), each bearing a tiny sucker; base of hectocotylus with 29–38 normal suckers; distal end of hectocotylised arm with sucker pedicels enlarged and tightly packed to form two double series of columnar



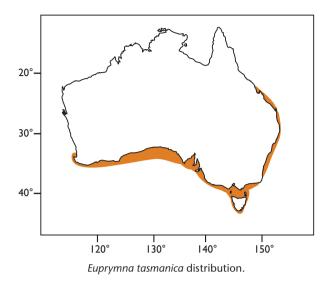
Dorsal view (M. Norman).



Arm crown, oral view (M. Norman).



Tentacular club (ABRS, K. Hollis).



structures; suckers reduced with tiny, fleshy, slit-like openings (30–38 in dorsal series, 29–38 in ventral series). Club suckers (many hundreds) all of similar minute size. Saddle-shaped bacterial photophore inside mantle cavity.

HABITAT AND BIOLOGY

This species lives in sandy and muddy areas, often in association with seagrass beds. It remains buried in sand during the day, and emerges at night to forage for small crustaceans and fishes. It can 'glue' sand grains to its dorsal body surface to aid in camouflage.

Multiple mating occurs in the laboratory and males increase the number of mantle contractions when mating with recently mated females, suggesting they are able to detect recent mating history. At the conclusion of mating the hectocotylus is enlarged. Spawning occurs in spring and summer, with females laying multiple clutches containing 6–163 eggs per clutch over 1–121 days. Egg number per clutch declines over the spawning period. Females lay pale orange eggs in loose clumps, usually at the base of seaweed or seagrass. In the laboratory, at higher ambient water temperatures, the rate of clutch production increased and egg size decreased (Squires *et al.* 2013).

SIZE

Up to 40 mm ML.

REMARKS

The taxonomic status of members of this genus is largely unresolved.

DISTRIBUTION

Southern Indo-Pacific: eastern and south-eastern Australia, from Brisbane to Shark Bay, Western Australia.

REFERENCES

Norman and Lu (1997), Squires et al. (2013).

Inioteuthis Verrill, 1881

DIAGNOSTIC FEATURES

Sepiolines without internal light organs. Suckers biserial on all arms. Tentacle club suckers in eight transverse rows; males with left arm 1 hectocotylised: a basal part, a broad copulatory apparatus with an apparent deep excavation caused by lengthening of sucker stalks of dorsal and ventral sucker rows, and a distal part. (Bello, personal communication.)

REMARKS

Three species belonging to *Inioteuthis* have been described: *I. capensis* Voss, 1962, I. japonica (Orbigny, 1845), and *Inioteuthis maculosa* Goodrich, 1896. Two additional species from northern Australia have been found by the author among museum collections. This genus has not previously been recognised from Australia and the status of these two species is currently under review. No descriptions of the female mantle cavity organs are available in the literature.

Sepiola Leach, 1817

DIAGNOSTIC FEATURES

Sepiolines with pair of internal kidney-shaped light organs on ventral surface of ink sac. Suckers biserial on arms 1 to 3 and at least proximally on arms 4. Tentacle club suckers in four to eight oblique rows. Females with ear-shaped bursa copulatrix on left ventral side of mantle cavity. Males with left arm 1 hectocotylised: suckers and sucker stalks typically arranged basally, a copulatory apparatus comprised of modified suckerless stalks, and a distal part. (After Bello 2013.)

REMARKS

Many species belonging to this genus are found in other parts of the world. The Australian representatives are yet to be formally described.

Sepiola sp.

COMMON NAME

Southern Bobtail Squid

DIAGNOSTIC FEATURES

Fins rounded and relatively small. Arm suckers biserial. Mature males with greatly enlarged suckers on arms 1 and 3. Males without modifications to left arm 1.

HABITAT AND BIOLOGY

Shallow water on sand and mud; often associated with seagrass.

SIZE

Up to 20 mm ML.

DISTRIBUTION

Southern Western Australia.

REMARKS

Only known from a few museum specimens and some live animal photographs and observations. Occurs with *Euprymna tasmanica* (Pfeffer, 1884) and is easily distinguished by the much larger purple-brown chromatophores over the body and arms.

Order Spirulida

Spirulidae Owen, 1836

The family Spirulidae is monotypic, represented by *Spirula spirula* (Linnaeus, 1758). The phylogenetic position of *Spirula* remains unresolved at this time, perhaps due to the difficulties of obtaining tissue; it has not been included in many molecular studies (Allcock *et al.* 2014). Lindgren *et al.* (2012) in a multi-gene cephalopod phylogeny study found *S. spirula* to be sister to a clade that included *Chtenopteryx* and *Bathyteuthis* (Bathyteuthoidea).

Spirula Lamarck, 1799

As for family.

Spirula spirula (Linnaeus, 1758)

Nautilus spirula Linne, C. (1758). Systema Naturae per Regna tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis. 824 pp. Holmiae. [710].

Type data: repository unresolved. Type locality: America.

COMMON NAME

Ram's Horn Squid

DISTINGUISHING CHARACTERS

Coiled internal shell comprised of a series of chambers that functions to regulate buoyancy.

DIAGNOSTIC FEATURES

Mantle cylindrical, thin, muscular; dorsal anterior margin triangular, acute (not fused to head). Ventral mantle with two tongue-like projections from between which the funnel protrudes. Fins narrow, ovate, with fringed anterior margins; short, do not exceed length of mantle anteriorly or posteriorly; attached dorsolaterally on posterior end of mantle (almost perpendicular to longitudinal axis of body). Mantle-locking cartilage a simple straight ridge; funnel-locking cartilage a simple, straight depression. Eyes large; ventral evelids present. Arms increase in length dorsally to ventrally. All arms except fourth pair united by broad webs. Non-hectocotylised arm sucker arrangement same in both sexes: arm suckers tetraserial, or in six series. Hectocotylus present, both ventral arms modified: right hectocotylised arm grooved, concave, with spoon-like expansion, pointed tip and two finger-like outgrowths; left hectocotylised arm round in cross-section with two spoonlike and one finger-like outgrowth with soft papillae at distal tip. Club straight, slender; not expanded, same width as stalk; with 12-16 suckers in each transverse row; all suckers of similar small size. Buccal membrane in females with spermatheca. Radula absent. Spirally coiled internal shell present, located in posterior end of animal; shell comprised of > 30 chambers in adults.

