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Table of Contents

Abstract ................................................................. 3
Introduction ............................................................... 4
Materials and Methods .................................................... 5
Descriptions ............................................................... 5
 *Okenia* Menke, 1830. .................................................. 5
   *Okenia echinata* Baba, 1949. ........................................ 6
   *Okenia purpurata* sp. nov. ......................................... 9
   *Okenia vena* sp. nov. ............................................... 13
   *Okenia virginiae* Gosliner, 2004 .................................. 16
   *Okenia mellita* sp. nov. ........................................... 19
   *Okenia barnardi* Baba, 1937. .................................... 22
   *Okenia pellucida* Burn, 1967 ...................................... 25
   *Okenia japonica* Baba, 1949. ..................................... 27
   *Okenia mija* Burn, 1967 ........................................... 29
   *Okenia zoobotryon* (Smallwood, 1910) .......................... 32
   *Okenia stellata* sp. nov. ......................................... 35
   *Okenia hallucigenia* sp. nov. .................................... 40
   *Okenia hinii* (Baba, 1938) ....................................... 42
   *Okenia pilosa* (Bouchet and Ortea, 1983) ....................... 46
   *Okenia plana* Baba, 1960 ......................................... 49
Discussion ............................................................... 53
Acknowledgements ...................................................... 64
References ............................................................. 64

Abstract

Five new species of the nudibranch genus *Okenia* Menke, 1830 (Goniodorididae) are described from Australian waters and the anatomy of another ten species from Australia and the Indo-West Pacific are described. *Okenia purpurata* sp. nov. and *O. vena* sp. nov. are reported from northern New South Wales where they feed on the bryozoan *Amathia tortuosa* Tenison Woods, 1880. *Okenia mellita* sp. nov. is reported from New South Wales, and a pair of species, *O. hallucigenia* sp. nov.
and *O. stellata* sp. nov. are reported from various locations in northern Australia where they both feed on the bryozoan *Pleurotoichus clathratus* (Harmer, 1902). *Okenia virginiae* Gosliner, 2004 is reported for the first time from Australia as is the Atlantic species *Okenia zoobotryon* (Smallwood, 1910). Anatomical information for *O. barnardi* Baba, 1937, *O. hiroi* (Baba, 1938) and *O. mija* Burn, 1967 is provided for the first time, as is further information on *O. plana* Baba, 1960 and *O. pilosa* (Bouchet and Ortea, 1983) from Australia and Hong Kong. New observations on the bryozoan prey of various species is reported: *O. mija* feeding on *Amathia wilsoni* Kirkpatrick, 1888, *O. zoobotryon* on *Zoobotryon verticillatum* (delle Chiaje, 1828), *O. hiroi* on an unnamed species of *Integripelta* Gordon, Mawatari & Kajihara, 2002, *O. plana* on *Membranipora membranacea* (Linnaeus, 1767), *Jellyella tuberculata* (Bosc, 1802) and *Cryptosula pallasiana* (Moll, 1803). *Okenia japonica* Baba, 1949 and *O. purpureolineata* Gosliner, 2004 are reported feeding on the same unidentified species of *Amathia* Lamouroux, 1812.

**Key words**: Mollusca, Goniodorididae, *Okenia*, new species, Australia, Indo-West Pacific

**Introduction**

In a recent revision of the Indo-West Pacific species of the goniodorid genera *Okenia*, *Sakishimaia*, *Hopkinsiella* and *Hopkinsia*, Gosliner (2004) proposed that they form a monophyletic clade and consequently synonymised all genera with the oldest name, *Okenia*. As Gosliner stated, our understanding of this group is still at a preliminary stage and we still have much to learn about the anatomy of many species of this group world wide. Thirteen species, including six new species are described by Gosliner from the Indo-West Pacific and a further 12 species, including five new species are described in this paper. There are at least six further species from the Indo-West Pacific we know little about, five from the eastern Pacific (Behrens 2004a, pers comm; Lance 1966; Millen *et al*. 1994) and at least 12 from the Atlantic (Cervera *et al*., 1991; Ortea & Espinosa 2000; Schmekel & Portmann 1982), giving us a group of over 40 species. Within this group there is a considerable variation in external shape and radular morphology, but until we know more about the anatomy and biology of individual species, it is difficult to interpret character variation within the group and analyse relationships. For example, the shape of the radular teeth changes very little within the family Goniodoridae, the radula of species of *Trapania* or *Goniodoris*, being indistinguishable from many species of *Okenia*, (see Rudman 1987), and yet in *Okenia* we find many species in which the radula has undergone considerable change in shape from the ‘typical’. Species such as *Okenia nakamotoensis* (Hamatani, 2001), *O. kondoi* (Hamatani, 2001), and *O. stellata* show little similarity to the teeth of ‘typical’ species such as *O. echinata* and *O. virginiae* (see Gosliner 2004; this paper). In some instances, such changes in form can be linked to functional changes. For example, it is not unreasonable to propose that a change in food could lead to alteration in the shape of the teeth. However within the Goniodoridae there are species of *Trapania* feeding on
entoprocts (Kamptozoa), species of Goniodoris feeding on ascidians, and species of Okenia feeding on both soft ctenostome bryozoans and hard calcareous cheilostome bryozoans, all with very similarly shaped teeth. We also have in Okenia two pairs of species with the most modified teeth (O. nakamotensis - O. kondoi and O. stellata – O. hallucigenia). The species within each pair feed on the same bryozoan, but in each case the teeth are quite different in shape and size.

Clearly at this stage of our knowledge, any phylogenetic consideration of the group must be considered to be preliminary. In this paper the anatomy of 15 species is described, including five new species from Australian waters. Further information is provided for five species previously reviewed by Gosliner.

Material and Methods

All species were either seen by me alive or were accompanied by colour photographs of the living animals. Full dissections of the general anatomy, and in particular the alimentary canal and reproductive system, were conducted. The morphology of the radular teeth and the jaw elements was studied and photographed using a scanning electron microscope. Identification of bryozoan prey was made with the assistance of Dr D. P. Gordon, National Institute of Water & Atmospheric Research (NIWA), Wellington, New Zealand. All material used in this study, including samples of the bryozoan prey, is housed in the collections of the Australian Museum, Sydney.

Descriptions

Okenia Menke, 1830

Okenia Leuckart in Bronn, 1826: 329 (nomen nudum)
Idalia Leuckart, 1828 (type species: Idalia elegans Leuckart, 1828 by original designation) not Huernber, 1819 (1820): 149 - Lepidoptera.
Okenia Menke, 1830 (type species: Idalia elegans Leuckart, 1828 by monotypy)
Idaliella Bergh, 1881 (type species: Idalia aspersa Alder & Hancock, 1845 by subsequent designation by Iredale & O'Donoghue, 1923)
Idaliana Norman, 1890 (type species: Idalia elegans Leuckart, 1828 by original designation).
Hopkinsia MacFarland, 1905 (type species: Hopkinsia rosacea MacFarland, 1905, by original designation)
Hopkinsella Baba, 1938 (type species: Hopkinsiella hiroi Baba, 1938, by original designation)
Cargoa Vogel & Schultz, 1970 (type species: Cargoa cupella Vogel & Schultz, 1970, by original designation)
Okenia Menke: Lemche, 1971, 265–266.
Sakishimaia Hamatani, 2001 (type species: Sakishimaia kondoi Hamatani, 2001, by original designation)
In general, species of *Okenia* are soft and elongate animals with a symmetrical arrangement of dorso-lateral papillae around the edge of the body. In many cases the papillae arise from a small ridge, which represents the mantle edge, but in species without such a ridge, papillae arise directly from the body wall. There can also be a number of dorsal papillae, usually arranged in a symmetrical pattern. In some species there is a single papilla in the dorsal midline, anterior to the gills, while in other species there can be up to eight papillae arranged in a characteristic, species-specific pattern. The gills are usually simple or bipinnate and although retractile, do not have the protection of a gill pocket. The internal anatomy is very similar to that described for *Trapania* (see Rudman 1987), although the shape of the radular teeth exhibits much greater interspecific variation than in related genera.

**Okenia echinata** Baba, 1949
(Figures 1, 2A, 9D, 25B, 26C, 28A)

*Okenia echinata* Baba, 1949: 46, 138, Pl.15, fig 53; Rudman 2003a
*Okenia cf. oputia*: Coleman 2001: 52 (misspelling of *opuntia*)

**Material:** Callala Point, Jervis Bay, New South Wales, Australia: 4 October 1975, 3 specimens, 7–9 mm long, found together on rock, AM C103305; 6 October 1975, 1 specimen, 8 mm long, AM C103287. Long Reef, Sydney, New South Wales, Australia, 29 January 1975, 1 specimen, 10 mm long, on short brown seaweed, AM C99401. Red Rock, N of Woolgoolga, New South Wales, Australia, 8 November 1977, 1 specimen, AM C109881. Arrawarra rock platform, Woolgoolga, New South Wales, Australia, 3 December 1990, Photo only, AM C164553.

**Geographic Distribution:** Japan (Baba 1949; Imamoto 2003; Kurihara 2003), eastern Australia (present study).

**External Morphology:** Body low, elongate, with mantle edge forming distinct overlap (Fig. 2A, 26C). Mantle edge with many (up to 14) short, bluntly pointed papillae on each side. In some specimens, anterior-most and posterior-most papillae are replaced by a cluster of two or three individual papillae. Slightly smaller, but similarly shaped papillae, scattered randomly over dorsum. Head separate from foot and best described as a large bilobed oral veil. At least eight bipinnate gills arranged in large arch around anal papilla. Grows to at least 10 mm long alive.

**Colour:** Animals from eastern Australia translucent white with many opaque white spots scattered over dorsum (Fig. 28A). Dorsal surface with dark brown to black pigmentation, some animals appearing a uniform dark brown to black coloration and others patterned with scattered dark brown to black patches, or even regions of dark spotting. Small opaque white spots scattered over regions of dark pigmentation. Anterior edge of head and oral lobes with broken orange line. Mantle papillae translucent white with orange band around mid-region; orange band sometimes extending to tip. Gills translucent white with
some orange markings on outside of rachis. Rhinophores translucent white with brown speckling, often with some orange speckling near tip. Foot with dark brown-black band down posterior midline merging with orange patch at posterior tip. Foot scattered with small white spots. Colour pattern of Japanese specimens compared below.

**Foregut anatomy:** Upper part of buccal bulb of 8 mm long animal (AM C103287) typical of Goniodorididae (see Rudman 1987) with large muscular buccal pump (Fig. 25B). Anterior end of buccal bulb surrounded by band of oral glands. Cuticular lining at anterior end of buccal cavity with some thickening on either side, consisting of raised elongate jaw elements with irregular papillae at tip (Fig. 1D). Radular formula $18(+1) \times 1.1.0.1.1$. Innermost tooth with broad base and long elongate pointed cusp with many (32+) narrow, relatively long, pointed denticles along cutting edge. Towards tip of cusp, denticles gradually shorten in length. Outer teeth much smaller, with broad quadrangular base and large recurved pointed cusp (Fig. 1A–C).

![FIGURE 1. Okenia echinata. Scanning electron micrographs of radula. A, Section across radular ribbon. B, outer teeth, showing single hooked cusp. C, inner teeth showing fine denticulation along cutting edge. D, section of jaws showing irregular band rodlets. Callala Point, Jervis Bay, New South Wales, Australia, 6 October 1975. AM C103287. Scale bar = 10 µm. Photo: G. Avern.](image-url)
Reproductive System: Reproductive opening on right side of body approximately below rhinophores (Fig. 9D). Vaginal duct branches distally, with short duct to large spherical bursa copulatrix and longer duct to slightly smaller elongate exogenous sperm sac.
Thin exogenous sperm duct runs from vaginal duct to fertilisation chamber lying within female gland mass. Exogenous sperm duct joins vaginal duct about halfway along its length. From ovotestis, spermoviduct expands into large ampulla, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into oviduct, opening into fertilisation chamber, and sperm duct, opening into large prostate gland. Long narrow vas deferens runs from prostate gland to penial bulb.