Photophores. Large photophore present between fins, surrounded by annular fold of skin.

Colour. Spirula spirula is normally covered in a redbrown to silvery skin that is often lost in trawled animals.

HABITAT AND BIOLOGY

This is a mesopelagic species, inhabiting 600–700 m during the day and found in depths < 300 m at night. Its common name is derived from the coiled shell, large numbers of which are frequently washed ashore. The capture of young at depths between 1000 and 1750 m suggests that females possibly lay eggs on the bottom of continental slopes. This observation is also supported by stable isotope analyses of the shell, which can be used as a biological proxy to interpret ontogenetically related environmental changes (Luckeneder *et al.* 2008). Luckeneder *et al*'s (2008) study showed that the young hatch in deep, cold seawater <1000 m depth at temperatures ~4–6°C but move to warmer (12–14°C) mid-water habitats during growth, and then move back into deeper water as adults. Eggs are small and the smallest known paralarva has a 1.5 mm ML with two shell chambers. The species attains sexual maturity at ~30 mm ML (after 12–15 months of life), and the lifespan is estimated to be ~18–20 months (based on a study of specimens caught by fisheries around Fuerteventura Island (Canary Islands)). Live animals have been seen to retract their head and arms into their mantle and close the opening with the pointed 'flaps' formed by the mantle. They take up a vertical position, head downwards, when at rest. The internal calcified shell provides osmotically regulated buoyancy control.

Interest to fisheries. No direct interest to fishery exists, but beachwashed shells are sold in the shell trade.

SIZE

Rarely exceeds 45 mm ML.

REMARKS

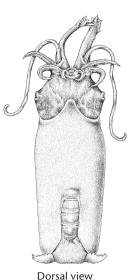
Only one species, *Spirula spirula*, has been recognised and described. Whether all *Spirula* belong to one species or more than one has yet to be fully examined. Neige and Warnke (2010) applied morphometric analyses to an examination of 110 *Spirula* shells from five geographical areas. Their findings challenge the monospecific status of *Spirula* in showing that shell characteristics varied with geographical origin: specimens from Madagascar, New Zealand and Brazil are larger than those from north-west Africa and Australia. Whether these differences reflect geographic variation or disjunction among populations will require detailed morphological and molecular analyses to unravel.

Warnke (2012) recently compared populations from disjunct ranges in the eastern Atlantic (South Africa and the Canary Islands, Morocco) using the amplified fragment length polymorphism (AFLP) technique. These results (although based on a limited number of samples) revealed a single genetic cluster, indicating there is probably only one population living in eastern Atlantic waters.

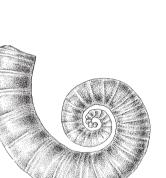
In addition, Haring *et al.* (2012) found through the analysis of three mitochondrial genes from a specimen collected off the eastern Australian coast (specifically Avalon Beach, New South Wales) that the molecular distances between populations from the Atlantic and Pacific are extremely low (<1%). The genetic data so far suggest continuous genetic exchange among *Spirula* populations that may reflect a much wider distribution of *Spirula* than currently indicated by live animal captures.

Based on comparison of haemocyanin sequences that have been used to calibrate a molecular clock for many

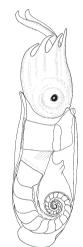




Fresh-caught specimen, dorsal view (K. Graham).



Shell (ABRS, K. Hollis).



(ABRS, K. Hollis).

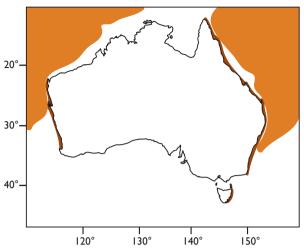
Diagram of whole animal in lateral view to show position of shell (A. Reid).

molluscan species, Warnke *et al.* (2011) estimate a divergence time of Spirulidae and Sepiida at 150 ± 30 million years ago.

Strugnell *et al.* (2006) successfully extracted 12S rDNA from beachwashed *Spirula* shells from Mission Beach, north Queensland. A 310 bp sequence was obtained and was subsequently shown to be identical to that of tissue obtained from a fresh specimen from Fuerteventura Island, Spain.

DISTRIBUTION

Spirula is distributed circumtropically worldwide from ~30°N to 30°S. As with many other epi- and mesopelagic circumtropical species, *Spirula*'s distribution is patchy.



Spirula spirula distribution. Note: The distribution is based on shell and whole animal data (shells may have drifted). Darker orange on the map refers to beachwashed shells.

It occurs near oceanic islands and the continental shelf in tropical and subtropical oceanic waters, where the water temperature at 400 m is 10°C or warmer. Current distribution maps are misleading because most include both beachwashed shell and whole animal distributions. A more accurate indication of the currently known distribution of *Spirula* is given in Haring *et al.* (2012, Fig. 1).

REFERENCE

Reid (2005c).

Superorder Octopodiformes

This taxon includes the orders Vampyromorphida and Octopoda.

DIAGNOSTIC FEATURES

Members of this group have eight arms and no tentacles (although the second pair of arms in *Vampyroteuthis* are modified as threadlike cirri). Head fused to mantle dorsally. Buccal crown absent. Arms 4 not modified, united by web (except in some argonautoids). Suckers radially symmetrical, without internal chitinous armature. Fins (when present) with cartilaginous axial support (cartilage lost in subadult *Vampyroteuthis*). Shell a gladius, cartilage-like fin support, pair of stylets, or absent.

Order Octopoda

This clade includes all benthic, demersal and pelagic octopods. It includes the suborders Cirrata and Incirrata. The classification shown below follows the family level revision of the order Octopoda proposed in Strugnell *et al.* (2014). Generic assignment follows Norman and Hochberg (2005).

Key to Octopoda suborders

- 1b. Fins absent. No cirri adjacent to arm suckers. Radula always present......Suborder Incirrata

Suborder Cirrata

This clade includes the cirrate (finned) octopods.