Remarks: This is the first record of this species outside Japan. The original description of *O. echinata* is of a uniformly brown animal with scattered white spots and triangular papillae. Baba likened it to a small holothurian. This colour pattern is rather different from that described here for animals from eastern Australia, but recent records from Japan (Imamoto 2003; Kurihara 2003) suggest this species is very variable in colour with animals ranging in colour from pale brown, as originally described by Baba, to animals with a bright red background colour or with a dark brown background colour and bright red papillae. Baba’s description of the jaws and radular morphology fit those described here for Australian material. The general shape, large bilobed head and many conical dorsal papillae all characterise this species externally. *Okenia opuntia* Baba, 1960 and *O. babai* Hamatani, 1961, both reported from Japan, are similar in general body shape, but not enough is known of their colour and anatomy to make a proper comparison. Coleman (2001: 52) has a photo of this animal from New South Wales, Australia, which he identified as ‘*Okenia cf. opuntia’.*

**Okenia purpurata** sp. nov.  
(Figures 2B, 3, 4B, 26D, 28D)

*Okenia* sp. Coleman, 2001: 52 (‘Carol’s Okenia’)

**Material:** East side of Split Solitary Is, Coffs Harbour, New South Wales, Australia, 22 m, on bryozoan, *Amathia tortuosa* Tenison Woods, 1880, 1 December 1990, 2 specimens: 7 mm long, AM C164523 [Paratype], 9 mm long, AM C434827 [Holotype]. North side of Split Solitary Is, Coffs Harbour, New South Wales, Australia, 20 m, on bryozoan, *A. tortuosa*, 20 March 1988, 11 mm long, AM C155753 [Paratype], Pig Is, Coffs Harbour, New South Wales, Australia, 20–22 m, on bryozoan, *A. tortuosa*, 8 December 1990, 3 & 6 mm long, AM C164605 [Paratypes].

**Etymology:** The name of this species is based on a Latin word for purple, a reference to its colour.

**Geographic Distribution:** Known only from northern New South Wales, eastern Australia (present study).

**External Morphology:** Body elongate with distinct mantle edge bearing seven cerata-like papillae on each side (Fig. 2B, 26D). Papillae ranging in length from relatively short anterior pair to four long, cylindrical posterior pairs, tapering to rounded tip. Papillae usu-
ally longer than width of body. Single mediodorsal papilla present, about midway between head and gills; three or four papillae in transverse line just in front of gills; small median papilla sometimes present just behind the gills. Four or five long, simple gills in arch around anal papilla in postero-dorsal midline. Head with pair of rounded, flattened oral tentacles. Head distinct from foot. Wide anterior end of foot rounded, with somewhat extended, anterior foot corners. Animal at least 11 mm long alive.

**FIGURE 3.** *Okenia purpurata* sp. nov. Scanning electron micrographs of radula. A, Section of right side of radula. Note faint denticulation restricted to the basal region of each cusp. Also note large pointed secondary spine on the outer corner of the inner teeth and the large bicuspid outer teeth. B, showing shape of inner lateral tooth. In fresh material, the prominent pointed spine on the outer edge of the tooth points upwards. The recurved shape in this photo is a result of some softening of the tooth occurring during preparation for SEM scanning. C, Magnified view of base of cusp of inner tooth to show the fine denticulation found only in this region. Pig Is., Coffs Harbour, New South Wales, Australia, 8 December 1990, AM C164605. A, B, Scale bar = 10 µm. C, Scale bar = 1 µm. Photo: A.C. Miller.

**Colour:** Background colour pinkish purple, deepening on rhinophores, gills and posterior tip of foot to deep reddish purple (Fig 28D). Rounded oral tentacles uniform purple.
Lateral papillae around mantle edge creamy white or yellow, except for anterior pair which are a watery purple with creamy white or yellow tip. Head, foot and sides of body purple, except for broad translucent cream band at edge of the foot.

**Foregut anatomy:** Whole of anterior end of buccal bulb lined with cuticle, but no distinct thickened regions or regions with cuticular rodlets. Roof of buccal bulb with relatively large buccal pump. Radular formula of two specimens: 22(+1) x 1.1.0.1.1 and 24 x 1.1.0.1.1. Innermost tooth with broad base and long elongate pointed cusp with very small remnant basal denticles; large pointed spine at upper inside corner of base of tooth (Fig. 3). Small outer teeth with broad quadrangular base and two very large, slightly recurved, pointed cusps.

**Reproductive system:** Reproductive opening on right side of body approximately below level of rhinophores (Fig. 4B). Vaginal duct elongate, leading back to spherical bursa copulatrix. Exogenous sperm duct narrow, running from junction of vaginal duct and bursa copulatrix to fertilisation chamber within female gland mass. Exogenous sperm sac large, elongate, opening about halfway along exogenous sperm duct. From ovotestis, spermoviduct expands into ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts, the oviduct, opening into fertilisation chamber, and sperm duct, broadening into long recurved 'vas deferens' which in dissection is impossible to separate into prostate gland, ejaculatory duct, and penial bulb.

**Remarks:** This species has a very distinctive colour pattern. On two occasions it was found with *Okenia vena* sp. nov. on the same bryozoan colony, and the two species are very similar in external shape and in the anatomy of the reproductive system. However the colour pattern of the two species is quite different with *O. purpurata* having a purple body and white papillae, while *O. vena* is white all over, with a pattern of brown veins over the dorsal surface. I have discussed the two species in more detail under the description of *O. vena*. *Okenia purpurata* can be characterised by its colour, the serial arrangement of the sperm sacs in the reproductive system, and the shape and denticulation of the radular teeth. It is one of a group of species in which the mantle is outlined by a ridge which extends out horizontally from the upper edge of the dorsum. In this species it runs all around the body, except in the posterior midline. The lateral papillae arise from this mantle ridge. The head, with its prominent oral tentacles, is distinct, extending out anteriorly in the space between the foot and the mantle. As well as the lateral papillae, there are a few large dorsal papillae forming a distinctive pattern. Two similarly shaped species with purple coloration have recently been described (Gosliner 2004) but both differ in many aspects of the colour pattern and internal anatomy. For example, *O. purpureolineata* Gosliner, 2004, is a uniform translucent purple with a pattern of dark purple sinuous lines on the mantle and *O. liklik* Gosliner, 2004 has orange on the mantle papillae and often a brown tip. Both also differ from *O. purpurata* in lacking both a secondary basal cusp on the inner radular tooth and a pair of large pointed cusps on the outer tooth.
**Diagnosis:** *Okenia purpurata* can be characterised by its colour, the serial arrangement of the sperm sacs in the reproductive system, and the shape and denticulation of the radular teeth. It differs in colour from two other purple species in having white papillae and lacking the sinuous dark lines of *O. purpureolineata* and the orange markings of *O. liklik*.

**Biology:** Found on the ctenostome bryozoan *Amathia tortuosa* Tenison Woods, 1880 (see also MacGillivray, 1895), sometimes with *O. vena*.

**Okenia vena** sp. nov.
(Figures 2C, 4A, 5, 26B, 28E)

**Material:** Pig Is, Coffs Harbour, New South Wales, Australia, 20–22 m, on bryozoan, *Amathia tortuosa*, 9 December 1990, 8 mm long, AM C164620 [Paratype], 9 mm long, AM C434826 [Holotype]. Pig Is, Coffs Harbour, New South Wales, Australia, 20–22 m, on bryozoan, *Amathia tortuosa*, 8 December 1990, 5 specimens, 7–9 mm long alive, AM C164606 [Paratypes]. East side of Split Solitary Is, Coffs Harbour, New South Wales, Australia, 22 m, on bryozoan, *Amathia tortuosa*, 1 December 1990, 10 mm long, AM C164524 [Paratype].

**Etymology:** The species is named from the brown vein-like pattern on the dorsum. The word *vena* is from the Latin for vein.

**Geographic Distribution:** Known only from northern New South Wales, eastern Australia (present study).

**External Morphology:** Body elongate. Mantle edge distinct, bearing seven or eight cerata-like papillae on each side (Fig. 2C, 26B). Papillae cylindrical, tapering to rounded tip; all of similar length, approximately the width of mantle, but most posterior pair sometimes longer. Single mediodorsal papilla about midway between head and gills; three or four papillae arranged in transverse line just in front of gills. One, sometimes two, papilla in dorsal mid-line, just behind gills. Up to seven gills arranged in arch around anal papilla in postero-dorsal midline. Head with pair of broad, flattened oral tentacles which taper to distinct point. Head distinct from foot. Anterior end of foot approximately twice width of rest of foot; with rounded foot corners. Animal at least 10 mm long alive.

**Colour:** Whole of body translucent white, with irregular pattern of dark brown lines arranged in longitudinal and diagonal network on dorsum and sides of body (Fig. 28E). Some specimens with some brown ‘smudging’ on papillae, and in others, translucent white gills can have inner edge of rachis lined with brown. Rhinophores orange-brown.

**Foregut anatomy:** Whole of anterior end of buccal bulb lined with cuticle, but no distinct thickened regions or regions with cuticular rodlets. Buccal pump relatively large. Radular formula of two specimens: \(20(\pm 2) \times 1.1.0.1.1\) and \(21 \times 1.1.0.1.1\) (Fig. 5). Innermost tooth with broad base and long elongate pointed cusp. One specimen with traces of up to 15 rounded denticles along the cutting edge of some teeth, while in second specimen
no sign of denticles present. As in *O. purpurata*, base of inner tooth with large pointed spine on dorso-lateral corner. Outer teeth much smaller, with broad quadrangular base bearing two very large, slightly recurved, pointed cusps.

**Reproductive system:** Reproductive opening on right side of body approximately below rhinophores (Fig. 4A). Vaginal duct elongate, leading back to large spherical bursa copulatrix. Exogenous sperm duct narrow, running from junction of vaginal duct and bursa copulatrix to fertilisation chamber within female gland mass. Exogenous sperm sac elongate, opening about halfway along exogenous sperm duct. Ampullar region of spermoviduct, running from ovotestis, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into oviduct, opening into fertilisation chamber, and sperm duct, opening into recurved prostate gland. Prostate gland opens directly into tapering penial sac.

**Remarks:** This species has a very distinctive colour pattern. On two occasions it was found with *O. purpurata*, on the same bryozoan colony, and the two species are very similar in external shape and in the anatomy of the reproductive system. However the colour pattern of the two species is quite different with *O. purpurata* having a purple body and white papillae, while *O. vena* is white all over, with a pattern of brown veins over the dorsal surface. The outer radular teeth of both species have an unusually large pair of pointed cusps, and both have a large secondary spine on the inner edge of the base of the first lateral tooth. However in *O. purpurata* the cusp of the innermost radular teeth has small denticles only at the base of the cusp, while in *O. vena*, there are signs of denticulation along the whole length of the cusp. *Okenia purpureolineata* Gosliner, 2004 has similarities in shape and colour, but in that species the network of lines on the dorsum are purple, the background colour and the papillae are purplish, there is a different arrangement of dorsal papillae, and the shape of the radular teeth are quite different, with prominent denticles on the innermost teeth and no distinct cusps on the outer teeth.

*Okenia vena* is one of a group of species in which the mantle is outlined by a ridge extending out horizontally from the upper edge of the dorsum. In this species it runs all around the body, except in the posterior midline. The lateral papillae arise from this mantle ridge. The head, with its prominent oral tentacles, is distinct, extending out anteriorly in the space between the foot and the mantle. As well as the lateral papillae, there are a few large dorsal papillae forming a distinctive pattern.

**Diagnosis:** *Okenia vena* can be characterised by its colour, the serial arrangement of the sperm sacs in the reproductive system, and the shape and denticulation of the radular teeth. The only similarly coloured species, *O. purpureolineata*, differs in its purple body colour and dark purple lines, and in the shape of the radular teeth, with prominent denticles on the innermost teeth and no distinct cusps on the outer teeth.