DIAGNOSTIC FEATURES

Body and arms semi-gelatinous; body with pair of round to elongate fins (two pairs in juvenile vampire squids), supported by cartilaginous structure. Mantle opening narrow, located on the ventral side of the body, tightly fitting around funnel. Arms with single longitudinal series of suckers between digits of thin skin (cirri). Arm webs usually deep and thin (in some groups as an inflatable layer). Small suckers embedded in flesh with soft lined cups (no horny sucker ring). Mature males of some groups with enlarged suckers; no arm tip modifications in males. Radula present, reduced, or absent. Ink sac absent.

Colour. Skin white to dark red-brown, uniform in colour. *Sculpture.* Skin sculpture absent.

REMARKS

Cirrate octopods include some of the largest invertebrates of the deep sea and are conspicuous members of benthopelagic and bathypelagic communities (Vecchione *et al.* 2002). Recent trawling, primarily in the northern hemisphere, has shown that the relative abundance of some cirrates, especially opisthoteuthids, may be quite high. Two of the three cirrate families, the Opisthoteuthidae and Cirroctopodidae, are found in Australian waters.

The phylogenetic relationships among cirrate octopods were investigated by Piertney *et al.* (2003) using mitochondrial 16S rDNA sequences. The derived phylogeny supported the traditional separation of cirrate families based on web form. The genera with a single web (*Opisthoteuthis, Grimpoteuthis, Luteuthis* and *Cirroctopus*) are clearly distinct from those with an intermediate or secondary web (*Cirroteuthis*, *Cirrothauma* and *Stauroteuthis*). The cirrates with a single web could be separated into three groups: (1) *Opisthoteuthis* species (with evidence of two groupings within this broader group); (2) *Grimpoteuthis* and *Luteuthis*; and (3) *Cirroctopus* species. These researchers suggest the following revisions in the classification of the cirrates: (1) *Cirrothauma*, *Cirroteuthis* and *Stauroteuthis* to be united in the Cirroteuthidae; (2) *Grimpoteuthis* and *Luteuthis* be placed in the Grimpoteuthidae; (3) *Opisthoteuthis* placed in Opisthoteuthidae; and (4) *Cirroctopus* placed in a new family, Cirroctopodidae.

This arrangement was reflected in the revised taxonomy of Collins and Villanueva (2006) and is the classification followed here. Only two families, Cirroctopodidae and Opisthoteuthidae, are found in Australian waters.

REFERENCE

Jereb et al. (2014).

Key to Cirrata families

- Fins large, paddle-like. Shell V-shaped Cirroctopodidae (C. mawsoni)
- 1b. Fins small, subterminal. Shell U-shapedOpisthoteuthidae

Cirroctopodidae

COMMON NAME

Finned Octopods

DIAGNOSTIC FEATURES

Relatively muscular, body not elongate. Eyes tilt dorsally; lenses present. Fins large. Secondary arm web absent. Suckers relatively small; enlarged suckers absent in mature males. Cirri of moderate length, equal to maximum sucker diameter. Gills hemispherical in form. Posterior salivary glands absent. Ink sac absent. Radula absent. Shell V-shaped with spike-like lateral walls.

SIZE

Mantle length to 180 mm. Total length > 600 mm.

DISTRIBUTION Southern hemisphere.

REFERENCE Hochberg *et al.* (2014).

Order Octopoda 299

Cirroctopus Naef, 1923

Cirroctopodidae is monogeneric, represented by *Cirroctopus*, with four species, one of which, *C. mawsoni* (Berry, 1917), is found in Australian waters.

Cirroctopus mawsoni (Berry, 1917)

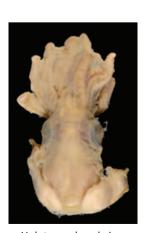
Stauroteuthis (?) mawsoni Berry, S. S. (1917). Cephalopoda. Scientific Reports of the Australasian Antarctic Expedition 1911–1914, (series C) 14(2), 1–39 [8, text figs 1–4; pl 10, fig. 1].

Type data: holotype AM C.40886.

Type locality: Antarctica, Southern Ocean, off Mertz Glacier, Adelie Land, 66°55'S, 145°21'E.

DIAGNOSTIC FEATURES

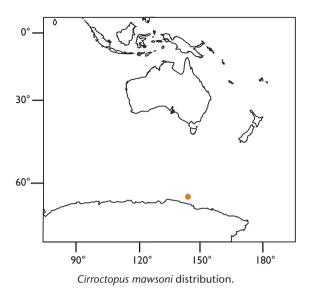
Body firm, smooth, almost sepioliform, compressed dorsoventrally, rounded below but only slightly arched over fins. Fins large with squared, truncate outer margins; anterior margins straight, posterior margin oblique; join to become continuous with each other posteriorly, forming a broad, flat fold of integument. Slight ridge along mantle margin from anterior junction with fins to anterior mantle margin. Funnel small, short. Arms unequal, formula 1 > 2 > 3 > 4. Oral surface with single series of small, closely packed discoidal suckers, flanked on each side by series of short, blunt, cylindrical papilliform cirri that alternate with suckers almost to tips of arms. Suckers with minute openings and indistinct radial grooves. Arm



Holotype, dorsal view (AM C.40886, R. Springthorpe).



Left dorsal arm (A. Reid, redrawn from original description).



webs deep, particularly on first pair of arms, which are connected almost to their distal tips. Webs decreasing in depth from dorsal to ventral arms and extend about halfway along ventral arms.

Colour. Fresh preserved specimens pale brownish cream; eyes and oral side of web slate coloured; integument reddish.

SIZE

Mantle length to 12 mm. Total length 32 mm.

REMARKS

This species is known only from the type specimen, which is immature.

DISTRIBUTION

Known only from the type locality: Antarctica, Southern Ocean, off Mertz Glacier, Adelie Land, 66°55′S, 145°21′E.

Opisthoteuthidae

DISTINGUISHING CHARACTERS

Cirri short (0.4–2.5 × largest sucker diameter) compared to members of the Cirroteuthidae with very long cirri (up to $8 \times$ largest sucker diameter).

DIAGNOSTIC FEATURES

Body foreshortened along anterioposterior axis. Secondary web absent; web nodules (support) present in some genera. Suckers and cirri extend to arm tips. Suckers not modified. Radula reduced or absent. Simple U-, V-, or W-shaped shell that reaches posterior end of body; lateral wings not expanded or only slightly expanded. Areolar spots present in some genera, including *Opisthoteuthis*.

HABITAT AND BIOLOGY

Opisthoteuthids alternate between sitting on the ocean floor and swimming just above it. The reduction of the radula is thought to reflect the habit of the prey being swallowed whole.

REMARKS

One genus, *Opisthoteuthis* Verrill, 1883 is recognised in this family (Collins and Villanueva 2006). It is represented by two species, both of which are found in Australian waters.

REFERENCES

Vecchione et al. (2008a), Hochberg et al. (2014).

Opisthoteuthis Verrill, 1883

COMMON NAME

Flapjack or Pancake Devilfishes

DISTINGUISHING CHARACTERS

Fins small. One or two regions (proximal and distal) of enlarged suckers in mature males. Sucker apertures without fleshy tooth-like structures. Optic lobe kidneyshaped; white body penetrated by two or more separate optic nerve bundles. Shell broad U-shaped. Areolar spots present.

DIAGNOSTIC FEATURES

Body flattened in anterioposterior axis (sometimes due to preservation), fresh specimens ovoid, mantle reduced to hump lying on extended arms, connected by thick webs. Tissue semi-gelatinous. Mantle aperture a narrow circular slit. Eyes large, diameter often 50% of head width. Fins small, fin cartilage U-shaped. Single barshaped cartilage for support of fins. Kidney-shaped optic lobe; white body penetrated by two or more separate optic nerve bundles. Funnel short, directed posteriorly. Proximal and/or distal region of arms of mature males with enlarged suckers, often with complex alignment. Arm suckers flanked by alternating short cirri; cirri may be retractile into pockets. Arm webs almost reach distal arm tips; web nodules, or web supports present or absent. Longitudinal gill axis perpendicular to body axis. Shell broad, U-shaped, lateral walls of wings not parallel; outer surface of saddle with groove; wing terminates in some species as elongate, simple pointed cone; termination complex in some species.

Colour. Areolar spots present, may be difficult to detect in some species.

HABITAT AND BIOLOGY

Opisthoteuthids are thought to be primarily benthic. They live in the bathyal depths (125–2250 m), on the bottom or above it but rarely ascend to midwater. However, they are capable of swimming by contraction of the armweb complex. In some species, swimming may be used for prey capture.

REMARKS

Reliable identification is only possible for mature males. Most species are not fully described and are poorly known.

REFERENCES

Villanueva et al. (2008), Hochberg et al. (2014).

Key to Opisthoteuthis species

Opisthoteuthis persephone Berry, 1918

Opisthoteuthis persephone Berry, S. S. (1918). Report on the Cephalopoda obtained by the F.I.S. 'Endeavour' in the Great Australian Bight and other southern Australian localities. *Biological Results of the Fishing Experiments carried on by the F.I.S. 'Endeavour', 1909–14,* 4(5), 201–298, 67 figures, 29 plates [290, text figs 66, 67, pls 81, 82, 85–88].

Type data: holotype AM C.148253.

Type locality: Australia: Bass Strait, 42 miles south and east of Genoa Peak.

DISTINGUISHING CHARACTERS

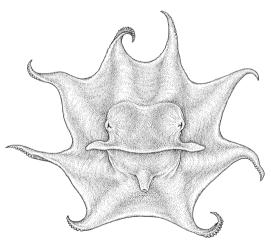
Funnel organ larger and more slender than that of *Opisthoteuthis pluto* Berry, 1918. Differs from *O. pluto* in



Aboral view (K. Graham).



Oral view (K. Graham).

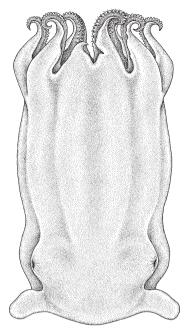


Aboral view (ABRS, K. Hollis).

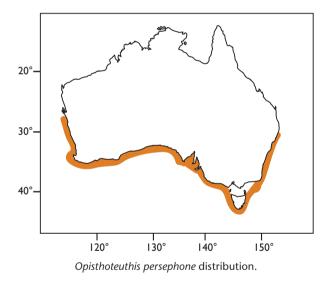
its distinctive colouration, particularly over the oral side of the arms and web, and the firm composition of arms.

DIAGNOSTIC FEATURES

Berry (1918) describes the eyes in this species as 'rather small and inconspicuous', and the fins as 'minute, tenuous'. Arm suckers small, even-sized, in single series of up



Dorsal view (ABRS, K. Hollis).



to 93. Funnel slender; funnel organ a pair of small, oval pads. Cirri with narrow pockets into which they can retract. Holotype specimen with arm suckers numbers: arm 1, 78 suckers; 2, 78; 3, 72; 4, 72. Digestive gland bilobed. Gills with six lamellae per demibranch. Shell broad U-shaped, saddle with posterior groove.

Colour. Aboral surfaces of preserved specimens nearly colourless or light grey with traces of superficial membrane lightly pigmented with streaks of brown. Oral surfaces of superficial integument colourless and transparent, interbrachial parts very loose; deeper layer dark bluish slate, paler along arms and over ring-like zone close to mouth. Suckers and cirri yellowish brown. Areolae very small, each with clear central area.

HABITAT AND BIOLOGY

Primarily benthic.

SIZE

The holotype has an arm span of 330 mm from arm tip to arm tip.

REMARKS

Opisthoteuthis persephone needs to be redescribed from new material from the type locality. It is sympatric with *O. pluto* Berry, 1918.

DISTRIBUTION

Off southern Australia: Great Australian Bight and Bass Strait, depths ~275–550 m.

REFERENCES

Young and Vecchione (2003a), Hochberg et al. (2014).