**Biology:** Found on the ctenostome bryozoan *Amathia tortuosa* Tenison Woods, 1880, sometimes with *O. purpurata*. 
FIGURE 5. Okenia vena sp. nov. Scanning electron micrographs of radula. A, Section showing left half of radular ribbon from the inside. Note large inner teeth show no sign of denticulation in this specimen. B, Whole radular ribbon. C, Section of right side of radular ribbon of a second specimen showing faint ridging along the edge of the inner teeth which represents remnant denticulation. Note also the large pointed secondary spine on the outer corner of the inner teeth and the large bicuspid outer teeth. D, magnification of part of inner teeth to show traces of denticulation along the edge of the tooth. Pig Is., Coffs Harbour, New South Wales, Australia, 8 December 1990, AM C164606. Scale bar = 10 μm. Photo: A.C. Miller.
**Okenia virginiae Gosliner, 2004**
(Figures 6, 7A, 9C, 26E, 28B,C)

*Okenia* sp. Gosliner, 1987: 92, fig. 159

*Okenia barnardi*: Debelius, 1996: 196, upper photo. NOT *O. barnardi* Baba, 1937

*Okenia* sp. Coleman, 2001: 52 (‘Arabian Okenia’)


**Material:** Strand, Townsville, Queensland, Australia, 2 specimens, 9, 11 mm long preserved, under rock at low tide, 23 April 1975, AM C99445. Cape Pallarenda, Townsville, Queensland, Australia, 2 specimens, 4, 12 mm long preserved, 22 May 1978, AM C112341.

**Geographic Distribution:** Durban, South Africa (Gosliner 1987, 2004), Oman, Arabian Gulf (Debelius 1996), Philippines (Coleman 2001), Queensland, eastern Australia (present study).

External Morphology: Body elongately ovate (Fig 7A, 26E) and relatively high; mantle edge indistinct, outlined by eight or nine large lateral papillae along each side, all of similar size, about twice width of body. Two most posterior papillae on each side usually arranged one above the other on common base. Papillae cylindrical with tapering...
pointed tip; highly motile, held horizontally, vertically or folded over body. Single mediodorsal papilla, similar in shape and length to lateral papilla, just in front of gills. Head partially merged with anterior foot but sole separated from head and mouth by distinct transverse groove. Dorsally, head region distinctly raised above foot and bears pair of tentacular oral tentacles. Gills long and simple, arranged in three clusters; anterior cluster of two gills with common base in midline, just in front of anal papillae; two posterior clusters, one on each side of anus, with two or three gills with common base. Rhinophores elongate, about half length of dorsal papillae, bearing numerous lamellae on upper half.

**Colour:** Background colour translucent white. Dorsum between lateral papillae, dark brown with network of longitudinal and diagonal narrow opaque white lines (Figs 28B, C). Lateral papillae translucent clear in basal region with upper half or third of most papillae being dark brown. Anterior four papillae with central dark brown band and white tip. Rhinophores similarly coloured, with translucent clear stalk, and dark brown, lamellate club. In some animals, thin opaque white lines from dorsum continue up rhinophore stalk.

**Foregut anatomy:** Anterior end of buccal cavity with cuticular lining but no sign of individual rodlets. Buccal pump on roof of buccal bulb, relatively large, similar to that of *O. mellita* (Fig. 25). Radular formula of animal, 11 mm long preserved, (AM C99445) (Fig. 6), is 26(+1) x 1.1.0.1.1. Innermost tooth with broad base and long elongate pointed cusp; many (40) narrow, relatively long, pointed denticles along the cutting edge; denticles at each end of cusp shorter. Outer teeth, much smaller than inner teeth, with broad quadrangular base and large recurved bluntly pointed cusp.

**Reproductive system:** Reproductive opening on right side of body approximately level with rhinophores (Fig. 9C). Vaginal duct leads back to large spherical bursa copulatrix. Exogenous sperm sac, small, spherical, connected to bursa copulatrix by short duct opening into bursa copulatrix alongside vaginal duct opening. Exogenous sperm duct, running from exogenous sperm sac to the fertilisation chamber within female gland mass, also opens nearby. From ovotestis, spermoviduct expands into large ampulla region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts; the oviduct, opening into the fertilisation chamber, and sperm duct, opening into prostate gland and from there to penial bulb.

**Remarks:** The animals described here from Queensland show some variation in colour pattern. As described above, the dorsum between the lateral papillae and down onto the midline of the posterior foot, is dark brown with a network of longitudinal and diagonal narrow opaque white lines. In some specimens (AM C112341) the white lines form a close reticulation, while in other specimens (AM C99445) there is a single white line around the dorsum, just outside the gills and rhinophores, and a double line down the midline between the gills and the rhinophores, with no diagonal or lateral lines.

These specimens have similarities to two recently described species, *O. virginiae* Gosliner, 2004 and *O. kendi* Gosliner, 2004. In colour, and most features of the anatomy, the Queensland specimens agree with his description of *O. virginiae*. The one point of differ-
ence is that the exogenous sperm duct (uterine duct) of that species is reported to run from near the base of the vagina to the fertilisation chamber within the female gland mass. In my specimens this duct runs from near the base of the bursa copulatrix. Gosliner notes that the position of this duct in his South African specimen is unique in the genus. Until further specimens are available for study it is not possible to say whether this is a variable character in *O. virginiae*. In radular morphology and reproductive anatomy the Queensland specimens are identical to *O. kendi*, which was reported from the Philippines. That species differs in colour details, with most of each papillae being dark brown and the dark brown dorsum lacking white lines.

*Okenia virginiae* was described from a single specimen from Durban, South Africa. There are other records of similar animals with a white reticulate pattern from Oman, Arabian Gulf, (Debelius 1996; Coleman 2001) and the records reported here from Queensland, show this species has a wide Indo-West Pacific distribution. As illustrated here (Fig 28B, C) the white lines are variable in this species, which may indicate that *O. kendi* and *O. virginiae* are colour extremes of a single species, the former representing an unlined form and the latter, a lined form.

**Biology:** We have no information on the natural history of this species.

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*Okenia mellita* sp. nov.
(Figures 7B, 8, 9B, 28F)

*Okenia* sp. Coleman, 1989: 17; Coleman 2001: 52 (‘black-tipped Okenia’)

**Material:** Split Solitary Is, Coffs Harbour, New South Wales, Australia, 15 February 1993, 18 mm long, AM C172896 [**Holotype**]. Montague Is, sthn New South Wales, Australia, 19 mm long preserved, AM C108509 [**Paratype**]. Montague Is, sthn New South Wales, Australia, 14 January 1978, 30 m, 1 specimen, 12 mm long preserved, AM C433973 [**Paratype**]. Fish Rock Cave, South West Rocks, nthn New South Wales, Australia, Val Taylor, Photo only.

**Etymology:** Latin for honeyed, a reference to the golden orange yellow colour of the animal.

**Geographic Distribution:** Known only from eastern Australian waters (Coleman, 1989; Coleman, 2001; present study).

**External Morphology:** Body elongately ovate (Fig 7B), relatively high and lacking distinct mantle edge, although this is indicated by five large lateral papillae along each side, with middle three papillae on each side being the longest, about twice width of body. Papillae cylindrical and gradually broaden in diameter, before tapering to pointed tip. Papillae quite motile, held horizontally, vertically or folded over body. Single mediadorsal papilla just anterior to gills, similar in shape and length to lateral papilla. Head merges with anterior foot and oral tentacles could be mistaken for tentacular anterior foot corners.
Gills long, simple, and arranged in three clusters; anterior cluster of two gills with common base in midline, just anterior to anal papillae; two posterior clusters, each of two or three gills with common base, on each side of anus. Rhinophores similar in shape and length to dorsal papillae; upper half of each rhinophore elongate and bearing lamellae.

**FIGURE 8.** *Okenia mellita* sp. nov. Scanning electron micrographs of radula. A, Section of whole radula. B, SEM of chitinised lining of the anterior buccal bulb folded out to show strong development of rodlets. C, Inner left radular teeth to show fine denticulation along cutting edge of tooth. D, Magnified section of jaw rodlets. Montague Is., New South Wales, Australia, 28 December 1977, ca.23m. AM C108509. Scale bar = 10 µm. Photo: G. Avern.
**Colour:** Background colour of body orange (Fig. 28F); mantle papillae and oral tentacles tipped with black; black spot on posterior tip of foot. Mantle with opaque white line running down dorsal midline from between rhinophores to base of mediodorsal papilla, just in front of gills. White line extends approximately halfway up anterior face of mediodorsal papilla. Lateral white line runs along each side and around anterior end of body, just below lateral papilla, with a branch of this line extending up ventral, or outer, face of each papilla to just below black tip. Rhinophore with translucent orange stalk and black club; white line runs up posterior midline of rhinophore, partly on stalk, partly on club. Gills translucent orange with opaque white edging.

**Foregut anatomy:** Anterior end of buccal cavity lined with cuticle with large regions on each side bearing raised elongate rodlets, tipped with irregular papillae (Fig. 8). Buccal pump on roof of buccal bulb relatively large (Fig. 25). Radular formula 30(+1) x 1.1.0.1.1. Innermost tooth with broad base and long elongate pointed cusp bearing many (30+) narrow, relatively small, pointed denticles along cutting edge; denticles at each end of row much smaller than rest. Outer teeth much smaller, with broad quadrangular base, and small recurved cusp [folded under in accompanying SEM photo]. In general, inner teeth and jaw elements appear strongly chitinised.

**Reproductive system:** Reproductive opening on right side of body, below and slightly posterior to rhinophores (Fig 9B). Vaginal duct leads back to large spherical bursa copulatrix. Exogenous sperm sac, small, spherical, with short duct opening into bursa copulatrix alongside vaginal duct opening. Also opening nearby is narrow exogenous sperm duct which runs to fertilisation chamber within female gland mass. From ovotestis, the spermoviduct expands into large ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into oviduct, which opens into the fertilisation chamber, and the sperm duct, which broadens into long recurved duct running to reproductive opening. In dissection I am unable to distinguish a prostate gland region or a muscular ejaculatory duct region.

**Remarks:** The orange colour pattern of *Okenia mellita*, with black-tipped papillae and white lines, is quite unique in the genus, and easily differentiates it from all other species. It is one of group of larger species in which there is no distinct ridge to differentiate the edge of the mantle, although this is indicated by the insertion points of the lateral papillae. The papillae are relatively large and mobile. Dorsal papillae are absent except for a single median one just in front of the gills. The cuticle lining the buccal bulb is well developed, with large recurved rodlets forming a complete band around the mouth. The heavy development of the buccal armature, both the radular teeth and jaw elements, suggest this species feeds on a bryozoan with a calcified skeleton.

**Diagnosis:** *Okenia mellita* can be distinguished by its unique colour pattern of orange, with white lines and black-tipped papillae, the well-developed jaw elements and the shape and denticulation of the radular teeth.

**Biology:** We have no information on the natural history of this species.

*Okenia barnardi* Baba, 1937
(Figures 7C, 9A, 10, 26F, 29A)

*Okenia barnardi* Baba, 1937: 295–296, fig. 3, pl. 2, fig. 6; Abe 1964: 43, pl. 18, fig. 63; Rudman & Darvell 1990: 39, Pl. 1H; Rudman & Darvell 2002b
Material: 2 specimens, 8 April 1983, Site 5.51, Heung Lo Po, Tolo Channel (Gruff Head), 5–10 m, Hong Kong, China, AM C139081. 2 specimens, 10 April 1983, Site 4.57, Bate Head, Mirs Bay, 5–10 m, Hong Kong, China, AM C139082. 14 April 1983, Site 2.66, Round Is. (W), Mirs Bay, 3–6 m, Hong Kong, China, AM C139083. 2 specimens, 19 April 1983, Site 4.8, Breaker Reef, Mirs Bay, 5–16 m, Hong Kong, China, AM C139084. 4 specimens, 16 March 1986, Site 11.87, South Ninepin (SE), 19 m, Hong Kong, China, AM C149770.

Geographic Distribution: Japan (Baba 1937, Abe 1964, Sato 2003), Hong Kong (Rudman & Darvell 1990, 2002b; Picton 2002). A supposed record of this species from the Arabian Sea (Debelius 1996: 196) is a misidentification for O. virginiae.

External Morphology: Body elongately ovate (Fig 7C, 26F); relatively high and lacking distinct mantle edge although this is marked by eight or nine large lateral papillae along each side, all of similar length, about equal to width of the body. Two most posterior papillae on each side are usually arranged one above the other on a common base. Papillae cylindrical, with tapering pointed tip; held horizontally, vertically or folded over body. Single mediiodorsal papilla, similar in shape and length to lateral papilla, just anterior to gills. Head partially merged with anterior foot but distinct ventral transverse groove separates sole from head and mouth. Dorsally, head region distinctly raised above foot and bearing pair of tentacular oral tentacles. Gills long and simple and arranged in three clusters; anterior cluster of one or sometimes two gills with common base in midline, just in front of anal papillae; two posterior clusters of between two and four gills with common base, one on either side of anus. Rhinophores elongate, similar in length to dorsal papillae, bearing numerous lamellae on upper half.

Colour: Body translucent white; dorsum dark brown, with opaque white spots of irregular size and shape, except for area in midline, between gills and rhinophores, which is a much lighter translucent brown, and has fewer and smaller opaque white spots (Fig. 29A). Posterodorsal part of foot with brownish tinge and broad, opaque, white median line running to posterior tip of foot. Rest of foot translucent white with scattered opaque white spots. Mantle papillae translucent whitish, with upper half of anterior four opaque white. In other papillae, white cap replaced by opaque white line running up outer edge. Posterior side of rhinophore stalk dark brown with white spots, rest of rhinophore translucent brown with dark brown tip. Gills translucent brown with dark brown line along outer edge.

Foregut anatomy: Anterior end of the buccal cavity with cuticular lining, but no sign of areas of thickening or jaw rodlets. Buccal bulb similar to that of O. mellita (Fig. 25) with relatively large buccal pump. Radular formula 20 x 1.1.0.1.1 (Fig. 10). Innermost tooth with broad base extending up into rounded but distinct dorso-lateral corner; cusp typically elongate and pointed with approximately 20 small, pointed denticles along cutting edge. Smaller outer teeth with broad triangular shape.

Reproductive system: Reproductive opening on right side of body below and just behind position of rhinophores (Fig. 9A). Vaginal duct broad, leading back to large termi-
nal spherical bursa copulatrix. Exogenous sperm sac elongate, slightly smaller than bursa, opens into vaginal duct, just before its junction with bursa copulatrix. Exogenous sperm duct narrow, joins vagina about halfway along its length and runs to fertilisation chamber within female gland mass. From ovotestis, spermoviduct expands into large ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts; oviduct opening into the fertilisation chamber; sperm duct, opening into large recurved prostate gland. From prostate gland, narrow vas deferens runs down to penial bulb.

**FIGURE 10.** *Okenia barnardi*. Scanning electron micrographs of radula. A, Section across radular ribbon. B, Showing fine denticles near tip of inner teeth, and bluntly pointed tip of outer tooth. Hong Kong, South Ninepin (SE), 19m, 16 March 1986, 19m, AM C149770. Scale bar = 10 µm. Photo: G. Avern.

**Remarks:** *Okenia barnardi* is known from very few records from Japan and China (Rudman & Darvell 1990, 2002b). It has similarities in external shape and reproductive anatomy to *O. virginiae* and *O. mellita*, and like both those species has large, strongly developed inner radular teeth. In both *O. barnardi* and *O. virginiae* the posterior pair of lateral papillae on each side arise from a single base. Externally this species can be characterized by its colour pattern, in particular, the dark brown band around the dorsum with scattered opaque white spots, the relatively numerous recurved lateral papillae, and the single mediodorsal papilla.

**Biology:** We have no information on the natural history of this species.
**Okenia pellucida** Burn, 1967

(Figures 4E, 11, 12A, 29B)


*Okenia* sp. Morton & Miller, 1968: 412, fig 153A.

**Material:** Neutral Bay, Port Jackson, Sydney, New South Wales, Australia, 20 April 1966, on *Zoobotryon verticillatum* (delle Chiaje, 1828), 3 specimens, AM C63092 [Holotype], AM C63093 [Paratypes]. Angourie Pool, nthn New South Wales, Australia: 1 specimen, 12 mm long preserved, 23 February 1975, AM C99406; 3 specimens, 8, 12, 20 mm long, on *Zoobotryon verticillatum*, 11 March 1982, AM C132964.


**Geographic Distribution:** New Zealand (Morton & Miller, 1968), Australia (NSW, Qld, WA) (Willan & Coleman 1984; Cranfield et al. 1998); Hawaii (Gosliner, Johnson & Bertsch 1986); Japan (Kurihara 1999), Palmyra Atoll, Oceania (Gosliner 2004); Malaysia (Gosliner 2004); United Arab Emirates (Behrens 2001).

**External Morphology:** Animal elongate with up to 11 or 12 lateral papillae along each side of mantle edge, which forms distinct ridge around edge of notum (Fig. 12A). Five or six dorsal papillae present, irregularly placed with no consistent pattern in different animals. Head quite separate from foot; with large triangular oral tentacles. Rhinophores approximately twice length of mantle papillae; club quite slender, tapering to rounded tip; rhinophore lamellae very reduced in size and number. Gills bipinnate, forming circle, or incomplete arch around anal papilla. Anterior gills quite large; others gradually decreasing in size posteriorly.
**Colour:** Body translucent white with network pattern of thin dark brown lines covering all parts of dorsum, foot, head and rhinophore stalk (Fig. 29B). Brown lines sometimes extend to tips of mantle papillae. Brownish band often present around bottom half of rhinophore club. Gill rachis with thin brown line.

Foregut anatomy: Anterior end of buccal cavity with cuticular lining, but no sign of individual rodlets. Buccal pump relatively large. Radular formula 26(+1) x 1.1.0.1.1 (Fig. 11). Innermost tooth with broad base and long elongate blade divided into two pointed cusps; inner cusp with approximately 12 long, pointed denticles along inner edge. Outer teeth small, with broad quadrangular base and large recurved pointed cusp.

Reproductive system: Reproductive opening on right side of body, approximately below level of rhinophores (Fig. 4E). Vaginal duct elongate, leading back to elongate bursa copulatrix. Exogenous sperm duct narrow, running from junction of vaginal duct and bursa copulatrix to fertilisation chamber within female gland mass. Exogenous sperm sac elongate, opening about halfway along exogenous sperm duct. From oovotestis, spermoviduct expands into ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts, the oviduct opening into fertilisation chamber, and long coiled and folded ‘vas deferens’ which in dissection is impossible to separate into prostate gland and ejaculatory duct. Muscular penial bulb present.

Remarks: The anatomy of this species has recently been described in detail (Gosliner 2004) but considering the widespread distribution of this species it is valuable to re-examine specimens from near the type locality. The anatomy of the specimens described here, and by Gosliner, agree with Burn’s original description (Burn 1967) in all essential features. One point of interest is the shape of the inner radular teeth with a bicuspid tip. This is unusual within the genus but also occurs in *O. purpureolineata* Gosliner, 2004. I have described it elsewhere in this paper from *O. hiroi* (Fig. 21D), and the deeply split tip of *O. kondoi* and *O. hallucigenia* is probably homologous. Since its original discovery in Sydney Harbour 40 years ago, this species has now been reported from much of the Indo-West Pacific. Its association with the fouling bryozoan *Zoobotryon verticillatum*, would suggest that its wide distribution has probably been aided by shipping.


**Okenia japonica** Baba, 1949
(Figure 13)

*Okenia japonica* Baba, 1949: 45, 138, fig. 45, pl. 15, fig. 52; Abe, 1964: 42, pl. 17, fig. 61; Rudman & Darvell 1990: 39–40, pl. 2A; Rudman & Darvell 2001b; Gosliner 2004: 131–133, figs. 6,7.

**Material:** Hong Kong, China: 1 specimen, 21 March 1982, Site 1.20, Village Rock, Double Haven, 10 m, AM C133749. 3 specimens, 14 April 1983, Site 2.66, Round Is. (W), Mirs Bay, 3–6 m, AM C139013. 1 specimen, 11 April 1983, Site 4.60, Kong Chau (NW), Mirs Bay, 5–10 m, AM C139014. 1 specimen, 11 February 1984, Site 10.98, Kiu Tau (S), Kiu Tsui Chan, Port Shelter, 4 m, AM C141478. 2 specimens, 5 April 1986, Site 2.67, Kai Kung Tau, Kat 0 Chau, Mirs Bay, 6 m, AM C150245. 2 specimens, 20 April 1986, Site 2.173, Kat 0 Chau (E of E tip), Mirs Bay, 2 m, AM C150246.
**Geographic Distribution:** Japan – main islands (Baba 1949; Sato 2003b; Sato 2003c); Okinawa (Gosliner 2004); China (Hong Kong – Rudman & Darvell 1990; Rudman & Darvell 2001b).

**External Morphology:** Body elongate with distinct, if narrow, mantle skirt with at least seven short, round-tipped, triangular papillae (Fig. 13B) on each side. Anteriormost and posteriormost lateral papilla more tentacular in shape, approximately twice length of other papillae. Single dorsal papilla in mid-line, half way between gills and rhinophores. Rhinophores relatively long and tapering to rounded tip; club occupying upper half, with approximately ten lamellae. Gills, six, in posterior dorsal midline, arranged in three groups, each group having common base; anterior group in dorsal midline just in front of anus; two lateral groups, one on each side of anus. Each group usually with two gills, but sometimes one or three are present. Head distinctly separate from mantle and foot; anterior edge with median notch. Oral tentacles lobe-like, triangular.

**Colour:** Animal translucent white with brownish dusting all over mantle and posterior foot; opaque white dusting on parts of gills and mantle papillae. Rhinophores with some brownish dusting, sometimes giving a brownish edging to rhinophore lamellae.

**Foregut anatomy:** Anterior end of buccal bulb lined with cuticle, but no distinct thickened regions or regions with cuticular roddlets. Radular formula 23(+1) x 1.1.0.1.1 (Fig. 13A). Innermost tooth with broad base and long elongate pointed cusp with up to 20 large, pointed denticles along cutting edge; denticles increasing in size towards tip of cusp. Outer tooth much smaller, with broad quadrangular base and two large recurved pointed cusps (AM C139013).
Remarks: The anatomy of this small elongate species of *Okenia* has recently been described in detail (Gosliner 2004). The external shape and radular morphology of Hong Kong specimens described here match Gosliner’s description of specimens from Okinawa.

Biology: Gosliner (2004) notes that specimens from Okinawa were reported by the collector (R.F. Bolland) to live on erect arborescent bryozoans. Dr Bolland has kindly sent photographs of the bryozoan, which appears to be a species of the ctenostome bryozoan genus *Amathia* Lamouroux, 1812, and from the spiral arrangement of the zooid groups along the erect stalks of the colony, it is not unlike *A. tortuosa*. *Okenia purpureolineata* Gosliner, 2004 is also found on this bryozoan (Bolland — pers. comm.). As reported elsewhere in this paper, both *O. vena*, and *O. purpurata* feed on *A. tortuosa*.

**Okenia mija** Burn, 1967  
(Figures 4C, 12B, 14, 29C)

*Okenia mija* Burn, 1967: 55–56, text-figs 4, 5; Rudman, 1999a  
*Okenia* sp. Coleman, 2001: 52 (“Sydney Okenia”)


Geographic Distribution: South-eastern Australia (Tasmania, Victoria, New South Wales) (Burn 1967; Coleman 2001; present study), and New Zealand (Rudman 1999a).

External Morphology: Animal small, elongate with distinct mantle edge, bearing series of lateral papillae; usually seven on each side; anteriormost pair in front of rhinophores. Papillae spindle-shaped when fully extended, being slightly wider in mid-region and tapering distally to rounded point (Fig. 12B). Papillae shape somewhat variable within individuals, stressed animals sometimes having cylindrical papillae with slightly swollen tip. Dorsal papillae, of varying size, also present; up to four in row down midline between gills and rhinophores, often flanked by row of papilla on each side. Usually a single papilla in dorsal midline on ridge between gills and posterior tip of foot. Sometimes an irregular row of up to six papillae present on each side of the body, midway between mantle edge and edge of foot. Head distinctly separate from mantle and foot; with pair of oral tentacles similar in length to lateral papillae, but more tentacular in shape. Rhinophores about twice length of lateral papillae, with up to six characteristic cup-shaped structures, each with notch in posterior mid-line. Gills bipinnate, six or seven, arranged in arch around anus; anterior three gills large and tripinnate; others smaller, bipinnate.