Opisthoteuthis pluto Berry, 1918

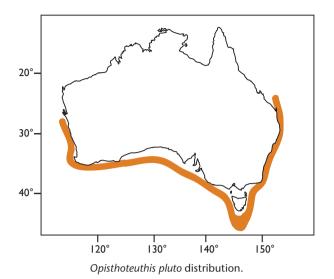
Opisthoteuthis (Teuthidiscus) pluto Berry, S. S. (1918). Report on the Cephalopoda obtained by the F.I.S. 'Endeavour' in the Great Australian Bight and other southern Australian localities. Biological Results of the Fishing Experiments carried on by the F.I.S. 'Endeavour', 1909–14, 4(5), 201–298, 67 figures, 29 plates. [284, text figs 64, 65, pls 81–84].

Type data: AM holotype not extant.

Type locality: Australia: Great Australian Bight, 129°28'E.

DIAGNOSTIC FEATURES

Eyes moderately large. Fins near posterior edge of eyes, large, flabby, oblong. Funnel long and narrow. Funnel organ a pair of small, well-separated oblique oval pads. Arms subequal in length; suckers in 80–85 rows on each arm. Female suckers five to seven largest, sucker rows one to three very small on all arms. Male with greatly enlarged suckers proximally and distally; proximal suckers equal in size on all arms; greatly enlarged suckers distally on arms 2 and 3 (or 2–4) near web edge. Both suckers and cirri appear to be completely retractile. Gills with eight lamellae per demibranch. Digestive gland bilobed. Shell broadly U-shaped, saddle with groove along posterior surface; wings with vertical thickening,



and then rapidly tapering, outer surface slightly excavated at point of expansion.

Colour. Aboral surfaces of preserved specimens dark brown or slate grey. Oral surface chocolate to purple, paler towards margins of webs and around mouth; dorsal surface with areolar spots with clear, sharply defined nucleus surrounded by narrower zone of dark chocolate, and then wider, paler region surrounded by paler slate zone, merging into colour of general integument.

HABITAT AND BIOLOGY

Primarily benthic.

SIZE

The largest specimen originally described is the holotype with an arm span of 540 mm.

REMARKS

Opisthoteuthis pluto is sympatric with *O. persephone*.

DISTRIBUTION

Off south-western Australia. Great Australian Bight, depth 275–1100 m.

REFERENCES

Nesis (1982/1987); Young and Vecchione (2003b), Hochberg *et al.* (2014).

Suborder Incirrata

This clade, which comprises all the non-cirrate octopods, includes the pelagic families Bolitaenidae, Vitreledonellidae, Amphitretidae, the argonautoids and the benthic cirrate octopods.

Key to incirrate superfamiles

- 1. Funnel-mantle locking apparatus present
- Funnel-mantle locking apparatus absent
-Octopodoidea

Superfamily Argonautoidea Naef, 1912

The Argonautoidea comprises a small group of pelagic incirrate octopods that inhabit most of the world's tropical and temperate oceans. The group is characterised by having marked sexual dimorphism with small or dwarf males and an unusual method of copulating that involves the transfer of a detached hectocotylus, which bears the spermatophores from the male into the female's mantle cavity. The group includes four monogeneric families – Argonautidae, Tremoctopodidae, Ocythoidae and Alloposidae – and appears to be the sister group to all other incirrate octopods (Allcock *et al.* 2014).

Strugnell and Allcock (2010) in the first phylogenetic study to include representatives of each of the four families showed a sister-taxon relationship between Argonauta and Ocythoe and between Tremoctopus and Haliphron (Alloposidae). Information from the fossil record was used to calibrate divergence times. Divergence times varied depending on which of two evolutionary scenarios are hypothesised: either that the early ocythoid has a shell and its absence is a secondary loss or that it never had a shell. The most recent common ancestor is estimated to date from the late Tertiary (~45.6 million years ago) if the absence of a shell in this lineage is a secondary loss. Ancestral Argonautoidea are assumed to have been benthic in habit. A transition to a pelagic existence may have been a response to global anoxic events that occurred in the Cenozoic (~60.5 million years ago) and also in the Cretaceous (124.5-97 million years ago).

Key to families of the Argonautoidea (after Lu and Dunning 1998)

- 1a. Cephalic water pores absent2

.....Anoposidae (Hauphion ananicus)

2b. Body muscular. Funnel not embedded in head tissue. Web shallow between all arms; dorsal arms

of female with distal expansion for secretion of shell. Third left arm of male hectocotylised, developed in sac under left eye.....Argonautidae

- 3b. One pair of cephalic water pores at base of ventral arms. Dorsal and ventral arms much longer than dorsolateral and ventrolateral arms; right ventrolateral arm of male hectocotylised. Web absent. Females do not construct a brood shell for carrying eggs......Ocythoidae (*Ocythoe tuberculata*)

Alloposidae Verrill, 1881

The family Alloposidae is currently monotypic, represented by *Haliphron atlanticus* Steenstrup, 1861.

Haliphron Steenstrup, 1861

DIAGNOSTIC FEATURES

Body tissue gelatinous, smooth. Cephalic water pores absent. Funnel embedded in head tissue. Funnel-locking apparatus simple; fused in adults. Third right arm of males hectocotylised, developed in sac anterior to right eye. Webs deep between all arms. Suckers biserial, can form single series basally. Ink sac present. Remnant of true shell, a short, thick gelatinous stylet present.

Haliphron atlanticus Steenstrup, 1861

Haliphron atlanticus Steenstrup, J. (1861). Foreviste derpaa en Afdeling af Museets seneste Forogelser af Blaeksprutteklassen, saerligen Octopodformer fra Middelhavet, og gav Bemaerkninger om de enkelte Arter, fornemlig efter det Veranyske Cephalopodvaerk. Videnskabelige Meddekekser fra deb Naturhistoriske Forening i Kjobenhavn, 1860, 332–333 [332].

Type data: holotype ZMUC.

Type locality: Atlantic Ocean.

DISTINGUISHING CHARACTERS

Haliphron has a remnant of a true shell, unlike other argonautouids: it is a short, thick, almost gelatinous stylet. It differs from *Argonauta* in having a hydrostatic



Live animal photographed in Monterey Bay (© 1995 MBARI).