Colour: Body translucent clear, with faint brownish tinge from underlying visceral mass and fine dusting of brown over skin (Fig. 29C). Small opaque white patches also present scattered over body and particularly in band around mantle edge, creating whitish border in some specimens. Irregular line of white patches present down dorsal midline from just behind gills to posterior tip of foot. Dorsum and sides of body with scattered yellowish brown, irregularly shaped patches, each with dark brownish black spot, often but not always, in centre of patch. Lateral papillae appear white, especially at tip, from concentration of white patches; rhinophores translucent clear, except for white patches on cup-shaped lamellae. Gills transparent, except for scattered white and brown patches.
**Foregut anatomy:** Anterior end of buccal cavity with cuticular lining, but no sign of individual jaw elements. Radular formulae of two animals, 22 x 1.1.0.1.1 (AM C151776), and 18 x 1.1.0.1.1 (AM C112203) (Fig. 14). Innermost tooth with broad base and long elongate pointed cusp bearing many (12–14) broad, pointed denticles along cutting edge; denticles at either end of row shorter than those in centre. Outer teeth smaller, with broad, quadrangular base and large recurved bicuspid tip; triangular projection present on outer edge, below bicuspid tip.

**Reproductive system:** Reproductive opening on right side of body, below and just behind rhinophores (Fig. 4C). Vaginal duct, short, broad, leading back to large spherical bursa copulatrix. Exogenous sperm duct narrow, running from junction of vaginal duct and bursa copulatrix to fertilisation chamber within female gland mass. Exogenous sperm sac small, spherical, opening about halfway along exogenous sperm duct. From ovotestis, the spermoviduct expands into large ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts; the oviduct opening into the fertilisation chamber; the sperm duct opening into large recurved prostate gland. Long, narrow, very coiled, muscular duct runs from prostate gland down to penial bulb.

**Remarks:** *Okenia mija* is one of a number of small brownish species of *Okenia* found in south-eastern Australia, but unfortunately apart for this species and *O. zoobotryon*, too few specimens are available of the other species or ‘forms’ to adequately determine their status. Externally, *O. mija* can be distinguished from *O. zoobotryon* by the lateral papillae, which are dorsoventrally flattened, and taper to a rounded tip, while in *O. zoobotryon* they have an inflated spherical tip. In *O. mija* there is also median row of dorsal papillae between the gills and the rhinophores and secondary papillae flanking the median row, while in *O. zoobotryon* there are only two dorsal papillae, and they lie in the midline. The rhinophores of *O. mija* have six very distinctive cup-shaped lamellae, each with a notch in the posterior midline, while in *O. zoobotryon* there are three cup-shaped rhinophoral lamellae, and they lack a posterior notch. Two distinctive features of the colour pattern are the translucent clear band around the mantle edge, with many opaque white specks, and the large light brown patches each with a central dark brown spot which are scattered over the dorsum and the sides of the body. In animals identified here as *O. zoobotryon*, the body is a uniform translucent brown, with small scattered white and dark brown patches.

The reproductive systems of *O. mija* and *O. zoobotryon* are very similar, with both having the sperm sacs arranged serially, and they both have a long coiled penial introvert, but in *O. zoobotryon* this is contained in a thin-walled sac while in *O. mija* it is not. During mating this introvert extends out almost the length of the body allowing animals to mate even when separated by 3 or 4 mm. In the preserved collection, three pairs of animals are still ‘in copula’. An identical situation occurs in *O. zoobotryon* and in one lot of specimens, two pairs of preserved animals are still ‘in copula’. The radular morphology of the two species shows some distinct differences. In *O. mija* there about approximately 12...
short broad denticles on the inner teeth while in *O. zoobotryon* the denticles are longer, narrower, and more numerous (approx 17). Both species have bifid cusps on the outer teeth but in *O. mija* they are much smaller and there is a triangular pointed flange below the cusps, a feature absent in *O. zoobotryon*. The two species also seem to differ in their food bryozoan, *O. mija* being found on *Amathia wilsoni* Kirkpatrick, 1888, and *O. zoobotryon* on *Zoobotryon verticillatum* (delle Chiaje, 1828).

**Biology:** In Tasmania, I have found *O. mija* feeding on the ctenostome bryozoan *Amathia wilsoni* Kirkpatrick, 1888 (see also MacGillivray, 1895). On other occasions, specimens have been found in mixed ‘algal washings’ which also contained pieces of unidentified ctenostome bryozoans.

**Okenia zoobotryon** (Smallwood, 1910)

(Figures 4D, 12C, 15, 26A, 29D)

*Polycerella zoobotryon* Smallwood, 1910: 137–145; Smallwood, 1912: 609–630
*Bermudella zoobotryon:* Odhner, 1941: 16
*Bermudella polycerelloides* Ortea & Bouchet, 1983: 49–54

**Material:** Point Turton Jetty, Yorke Peninsula, SA, on bryozoan, *Zoobotryon verticillatum* (delle Chiaje, 1828), 3 m, 19 February 1985, many hundreds seen, approx 50 specimens collected, 4–6 mm long, AM C145165.

**Geographic Distribution:** Western Atlantic (Caribbean region) (Smallwood 1910; Clark 1984; Redfern 2001). Possible records also from Canary Islands (Ortea & Bouchet 1983), and Australia (present study), but as discussed below, our knowledge of this species needs to be improved before identifications can be confirmed.

**External Morphology:** Animal small, elongate, with distinct mantle edge bearing approximately six papillae on each side, including anterior pair in front of rhinophores. Papillae slightly swollen, tentacular, rounded at tip (Fig. 12C, 26A). Two dorsal papillae in midline, one just in front of gills, one just behind rhinophores. Head distinctly separate from mantle and foot. Oral tentacles similar in size and shape to lateral papillae. Rhinophores about twice length of lateral papillae, with three characteristic cup-shaped structures on the posterior side. Gills bipinnate, three or four arranged in arch around anus in posterodorsal midline.

**Colour:** Body translucent straw, with opaque white speckling and microscopic brown spots scattered all over (Fig. 29D); few larger darker brown spots also present. Lateral papillae translucent clear with scattered opaque white patches. Rhinophores translucent clear with white patches mainly confined to edge of cup-shaped ‘lamellae’ and tip.

**Foregut anatomy:** Anterior end of buccal cavity with cuticular lining but no sign of individual jaw elements. Buccal pump on roof of buccal bulb, relatively large. Radular for-
central tooth formula of three animals; 23, 22, 25 x 1.1.0.1.1 (AM C145165) (Fig. 15). Innermost tooth with broad base and long, elongate pointed cusp bearing many (22+) narrow, relatively long, pointed denticles along cutting edge. Denticles at either end of row shorter. Outer teeth small, with broad quadrangular base and large recurved bicuspid tip.

**Reproductive system:** Reproductive opening on right side of body, below and just behind rhinophores (Fig. 4D). Vaginal duct short, broad, leading back to large spherical bursa copulatrix. Exogenous sperm duct narrow, running from junction of vaginal duct and bursa copulatrix to fertilisation chamber within female gland mass. Exogenous sperm sac small, spherical, opening about halfway along exogenous sperm duct. From ovotestis, spermoviduct expands into large ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts; the oviduct, opening into fertilisation chamber; the sperm duct, opening into large recurved prostate gland. From prostate gland, a thin-walled sac, enclosing a long, narrow, very coiled duct, runs down to penial opening. Coiled duct possibly muscular vas deferens or perhaps long penial introvert, capable of eversion during copulation.

**Remarks:** This small brown goniodorid was originally described from Bermuda (Smallwood 1910) where it was found in large numbers on the ctenostome bryozoan *Zoobotryon pellucidum* Ehrenberg, 1828. The rhinophores were described as having 'three to six cup-like, equidistant folds on the posterior surface of its distal two-thirds' (Smallwood 1910: 143), and the 16–19 dorsal and lateral papillae were described as ‘clavate… the tips of which are translucent’ (Smallwood 1910: 144). The dorsal papillae were arranged in a distinct pattern, with two in the midline between the gills and the rhinophores, two on either side of the midline in front of the rhinophores, two just in front of the gills and two behind the gills. There are also 4 – 6 lateral papillae on each side. From Smallwood’s drawing I would consider the anterior pair of dorsal papillae to be the most anterior of the lateral papillae and the posterior pair to be the most posterior of the lateral papillae. Determining the nature of these papillae is important because the arrangement of the dorsal papillae is often a species-specific character. In a later anatomical description (Smallwood 1912), he described the reproductive system in some detail. Unfortunately his description, based on dissection and histological sections, doesn’t seem to make sense, and his only illustration misidentifies the bursa copulatrix as the prostate gland, and the male part of the system is completely absent. This is unfortunate because it means we have no knowledge of the reproductive system of this species. Clark (1984) redescribed specimens from Bermuda and reported populations from Florida. Externally his description follows Smallwood’s except for the report of two dorsal papillae on each side of the pericardium, instead of a single pair. He also corrected the radula description. As I discuss elsewhere, (Rudman 2004a), Clark’s suggestion that *O. evelinae* Marcus, 1957 is a synonym of *O. zoobotryon* is most unlikely. Redfern (2001) describes and illustrates the external features of animals from Bermuda and confirms they match Valdés & Ortea’s (1995) illustration of a Cuban specimen which shows two pairs of secondary dorsal papillae as described by Clark.
The question that then arises is whether the specimens I have reported here from South Australia are the same species? In general external shape and colour they agree, and they
have the characteristic cup-shape lamellae on the rhinophores, but the 20 or more preserved specimens I examined all lacked the secondary dorsal papillae which are characteristic of Atlantic specimens of *O. zoobotryon*. Unfortunately our knowledge of the anatomy of Atlantic specimens of *O. zoobotryon* is poor. Drawings of the radular teeth (Clark 1984; Valdés & Ortea 1995) suggest they are very similar to the radula of Australian specimens, but it would be valuable to have information on the reproductive system. If the long coiled penial introvert of Australian specimens is present in Atlantic animals it would a valuable confirmation. By coincidence, there is another small brown species, *O. mija*, found in Australian waters which has a similar arrangement of dorsal papillae to that of Atlantic *O. zoobotryon*. It differs in having papillae with pointed, rather than swollen, tips, and feeds on a related bryozoan *Amathia wilsoni*. The differences between that species and Australian specimens of *O. zoobotryon* are discussed under *O. mija*.

Until further information is available on the anatomy of Atlantic specimens of *O. zoobotryon* it would seem appropriate to identify these specimens from South Australia with that species despite the obvious zoogeographic anomaly. The ctenostome bryozoan *Zoobotryon verticillatum* (=*Z. pellucidum* — see Osburn 1953: 742–3) is a well-known ‘tramp’ species with a worldwide distribution considered to be the result of shipping and perhaps drifting on pieces of brown algae. *Okenia pellucida*, which also feeds on *Z. verticillatum*, has a wide distribution which is also considered, at least partially, to be the result of the ‘unnatural’ distribution of *Zoobotryon*.

**Biology:** Found only on its food, the ctenostome bryozoan *Zoobotryon verticillatum*.

*Okenia stellata* sp. nov.
(Figures 16A, 17, 18B, 25A, 27C, 30D)

*Hopkinsia* sp. 1. Wells & Bryce, 1993: 74, Fig 80.
*Hopkinsia* sp. 2. Marshall & Willan, 1999: 68–69, Fig. 114.
*Okenia* sp. Coleman, 2001: 52 (‘orange Okenia’) (‘red stripe Okenia’)

Material: Blue Pools, Heron Is, Queensland, Australia, 31 August 1981, 1 specimen, 9 mm long preserved, AM C434824 [Holotype], 9 specimens, 3–10 mm preserved, AM C131365 [Paratypes]. Rope Trails, Lady Eliot Is., Queensland, Australia, 17 m, 15 January 1983, 1 specimen, 18 mm long alive, AM C137440 [Paratype]. N side of Mutton Bird Island, Coffs Harbour, New South Wales, Australia, 6 December 1990, 1 specimen, rocky reef, 11m. AM C433966 [Paratype].