Dorsal view, female (Plate L, Fig. 2a, from orginal description).

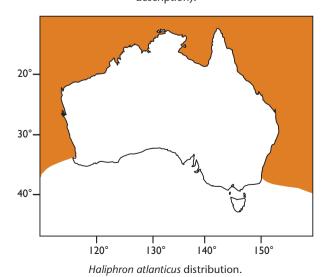




Ventral view, female (Plate L, Fig. 2, from original description).

e Lateral view, male (Plate L, Fig. 1, from orginal description).

Hectocotylus (Plate L, Fig. 1a, from orginal description).



organ. In addition *Haliphron* attains giant sizes, reaching 400 mm mantle length and a total length of 2 m.

DIAGNOSTIC FEATURES

Mantle short and broad, head wide; eyes large, diameter up to one-third ML. Arms short with deep webs; formula 1 > 2 > 3 > 4. Funnel long; opens anterioventrally to eyes. Funnel-locking apparatus complex, comprised of hook-like muscular folds on funnel corners with corresponding ridge/ grooves on mantle, fused in adults. Funnel organ W-shaped. Arms short; suckers biserial distally, uniserial proximally; enlarged suckers absent. Hectocotylus develops in an inconspicuous pocket in front of right eye (males appear to have only seven arms); when mature, hectocotylus protrudes from pouch, it detaches at mating; hectocotylus with papillate lateral fringe from base to spermatophore reservoir; open spermatophore groove leads to terminal spermatophore reservoir branched off arm at base of penile filament; penile filament hangs free, not enclosed within sac; two rows of large suckers present. First lateral tooth of radula much smaller than rhachidian or second lateral tooth. Hydrostatic organ (swim bladder dorsal to the digestive system) present. Water pore absent. Stylets relatively small, wide, thick, drop-like bodies embedded in lateral walls of mantle.

Colour. Densely pigmented reddish purple.

HABITAT AND BIOLOGY

Females brood their eggs, which are attached to the oral side of the arm bases near the mouth. It has been suggested that *H. atlanticus* may not be entirely pelagic, spending more of its life at the bottom, especially on continental slopes. It may undergo diel migration, moving to surface water at night. Observations of live animals made from a submersible show that they use the deep arm webs to swim with a medusoid motion.

SIZE

Females very large, up to 690 mm ML, or total length up to 2 m; males up to 100 mm ML, 300 mm total length (i.e. smaller than females, but not dwarf).

DISTRIBUTION

Circumglobal in the Atlantic, Indian and Pacific Oceans between 43°N and 45°S. Depth range surface to at least 1260 m and up to 6787 m.

REFERENCE Finn (2014a).

Argonautidae Cantraine, 1841

Argonauta Linnaeus, 1758

COMMON NAME Paper Nautilus

DISTINGUISHING CHARACTERS

Third left arm of males hectocotylised. Males of other Argonautoidea (Alloposidae, Ocythoidae and Tremoctopodidae) possess modified third right arms. Within the family, species are distinguished based on the following traits (as determined by Finn 2013): males – relative arm sucker counts, hectocotylised arm sucker counts, gill lamellae counts; females – arm formulae, relative arm sucker counts, gill lamellae counts, presence or absence of shell rib tuberculation, inter-keel tuberculation (paired or paired or alternating), keel width uniform or widening during growth.

DIAGNOSTIC FEATURES

Body firm, mantle thin and muscular. Mantle-locking apparatus well developed with pit and nodule lock; funnel organ Λ / shape. Suckers biserial on long stalks, connected to marginal membrane; interbrachial web narrow, cephalic water pores absent. Distal tips of dorsal arms of female with broad, expanded, membranous, glandular flaps that secrete and hold shell; sexual dimorphism pronounced; males dwarf, with entire left third arm hectocotylised, developed in pouch beneath eye, and with further growth hangs free in the arm crown and reaches around same size as body; autotomised when mature; female produces large, fragile external shell in which she broods her eggs. Stylets absent.

HABITAT AND BIOLOGY

This pelagic octopus spends its entire life in the open ocean. Little is known about its biology, but it probably feeds on pelagic molluscs, small fishes and crustaceans. During mating, males rupture the pouch containing the modified arm. This is then loaded with sperm, detaches, and is presented to the female. This detached arm manoeuvres to the gill cavity of the female where it attaches to her gills until required for fertilisation. Single females have been found with multiple male arms attached to the gills. The shell is secreted using enlarged webs on the end of the first arm pair and functions as a brood chamber for the eggs and a flotation device for the female argonaut. The shell is not homologous with the true molluscan shell. Young are brooded first in the oviducts (as is the case in *Ocythoe*), and then eggs are laid in strings and attached to the shell until the planktonic larvae hatch. Members of this genus are continuous spawners.

Mass strandings of female argonauts occur at various times, particularly along the southern Australian coastline, perhaps due to currents, winds, or perhaps following massing due to a favourable and concentrated food source. The shells are popular for sale in the shell trade. In the northern hemisphere (where more studies have been undertaken), argonauts form a significant component of the diets of pelagic fishes.

REMARKS

This genus has been recently revised by Finn (2013), who showed that there are only four species of *Argonauta* worldwide: *A. argo* Linnaeus, 1758; *A. hians* Lightfoot, 1786; *A. nodosus* Lightfoot, 1786 and *A. nouryi* Lorois, 1852, despite > 50 species names occurring in the literature. The plethora of names has resulted from new species being coined on the basis of variation in shell morphology. Finn's (2013) revision has shown that this variation can often be explained by changes in the shape of the shell during growth. All but *A. nouryi* are found in Australian waters.

Female argonauts continue to grow when mature and indices using dorsal ML as a size standard tend to decrease with increasing mantle lengths. This makes comparison among descriptions difficult.

Argonauta, unlike other argonautids, does not possess a swim bladder. Females appear to compensate by trapping air in the shell and using it as a flotation device.

DISTRIBUTION

Worldwide in tropical and temperate oceans.

REFERENCES

Finn and Norman (2011a), Finn (2013), Finn (2014b).

Key to Argonauta species

(After Finn 2013, with information on male *A. argo* from Naef 1923 and Voss 1956 *fide* Finn 2013.)

Males

Females

- 1a. Arms 4 longer than arms 2 A. argo
- 1b. Arms 2 longer than arms 4.....2
- 2a. Arms 1 with 280–360 suckers, arms 2 and 3 with 140–220 suckers, arms 4 with 80–135 suckers.
 14–21 gill lamellae per demibranch.......A. nodosus

Shells

- 1a. Lateral ribs smooth, continuous2

Argonauta argo Linnaeus, 1758

Argonauta argo Linnaeus, C. (1758). Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 824 pages. Holmiae [708].

Type data: syntypes.

Type locality: 'Pelago, M. Indico, Mediterrane'.

COMMON NAME

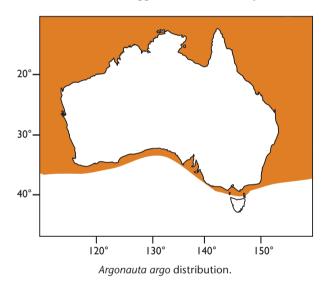
Greater Argonaut

DIAGNOSTIC FEATURES

Males with 12 or 13 suckers on normal arms, 95 suckers on hectocotylised arm. Female arms 4 longer than arms 2 (arm formula 4 > 2 > 3), typically $2.1-3.6 \times ML$, reflexed posteriorly; arms 4 longer than arms 2; 350-380 suckers on arms 1, 190–270 suckers on arms 2 and arms 3, 180– 240 suckers on arms 4. Gills with 16 or 17 lamellae per demibranch. Radula with seven teeth and two marginal plates in each transverse row, rhachidian teeth without lateral cusps (acuspid). Shell with smooth, continuous lateral ribs; keel narrow and of uniform width; keel



Live female with egg case, side view (V. Taylor).



tubercles consistent size and shape; no inter-keel tuberculation.

Colour. Deep maroon to silver.

HABITAT AND BIOLOGY

Little is known of the biology of *Argonauta argo* in Australian waters. Some Japanese specimens were observed using surface-acquired air trapped in their shells to attain neutral buoyancy (Finn and Norman 2010; Finn 2010).

SIZE

Females up to 97 mm ML, shells of Australian females up to 206 mm long. Largest shell examined by Finn (2013) measured 268 mm.

REMARKS

According to Finn (2013), *A. argo* can display considerable variation the shape of the aperture edge near the axis. In the past this has led to confusion in defining the species.

DISTRIBUTION

Argonauta argo is found circumglobally in both hemispheres between ~40°N and 40°S. In Australian waters, this species is most commonly encountered in southern Western Australia from Rottnest Island to Albany. It is occasionally found over the North West Shelf, Western Australia and southern Australia, including South Australia, Bass Strait, northern Tasmania and eastern Victoria; and shells have been found on beaches from Frazer Island, Queensland to Sydney and Lord Howe Island. While relatively common in the Indian Ocean and southern Western Australia it is rare in South Australia and Victoria, probably drifting from western Australia on the easterly flowing Leeuwin current.

REFERENCES

Finn (2013), Finn (2014b), Grove and Finn (2014).

Argonauta hians Lightfoot, 1786

Argonauta hians Lightfoot, J. (1786). A Catalogue of the Portland Museum. 194 pp. [44, 139, 174].Type data: repository unresolved.Type locality: not designated.

COMMON NAME

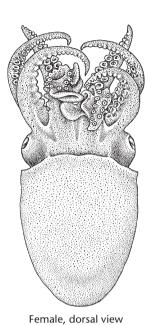
Brown Argonaut

DIAGNOSTIC FEATURES

Male hectocotysed third left arm extremely long, $\sim 4 \times ML$ and 8 × opposite arm length (arm formula $1 \ge 4 = 2 > 3$). Males with 10 or 11 suckers on all normal arms; 37–44 suckers on hectocotylised arm. Female arms moderate length, ~ 1 or 2 × ML, reflexed posteriorly over mantle. Female arms 2 longer than arms 4, arm formula $2 \ge 3 > 4$. 135–160 suckers on arms 1, 70–115 suckers on arms 2 and 3; 30–50 suckers on arms 4. Males with six or seven gill lamellae per demibranch; females with 9–13 lamellae per demibranch. Radula with seven teeth and two marginal plates in each row. Rhachidian tooth with well-developed single lateral cusp (tricuspid).



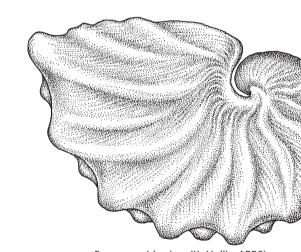
Fresh-caught female specimen with egg case (K. Graham).



(K. Hollis, ABRS).



Male, dorsal view (male and female drawn to scale) (K. Hollis, ABRS).

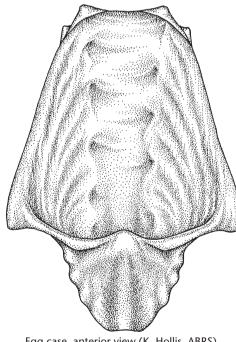


Egg case, side view (K. Hollis, ABRS).

Colour. In life deep maroon to silver. Dorsal mantle with large chromatophores grading to small chromatophores ventrally. Dorsal surface of anterior funnel covered with dense chromatophores.

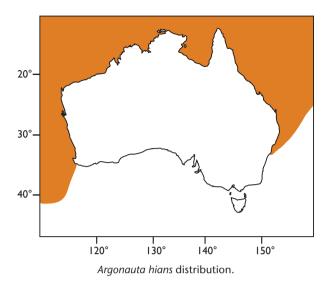
HABITAT AND BIOLOGY

Detatched male hectocotyli found within the mantle cavity and funnel of females. According to Finn (2013) Australian females are mature between 17-19 mm ML and egg laying begins between 19-21 mm ML. There have



Egg case, anterior view (K. Hollis, ABRS).