**Etymology:** From the Latin adjective *stellatus*, meaning starry, in reference to the star-like shape of this animal when its lateral processes are held erect.

**Geographic Distribution:** Northern Australia from Western Australia (Wells & Bryce 1993; Coleman 2001), Northern Territory (Marshall & Willan 1999); Queensland, northern New South Wales (Marshall & Willan 1999; present study).
FIGURE 16. A, Okenia stellata sp. nov. Heron Is, Queensland, Australia, August 1981, 10 mm preserved, composite drawing from photos by G. Avern., AM C131365. B, Okenia hallucigenia sp. nov. Port Stephens, New South Wales, Australia, July 1986, 18 mm long alive, AM C150357.

**External Morphology:** Animal ovate, dorso-ventrally flattened (Fig. 16A, 27C), lacking mantle ridge, but edge of dorsal ‘mantle’ marked by position of five large lateral papillae on each side. Papillae relatively large for size of body, their length reaching 1 to 1.5 times the length of body. Papillae held out at right angles to edge of body to form a star-like radiating pattern. Papillae usually held out horizontally, with tips curved slightly upwards. Basal part of lateral papillae cylindrical, but outer half to two-thirds become
broader and dorso-ventrally flattened before tapering to a pointed tip. Single, similarly shaped, dorsal papilla in dorsal midline, just in front of gills, usually held erect. Rhinophores short, about one third the length of lateral papillae; lamellate tapering club often held recurved posteriorly. Gills, small, usually five, arranged in arch around anus. From above, head indistinguishable from foot; no oral tentacles; ventrally, distinct groove differentiates anterior edge of foot from head.

**Colour:** Body pink with pattern of thin red lines, including one around body just below papillae, usually hidden from above, but visible in anterior and posterior midline, where papillae absent. Single red line also runs from posterior base of each rhinophore back around gills to join in dorsal midline behind gills. Red line also runs up posterior midline of each rhinophore stalk to the base of the lamellate club. Secondary transverse line sometimes present, running across in front of gills. Parts of lines often missing in individual animals. Mantle papillae and rhinophore clubs with deeper red tips (Fig. 30D); gills with deep red band up smooth outer edge.

**Foregut anatomy:** Anterior buccal bulb lined with cuticular rodllets, densely packed together in continuous band (Fig. 17, 25A). Buccal pump relatively large (Fig. 25A). Radular formulae of 2 specimens; 14 x 1.1.0.1.1 (AM C131365) and 16 x 1.1.0.1.1 (AM C137440). Inner teeth with wide base and long rod-like blade, bluntly rounded at tip; rounded groove present, running length of posterior face of blade; no sign of denticles. Outer teeth small, with broad rounded base and up to four recurved pointed cusps along outer edge of tooth.

**Reproductive system:** Reproductive opening on the right side of body, below and slightly posterior to level of the rhinophores (Fig. 18B). Vaginal duct elongate, leading back to large spherical bursa copulatrix. Exogenous sperm duct narrow, running from junction of vaginal duct and bursa copulatrix to fertilisation chamber within female gland mass. Exogenous sperm sac elongate, opening about halfway along exogenous sperm duct. From ovotestis, spermoviduct expands into ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts; the oviduct, opening into the fertilisation chamber; the sperm duct, opening into recurved prostate gland. Vas deferens short, narrow, joining prostate gland to long tapering penial sac.

**Remarks:** *Okenia stellata* has similarities to *O. nakamotoiensis* (Hamatani, 2001), both having five pairs of lateral papillae, but in *O. nakamotoiensis* they are shorter and the tips are swollen with a rounded point. In both species the head and foot have merged, except for a lateral groove on the sole of the foot. In both, the inner radular teeth are long and rod-like but in *O. stellata* they are stout, with a dorsal groove and a bluntly rounded tip, while in *O. nakamotoiensis*, they are slender with a recurved hook-like tip, a feature also present in *O. rosacea* (MacFarland, 1905). In both species the outer teeth are very reduced. As I discuss elsewhere in this paper, the foregut of *O. hallucigenia* and *O. stellata* are quite different in relative size and shape. The reproductive system of *O. nakamotoiensis* (see Gosliner 2004) is very similar to that of *O. stellata* with both having the sperm ducts in a serial arrangement. Like many of the group which were previously placed in the genera *Hopkinsia* and *Hopkinsiella*, both these species are bright pink. In *O. nakamotoiensis* the base of the papillae are white as is a line up the anterior (dorsal) side of each gill. In *O. stellata* there is no white, but there is a pattern of red lines on the dorsum. Interestingly, *O. nakamotoiensis* occurs with another species, *O. kondoi* (Hamatani, 2001), on a branching,
erect, but calcareous, bryozoan, *Tropidozoum cellariforme* Harmer, 1957 (Family Euthyrissellidae) (see Gosliner 2004). *Okenia stellata* also lives on a similar euthyrissellid bryozoan, in this case, *Pleurotoichus clathratus* (Harmer, 1902). Just as *O. nakamotoensis* and *O. kondoi*, are often found together on the same bryozoan colony, *O. stellata* is often found with another species, *O. hallucigenia*, on the same colony of its food bryozoan.

**Diagnosis:** *Okenia stellata* can be distinguished by its bright pink color and pattern of red lines, its 10 symmetrically arranged large lateral papillae and its blunt rod-like inner radular teeth.

**Biology:** Observations from Western Australia, Queensland and New South Wales all note its association with *Pleurotoichus clathratus*.

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**FIGURE 18.** Reproductive System. A, *Okenia hallucigenia* sp. nov. Blue Pools, Heron Is, Queensland, Australia, December 1981, 9 mm long preserved, AM C132326. B, *Okenia stellata* sp. nov. Heron Is, Queensland, Australia, August 1981, 10 mm preserved, AM C131365. **amp** ampullar region of spermoviduct; **bc** bursa copulatrix (gametolytic gland); **es** exogenous sperm sac (receptaculum seminis); **pro** prostate gland; **ps** penial sac. Scale bar = 1 mm.
**Okenia hallucigenia sp. nov.**
(Figures 16B, 18A, 19, 27E, 30C)

*Hopkinsia* sp. Rudman & Avern, 1988: 388; Rudman, 1998a: 992, pl. 35.6; Rudman, 1998b

*Hopkinsia* sp. 1. Marshall & Willan, 1999: 68–69, Fig. 113

*Okenia* sp. Coleman, 2001: 52 (‘pink Okenia’)

**Material:** Blue Pools, Heron Is, Queensland, Australia: May 1980, AM C124290; 31 August 1981, 6 specimens, 5–12 mm long preserved [largest 18 mm long alive], AM C433967 [Paratypes]; 11–14 December 1981, 40–50 ft, 1 specimen, 10 mm long preserved, AM C434825 [Holotype], 6 specimens, 7, 7, 8, 9, 9, 9 mm long, AM C132326 [Paratypes]. Gorgonia Hole, Heron Is, Queensland, Australia, 12 m, 7 September 1982, 1 specimen, 5 mm long preserved, AM C135363 [Paratype]. (3) North Solitary Is, Coffs Harbour, New South Wales, Australia, 17 January 1989, 1 specimen, 10 mm long alive, AM C157164 [Paratype]. North side of Mutton Bird Island, Coffs Harbour, New South Wales, Australia, 6 December 1990, 1 specimen, on rocky reef covered in kelp, 11 m. on pink bryozoan preserved separately. AM C164590 [Paratype]. Halifax Park, Port Stephens, New South Wales, Australia, 21 m, 5 July 1986, 2 specimens, 15 & 18 mm long, AM C150357 [Paratypes].

**Etymology:** This species is named for its likeness to the Burgess Shale ‘onycophoran’ fossil, *Hallucigenia sparsa* Morris, 1977, as reconstructed by Lars Ramsköld (1992).

**Geographic Distribution:** Northern Australia from Western Australia (Kimberley, Exmouth Gulf), Northern Territory (Marshall & Willan 1999; Coleman 2001), Queensland, central New South Wales (Rudman & Avern 1988; Rudman, 1998b; Marshall & Willan 1999; present study).

**External Morphology:** Animal very elongate, with high profile (Fig. 16B, 27E); mantle ridge absent but position indicated by presence of four pairs of prominent, very large, mantle papillae on each side. Anteriormost papilla on each side sits just in front of adjacent rhinophore and points anteriorly; approximately half the width and length of other papillae and tapering to a point. Other three lateral papillae on each side point outwards and somewhat upwards; length approximately twice width of body, with bluntly rounded tip. Papillae quite rigid and not as motile and flexible as long papillae of many other species of *Okenia*. Single dorsal mantle papilla, in midline, just in front of gills. Gills, usually five, arranged in arch around anal papilla; sometimes only three gills present, with bases merged into a single trunk. Gills simple, with broad smooth band up outside edge. Rhinophores long and tapering; club with up to 16 lamellae, occupies upper two-thirds of rhinophore. Head very distinctive, with wide bilobed ‘oral veil’ at least twice width of body; lateral tips of head can extend into tentacular foot corners. Head, and much narrower foot, merge into one another seamlessly, with no sign of transverse ventral groove seen in many species, although transverse groove at level of mouth may represent junction of foot and head.
**Colour:** Animal bright pink (Fig. 30C) except for tips of mantle processes; gills, rhinophores, which are a deeper, redder shade of same colour.

**Foregut anatomy:** Anterior end of buccal bulb lined with cuticle, but no distinct thickened regions or areas with cuticular rodlets. Buccal bulb relatively small for size of animal, with long oral tube, not previously reported from any other species of *Okenia*. Radula (Fig. 19) very similar in shape to that of *O. kondoi*; formula 20 x 1.1.0.1.1. (AM C157164). Innermost tooth with broad base and blade with bicuspid tip; mediodorsal groove down distal half of tooth; up to 16 very long denticles along cutting edge. Outer teeth, much smaller, with broadly quadrangular shape and three or four remnant cusps.

**FIGURE 19.** *Okenia hallucigenia* sp. nov. Scanning electron micrographs of radula. A, Section of whole radula. B, Section of left side of ribbon showing large denticulate inner teeth and small reduced, plate-like outer teeth. C, Inner tooth from left side of radula showing groove along the top of the blade and the bifid tip of the cusp. D, section of right side of radula. North Solitary Is., Coffs Harbour, New South Wales, Australia, 17 January 1989, AM C157164. Scale bar = 10 µm. Photo: A.C. Miller.
**Reproductive system:** Reproductive opening on right side of body, below and just posterior to level of rhinophores (Fig. 18A). Vaginal duct elongate, leading back to spherical bursa copulatrix. Exogenous sperm duct narrow, opening into vaginal duct just before it reaches bursa copulatrix, and running to fertilisation chamber within female gland mass. Exogenous sperm sac elongate, about half the size of bursa copulatrix and opening into exogenous sperm duct via a short duct, about halfway along its length. From ovotestis, spermoviduct expands into an ampullar region, usually distended with endogenous sperm. Spermoviduct divides into two short ducts inside female gland mass; one, the oviduct, opens into fertilisation chamber; the other, the sperm duct, runs into a long recurved prostate gland, a relatively long ejaculatory duct and then the penial bulb.

**Remarks:** As I have discussed under *O. stellata*, this species is often found with that species on the bryozoan *Pleurotoichus clathratus*. This pair of species is matched by another pair of similarly shaped and coloured species (*O. nakanotoensis, O. kondoi*) which are reported from southern Japan, the Marshall Ids and the Philippines. *Okenia kondoi* is very similar to *O. hallucigenia* in external shape and radular morphology, the main anatomical difference being its very short vaginal duct, the bursa copulatrix opening almost directly into the genital vestibule. *Okenia kondoi* was originally placed in a monotypic genus *Sakishimaia* Hamatani, 2001 on the basis of its cylindrical body shape and the absence of a second lateral radular teeth. Gosliner (2004) has shown the second radular tooth is present, if greatly reduced, and argues, after cladistic analysis, against retaining the genus *Sakishimaia*. Externally, *O. kondoi* appears to be even more cylindrical in shape than *O. hallucigenia*, its diameter matching that of the cylindrical branches of the bryo- zoan on which it lives and feeds. It also differs from *O. hallucigenia* in its colour pattern, with the bottom half of each papilla being creamy white. There is also a broken creamy white band running along each side of the dorsum, joining the bases of the lateral papillae. There are also creamy white streaks along each side of the body. By comparison, *O. hallucigenia*, is a uniform pink. As I discuss elsewhere, the foregut of *O. hallucigenia* and *O. stellata* are quite different in relative size and shape.