Shells. Shells (found around Australia) 75 mm length; ribs smooth, continuous, radiating from central axis towards keel; keel width and tubercle size increase with shell growth. Rib count up to 41 in large shells with ~1.5 ribs per keel tubercle; up to 29 tubercles in larger shells; ears often present. Stain pigmentation > 67% of keel tubercles.



been no live observations of these animals in Australian waters.

SIZE

Small. Males up to 7 mm ML, 40 mm total length. Females up to 40 mm ML, 118 mm TL. Largest shell found in Australian waters 75 mm long.

REMARKS

The shell of this species is highly variable. *Argonauta boettgeri* Maltzan, 1881 is considered by Finn (2013) to be a synonym of *A. hians*.

DISTRIBUTION

In Australia, found from the North West Shelf, between Exmouth Gulf and Rowley Shoals, known from Cape Peron (south of Fremantle), Western Australia to Groote Eylandt, Gulf of Carpentaria, Northern Territory and from Cape York, Queensland, south to Botany Bay, New South Wales and Lord Howe Island.

REFERENCES

Finn (2013), Finn (2014b).

Argonauta nodosus Lightfoot, 1786

Argonauta nodosa Lightfoot, J. (1786). A Catalogue of the Portland Museum. 194 pp. [96, 172].Type data: repository unresolved.Type locality: South Africa: Cape of Good Hope.

COMMON NAME(S)

Southern Argonaut, Tuberculated Argonaut

DIAGNOSTIC FEATURES

Female mantle conical, posterior mantle with upward torsion following shape of shell. Head small, embedded within mantle. Eyes large, protruding, constricted basally. Funnel-locking cartilage comprised of rounded, posteriorly directed nodules on inside of mantle wall corresponding to depressions on outer edges of funnel. Arm lengths unequal, $1.7-2.4 \times ML$ (arm formula $2 > 3 \ge 4$ or $2 > 4 \ge 3$); dorsal arms of females with wing-like webs; arms 2 longer than arms 4 in females. Web deepest between dorsal arms. Arms with two series of suckers; without enlarged suckers; females with 280-360 suckers on arms 1, 140-220 suckers on arms 2 and arms 3, 80-135 suckers on arms 4. Radula with seven teeth and two marginal plates in each row, without lateral teeth. Males with 17-20 suckers on all normal arms; 58-64 suckers on hectocotylised arm. Male arm formula $4 \ge 1 = 2 > 3$. Detached hectocotylus with 58-64 suckers in two rows. Gills with 14-21 lamellae per demibranch (females); 8-11 lamellae per demibranch (males).

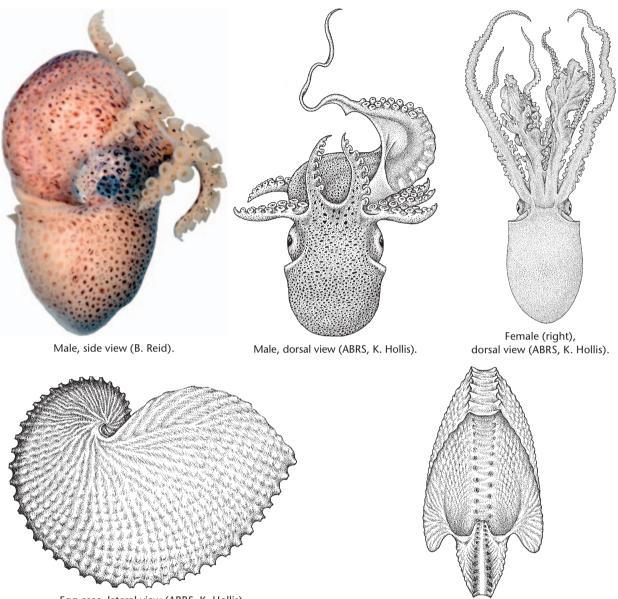
Shell. Shell with concentric series of knobbled ridges, laterally flattened. Ribs numerous, close together, sometimes branching as they radiate towards keel. Lateral ribs composed of rows of separate tubercles; keel width and keel tubercle sizes increase with shell growth; no interkeel tuberculation. Flared shell 'ears' or 'horns' may be present in small specimens, becoming less conspicuous in larger animals. Dark staining on keel tubercles on first third of shell.

Colour. In life orange to deep maroon and purple dorsal webs covering external shell surfaces maroon to reflective silver.

HABITAT AND BIOLOGY

Female *Argonauta nodosus* strand in large numbers in particular years in southern Australia, New Zealand and elsewhere. Based on museum collections, this appears generally to occur from April to October and December to January. There is no regular periodicity in this occurrence. There may be a correlation between the occurrence of *A. nodosus* in southern Australian waters and schools of euphausiids (small shrimp-like crustaceans, or krill) on which they feed.

Eggs of different stages have been recovered from shells, suggesting there is a periodicity in egg laying. The eggs are tiny, numbering many thousands and the young hatch as planktonic larvae.



Egg case, lateral view (ABRS, K. Hollis).

SIZE

Females up to 13 cm ML (shell length up to 24 cm); males up to 11 mm ML and 61 mm total length.

REMARKS

Immature females may be confused with A. hians.

Wolfe *et al.* (2012, 2013) and Smith *et al.* 2012) have examined the shell, or brood chamber, of *A. nodosus* shells using electron backscatter diffraction to characterise the crystallography of biomineralisation and changes that occur after exposure of the shell to reduced pH. The mineralogy of the shell was shown to be 100% calcite with an intermediate Mg-calcite concentration (5.1 Wt%).

Egg case, anterior view (ABRS, K. Hollis).

Magnesium calcite is more susceptible to dissolution at low pH than other skeletal mineral forms, making argonaut brood chambers particularly susceptible to loss of structural integrity and strength as a result of ocean acidification. These studies, however, were conducted only on the shells in the absence of the animal. It is not known whether the females may be able to compensate for this loss of mineralisation at low pH.

DISTRIBUTION

Southern hemisphere between 10°S and 44°S. Known within Australia from Queensland, Great Barrier Reef, Capricorn Bunker Group, south to Bruny