**Diagnosis:** *Okenia hallucigenia* can be distinguished by its shape, radular morphology, and uniformly pink colour pattern.

**Biology:** Observations from Western Australia, Queensland and New South Wales all note its association with *Pleurotoichus clathratus*.

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*Okenia hiroi* Baba, 1938
(Figures 20B, 21, 24D, 27B, 30B)

*Hopkinsiella hiroi* Baba, 1938: 9–11, fig. 7; Baba, 1949: 47, 139–40, fig. 49, pl. 16, fig. 56
*Hopkinsia hiroi*: Bouchet and Ortea, 1983: 227–233; Rudman & Darvell, 1990: 38, Pl. 1G; Rudman & Darvell, 2001a

**Material:** 4 specimens, 18 April 1982, Site 4.8, Breaker Reef, Mirs Bay, 15 m, Hong Kong, China, AM C133758. 2 specimens, 23 January 1983, Site 9.40, Wai Kap Pai,
Rocky Harbour, 5–6 m, Hong Kong, China, AM C138136. 1 specimen, 10 April 1983, Site 4.57, Bate Head, Mirs Bay, 5–10 m, Hong Kong, China, AM C139024. 4 specimens, II April 1983, Site 4.59, Gau Tau (N), Mirs Bay, 5–12 m, Hong Kong, China, AM C139025. 1 specimen, 31 March 1984, Site 10.99, Kiu Tau (W), Kiu Tsui Chau, Port Shelter, 6 m, Hong Kong, China, AM C142172.

**Geographic Distribution:** Pacific coast of Japan (Baba 1938; 1949; Nishina 2001; Sato 2003d); Korea (Koh 2003); China (Hong Kong — Rudman & Darvell 1990; 2001a; Chan 2001).

**External Morphology:** Animal elongately ovate with low flattened profile (Fig. 20B, 27B). From above, mantle, foot and head are merged into one, but ventral groove indicates separation of head and foot. Oral tentacles absent. Elongate lateral papillae in single row around body; 11 or 12 on each side, but no indication of symmetrical pairing of papillae as found in other species of *Okenia*. Few dorsal papillae also present, one in midline, halfway between the gills and rhinophores, another on each side, just behind this central one, forming a staggered transverse row; another two papillae just behind gills, one on each side. Arrangement and number of dorsal papillae variable; some specimens with up to seven, others with as few as three dorsal papillae. Rhinophores similar in size and shape to lateral papillae; lamellae reduced to series of ridges on posterior face of upper half of each rhinophore. Gills, four or five, forming arch around anal papilla.

**Colour:** Animal pink, matching colour of the bryozoan on which it is feeding (Fig. 30B). Tips of all the dorsal processes (papillae, rhinophores) white.

**Foregut anatomy:** Anterior end of buccal bulb lined with cuticle but no distinct thickened regions or regions with cuticular rodlets. Buccal bulb with prominent buccal pump and large radular sac. Radular formula 39(+2) x 1.1.0.1.1 (AM C138136) (Fig. 21). Inner teeth with wide base and long rod-like blade narrowing to bicuspid tip; cutting edge lined with large bluntly rounded denticles. Outer teeth, much smaller, with broad rounded base and up to four recurved pointed cusps along outer edge of tooth.

**Reproductive system:** Reproductive opening on right side of body, below and just posterior to rhinophores (Fig. 24D). Vaginal duct leads back to large spherical terminal bursa copulatrix. Exogenous sperm sac small, elongate, joins vagina just below bursa copulatrix. Exogenous sperm duct narrow, joins vagina just below exogenous sperm sac, and runs to fertilisation chamber within female gland mass. From ovotestis, spermoviduct expands into large ampullar region, usually distended with endogenous sperm. Inside female gland mass spermoviduct divides into two short ducts; the ooviduct, opening into fertilisation chamber, and the sperm duct, opening into relatively narrow, recurved, prostate gland. Prostate gland joined to penial bulb by short, narrow vas deferens.

**Remarks:** I follow Gosliner (2004) in synonymising the genera *Hopkinsia* and *Hopkinsiella* with *Okenia*. Like many of the ‘Hopkinsia-group’ of species, *O. hiroi* has a relatively broad flattened body in which the head and foot are fused, the lateral papillae are relatively large and crowded, and the body, like its food, is reddish pink. The inner radular
teeth of this species have two interesting features that link it with both ‘typical’ species of *Okenia* and some more extreme forms. The teeth have a distinctive rounded groove along the upper edge of the blade which is also found in the unusually shaped *O. stellata*, and they also have a bicuspid tip, an unusual feature also found in *O. pellucida*, and *O. purpureolineata*. This grooved and bifid tooth may also indicate the origin of the strange tooth found in *O. hallucigenia* and *O. kondoi* in which the groove, the bifurcation, and the denticle appear to have become greatly accentuated.

**Biology:** *Okenia hiroi* in Hong Kong, is often found associated with a similarly coloured encrusting bryozoan (Rudman & Darvell, 2001), which has been identified by Dr D.P. Gordon as a ‘new species of *Integripelta* Gordon, Mawatari & Kajihara, 2002 (Eurystomellidae; Cheilostomata).”

Okenia pilosa (Bouchet & Ortea, 1983)
(Figures 20A, 22, 24A,C, 27A, 29E)


Material: 19 specimens (4–10 mm long preserved), 11 April 1983, Site 4.59, Gau Tau (N), Mirs Bay, 5–12 m, Hong Kong, China, AM C139137. 2 specimens (9, 9.5 mm long preserved), 13 April 1983, Site 4.65, Chek Chau (NE), Mirs Bay, 2–6 m, Hong Kong, China, AM C139138. 1 specimen (3.5 mm long preserved), 12 April 1983, Site 2.61, Bluff Head, Tolo Channel, 4–7 m, Hong Kong, AM C139054. 5 specimens (4.5, 5, 7, 8, 10 mm long preserved), 14 April 1983, Site 2.32, Round Is. (E), Mirs Bay, 3–10 m, Hong Kong, AM C139055. 6 specimens (3, 4, 4.5, 7, 10 mm long preserved), 24 February 1984, Site 14.41, Tai Tam Harbour, Hong Kong Is., 0.5 m, Hong Kong, China, AM C141494. 4 specimens (4.5–13 mm long preserved), 25 February 1984, Site 10.99, Kiu Tau (W), Kiu Tsui Chan, Port Shelter, 4–7 m, Hong Kong, China, AM C141495. 1 specimen (4 mm long preserved), 14 April 1986, Site 2.61, Bluff Head, Tolo Channel, 2 m, Hong Kong, China, AM C150284. 1 specimen (4 mm long preserved), 19 April 1989, Round Island, Hong Kong, China, AM C158188.

Geographic Distribution: Hong Kong, China (Rudman & Darvell 1990; 2002b; present study); Japan (Imamoto 2004); New Caledonia (Bouchet and Ortea 1983); Papua New Guinea (Gosliner 2004); Queensland, Australia (Marshall & Willan 1999).

External Morphology: Body round, flattened, as in O. plana, but with many more finger-like papillae arranged in series of irregular rows around sides of body (Fig. 20A, 27A). Some papillae also present in central part of mantle, including single papilla on outside of each rhinophore and another on each side of gill circle. Three papillae arranged in transverse row across dorsum, midway between gills and rhinophores. Rhinophores and gills elongate, looking much like papillae. Approximately 12 bipinnate gills arranged in circle around anus. From above, mantle, foot and head are indistinguishable, but ventrally, head and foot separated by transverse groove. Oral tentacles absent.

**Colour:** Body translucent white, closely speckled with brown and with irregular net-work of white lines (Fig. 29E). Brown markings usually consist of pale brown patches, each with a central dark brown spot. Mantle papillae transparent with dark brown specks and some opaque white spots or streaks. Rhinophores and gills similar in colour to papillae.

**Foregut anatomy:** Cuticular lining at anterior end of buccal cavity with band of irregularly shaped, thickened rodlets, sometimes tipped with papillae (Fig. 22). Buccal bulb with large dorsal buccal pump and prominent radular sac. [the foregut is at least 2–3 times larger than similar sized O. plana (4 mm long buccal bulb in 13 mm long O. pilosa compared with 1.5–2 mm long in 12.5 mm O. plana).] Radular formula: 24(+1) x 1.1.0.1.1 (AM C141494, AM C139137, AM C141495 (approx 13 mm long preserved); 16 x 1.1.0.1.1 (AM C141495A, AM C141495B (approx 4.5–5 mm long preserved). Innermost tooth with broad base and long elongate pointed cusp; no sign of denticles along cutting edge. Outer teeth, much smaller, with broad quadrangular base with large recurved pointed cusp at tip, then two or three large pointed denticles, and a basal cusp similar in size to uppermost. In two juveniles, (4.5–5 mm long preserved), outer teeth with upper cusp, up to six pointed denticles, and in all cases, a prominent, pointed, triangular, basal cusp (Fig. 22G-I).

**Reproductive system:** Reproductive opening on right side of body below and just posterior to rhinophores (Figs 24A,C). Vaginal duct, narrow, leading back to extremely elongate terminal bursa copulatrix lying folded around female gland mass. Exogenous sperm sac, small, elongate, opening off vagina just below opening to bursa copulatrix. Exogenous sperm duct, thin, joining vagina about halfway along its length and running to fertilisation chamber within female gland mass. From ovotestis, spermoviduct expands into large ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts; the oviduct, opening into fertilisation chamber; and the sperm duct, opening into large recurved prostate gland. Narrow vas def-erens runs from prostate gland down to penial opening. In dissection, it is not possible to distinguish a penial bulb from the vas deferens. Because of the unusual nature of the bursa copulatrix, three specimens were dissected, and all showed the same shape (Figs 24A,C).

**Remarks:** The round flattened body is very similar to that of O. plana but there are many more of the finger-like papillae in O. pilosa than in O. plana. Like O. plana, the colour of the body and its round flattened body make it very well camouflaged on its bryozoan food. Okenia pilosa differs from O. plana externally, in having many more of the finger-like lateral papillae. The animals grow to approximately 25 mm in length and feed on encrusting bryozoan colonies on which they are found. Gosliner (2004) recently identified a single specimen from Papua New Guinea as O. pilosa but differences in colour and anatomy suggest there may be more than one species with multiple mantle papillae. Gosliner’s animal has a white reticulate pattern and yellow spots on the mantle and yellow edging to the gills. It also had scattered brown spots, which appear very obscure in the colour photo-
graph accompanying the description. In Hong Kong specimens there is no yellow pigmentation and the white reticulation and brown markings are very prominent. There are also some anatomical differences. Firstly the outer radular teeth in large specimens from Hong Kong have two prominent pointed cusps with a few smaller pointed denticles between them, very similar to the teeth of *O. plana*. However in smaller specimens (4–5 mm long preserved) there are up to six smaller denticles, although the basal cusp is still prominent. This differs from Gosliner’s specimen which is illustrated as having quite fine denticles. In the original description of this species (Bouchet & Ortea 1983), the outer teeth are described as ‘pectinate’ and in the accompanying drawing there are fine denticles as in Gosliner’s SEM photo. However Bouchet & Ortea’s drawing also shows the presence of a prominent basal cusp as in Hong Kong material. The other difference concerns the shape of the bursa copulatrix, which in Hong Kong specimens is a long elongate structure lying over the top of the female gland mass. It is so conspicuous that when I first dissected a specimen I thought it was part of the intestine running back to the anus. Again, this shape is quite unusual, but found in five animals I dissected. This differs from Gosliner’s description of a small spherical bursa. The original description included information on the external shape, the colour of the animal and the radular morphology. Both the animals from Hong Kong and Papua New Guinea are similar in shape to the original description. The animals from Hong Kong are a better colour match than those from Papua New Guinea, but the Papua New Guinean animals are perhaps a better match in radular morphology. Until more material is found and studied it is not possible to say whether the differences represent intraspecies variability or interspecies differences.

**Biology:** Bouchet & Ortea (1983) report this species feeding on an encrusting bryozoan, *Calpensia sp.*

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**Okenia plana** Baba, 1960
(Figures 20C, 23, 24B, 27D, 29F, 30A)

*? Doris eolida* Quoy & Gaimard, 1832: 263–264, pl. 18, figs. 11–15; Rudman, 1995: 8–9.

*Okenia plana* Baba, 1960: 80–81, pl. 7, figs.2A–D; Steinberg, 1963: 63–67; Morton & Miller, 1968: 169, 412, pl. 21, fig. 2; Willan & Morton, 1984: 91; Willan & Coleman, 1984: 18, fig. 34, 52; Behrens, 1991: 45, fig. 51; Gosliner, 2004: 144–147, Figs 20B, 21–22.


**Material: Australia:** Green Point, Woolgoolga, New South Wales, Australia, on bryozoan, *Jellyella tuberculata* (Bosc, 1802), on brown algae, ELWS pool, 1 November 1982, 1 specimen, 10 mm long, AM C136131. Five Dock Point, Drummoyne, Sydney, New South Wales, Australia, intertidal on bryozoan, *Cryptosula pallasiana* (Moll, 1803), 14 May 1984, 1 specimen, 10 mm long, AM C142137. Jervis Bay, New South Wales, Australia, removed from unidentified encrusting bryozoan, growing on *Ecklonia* on fouled ropes
hanging from mussel culture raft, 3 June 1980, 1 specimen 8 mm long, AM C122198; 2 specimens, AM C123570. **China:** 1 specimen, 5 April 1986, Site 5.128, Heung Lo Po (E), Tolo Channel, 1 m, Hong Kong, (on prey bryozoan, *Membranipora membranacea* (Linnaeus, 1767)), AM C150268. 1 specimen (4.5 mm long preserved), 20 February 1983, Site 14.41, Tai Tam Harbour, Hong Kong Is., 1 m, Hong Kong, AM C138144. 20 specimens (5–8 mm long preserved), 11 April 1983, Site 4.59, Gau Tau (N), Mirs Bay, 5–12 m, Hong Kong, AM C139053. 5 specimens, 25 February 1984, Site 10.99, Kiu Tau (W), Kiu Tsui Chau, Port Shelter, 4–7 m, Hong Kong, AM C141489.

**Geographic Distribution:** This species has a wide distribution in the western Pacific being reported from Japan (Baba 1960), Hong Kong (Rudman & Darvell 1990), New Zealand (Morton & Miller 1968), Australia (Rudman 1998c), and recently from the Philippines (Gosliner 2004). Its presence in California (Behrens 1991) is considered an artificial distribution brought about by its food, the fouling bryozoans, being transported long distances by shipping.

**External Morphology:** Body with low flattened profile, ranging in shape from almost circular to broadly ovate (Fig. 20C, 27D). From above, mantle, foot and head merge into one. Raised visceral hump in dorsal midline outlined by five elongate, lateral, mantle papillae on each side. Foot extends out all around body as a thin layer, hugging contours of substrate. Single mediodorsal papilla midway between gills and rhinophores; Twelve gills form circle in posterior midline around anal papilla. Ventrally, a slight transverse groove separates head from anterior foot. Oral tentacles absent.

**Colour:** Specimens from Australia and New Zealand, are translucent white with closely packed, relatively large, brown patches, the spaces between the brown patches creating a network of whitish lines (Figs 29F, 30A). On close examination, each brown patch is edged with a thin opaque white line. Sometimes the white lines of adjacent brown patches merge, and in other cases they are separated by a translucent whitish region. In some specimens the opaque white pigment is absent, or there are only traces of it here and there. In these animals the network pattern between the brown patches is basically translucent white or straw coloured. The mantle papillae, the rhinophores, and the gills all have the same colour pattern, making the animals very cryptic when sitting on its bryozoan food. Specimens from Japan & Hong Kong (Rudman & Darvell 1990) have traces of the opaque white lines that outline each large brown patch in Australian specimens, but instead of having a large brown patch, Hong Kong specimens have a small dark brown spot in the centre of each ‘mesh’.

**Foregut anatomy:** Anterior end of buccal cavity with cuticular lining and anterior band of irregularly shaped thickened rodlets, some bearing a few terminal papillae (Fig. 23B). Buccal bulb with large dorsal buccal pump and prominent radular sac. [Compared with *O. pilosa*, the foregut is at least 2–3 times smaller (4 mm long buccal bulb in 13 mm
long *O. pilosa* compared with 1.5–2 mm long in 12.5 mm *O. plana*). Radular formula 25(+1) x 1.1.0.1.1 (AM C139053, AM C123570). Innermost tooth with broad base and long elongate pointed cusp (Fig. 23); no sign of denticulation along cutting edge. Outer teeth much smaller, with broad quadrangular base and large recurved pointed cusp at the tip. Below cusp are two or three large elongate denticles, and a basal cusp. No regional differences in morphology between specimens from Australia and Hong Kong.

Reproductive system: Reproductive opening on right side of the body, below and just posterior to rhinophores (Fig. 24B). Vaginal duct narrow, leading back to large spherical bursa copulatrix. Exogenous sperm sac small, elongate, joining bursa copulatrix alongside openings to vaginal duct and narrow exogenous sperm duct. From ovotestis, spermoviduct expands into large ampullar region, usually distended with endogenous sperm. Inside female gland mass, spermoviduct divides into two short ducts; the oviduct, opening into fertilisation chamber; the sperm duct, opening into large recurved prostate gland. Vas deferens, long, narrow, running from prostate gland to penial opening. No distinct penial bulb could be distinguished in dissection.

Remarks: Okenia plana is very similar to O. pilosa in shape and colour but differs in having only a few long rounded lateral papillae on the mantle. There is usually one in the middle of the back and about five down each side near the mantle edge. In Japanese and Hong Kong specimens there are small brown specks all over the mantle and body but in Australia and New Zealand there are much larger brown patches. The radular morphology of O. plana is very similar to that of O. pilosa as reported here from Hong Kong, but there are some puzzling differences in descriptions of the outer teeth of O. pilosa by other workers. I have suggested (Rudman, 1995) that the earliest name for this species may be Doris eolida Quoy & Gaimard, 1832, which was proposed for a small 5 mm animal found clinging to floating Sargassum weed in the South China Sea. However as no specimens bearing that name can be found in the Museum National d'Histoire Naturelle, Paris, this name should be treated as a nomen dubium as its identity cannot be confirmed.

Biology: Okenia plana has previously been reported living and feeding on the colonial bryozoan, Membranipora membranacea, (Linnaeus, 1767), a cosmopolitan fouling organism on wharf piles, and algae (Morton & Miller 1968, Ryland 1976). It is also reported here from Hong Kong on M. membranacea and from New South Wales, eastern Australia, on two other cosmopolitan cheilostome bryozoans, Cryptosula pallasiana, a fouling organism on wharf piles and algae, and Jellyella tuberculata, which is usually found on attached and floating brown algae.

Discussion

Gosliner’s (2004) recent cladistic analysis of the genus Okenia (including Sakishimaia, Hopkinsiella and Hopkinsia), is a valuable addition to our understanding of the Goniodorididae. As all such studies should do, it gives us a much better understanding of what we do not know as well as clarifying what we do know. Although Gosliner’s study suggests there is insufficient anatomical evidence at present to justify the use of more than one genus for this group of species, there certainly appear to be ‘intrageneric’ groups of species with characteristics related to their natural history, and in particular, their food.

Species of Okenia show a much greater diversity in body form and radular morphology than other goniodorid genera, such as Trapania and Goniodoris. The genus Trapania
ZOOTAXA

695

has a worldwide distribution and consists of approximately 30 species. All that have been studied have a very uniform shape and anatomy, differing in slight differences of radular morphology and colour pattern (Rudman, 1987), and recent discussions (Picton 2001) confirm that many species feed on entoprocts (Kamptozoa). *Goniodoris* would seem to be a much less speciose genus and to be uniform in shape and anatomy, with a relatively high body, mantle ‘ridge’ around the edge of the body, no mantle papillae, and a distinct head with the anterior corners extended into triangular oral tentacles. Little is known about the anatomy and biology of the described species except for the Atlantic species, *G. nodosa* (Montagu, 1808) and *G. castanea* Alder & Hancock, 1845. Species of *Goniodoris* feed on ascidians, but juveniles of *G. nodosa* are reported by Picton & Morrow (1994) to feed on bryozoans, particularly the ctenostome *Acleonidium diaphanum* (Hudson, 1762).

The main character distinguishing the genus *Okenia* from *Goniodoris* is the presence, in *Okenia*, of multiple mantle papillae, ranging from species with a few, very long papillae, to species with many short papillae, which are little more than outgrowths of the mantle edge. Much of this variation is illustrated in this paper, but one which is not, is that of the ascidian-eating species of the North Atlantic, such as *Okenia aspersa* (Alder & Hancock, 1845), whose high body form, general shape, anatomy and ascidian food, are identical to species of *Goniodoris*, except for the presence of anterior and posterior lateral papillae (see Thompson & Brown, 1984; Morse, 1972 as *O. ascidicola*; Valdés & Ortea, 1995 as *O. quadricornis*). It could be suggested that species of *Goniodoris* have evolved from an *Okenia*-like ancestor, such as *Okenia aspersa*, which has begun to feed on ascidians, or conversely, bryozoan-feeding in species of *Okenia* may have evolved as a neotenic event from an ascidian-feeding ancestor. The behaviour of juvenile *G. nodosa*, feeding on encrusting bryozoans while adults feed on ascidians, certainly shows that such a feeding change is possible without a major change in shape or buccal armature.

Although there are some species of *Okenia* for which we have no biological information, the genus can be separated into three or four groups, in which body shape and general anatomy seem to match feeding behaviour.

**Group 1 [Ascidian prey]:** *Okenia aspersa, O. elegans, O. leachii* (see Picton & Morrow, 1994) all have a *Goniodoris*-like high body, traces of a caudal crest, and a mantle ridge with multiple mantle papillae. The head is separate from the foot and the mantle, but lacks any distinct oral tentacles. The high body in *Goniodoris* seems to be associated with its feeding behaviour. *Goniodoris meracula* Burn, 1958 (see Rudman, 2003b) and *G. castanea* Alder & Hancock, 1845 (see Thompson & Brown, 1984) both nestle in cavities they eat out of their ascidian prey, deep enough to enclose the animal. While sitting in the cavity the edge of the foot extends out and up, as a thin layer, to completely line the walls of the cavity. Thompson & Brown (1984) report that the ascidian-feeding *O. elegans* also burrows into its prey in a similar manner. In this group, there is a clear correlation between body shape and food.

**Group 2 [Ctenostome bryozoan prey]:** These species feed on erect, arborescent, non-calcareous bryozoans such as *Amathia* spp. and *Zoobotryon*. They have an elongate, flattened body, relatively short lateral papillae, and the head is separate from the mantle and the foot and bears distinct oral tentacles (Fig. 26). Many, but not all, have an inner basal spine on the inner radular tooth, and two prominent cusps on the outer tooth (Figs 3, 5).

- *O. pellucida*: *Zoobotryon verticillatum* [Vesiculariidae]
- *O. zoobotryon*: *Zoobotryon verticillatum* [Vesiculariidae]
- *O. mija*: *Amathia wilsoni* [Vesiculariidae]
- *O. vena*: *Amathia tortuosa* [Vesiculariidae]
- *O. purpurata*: *Amathia tortuosa* [Vesiculariidae]
- *O. japonica*: *Amathia cf. tortuosa* [Vesiculariidae]
The species of the ctenostome-feeding group are either small and cryptic or relatively large, brightly coloured and conspicuous. Cryptic species, such as *O. zoobotryon*, *O. cupella*, and *O. mija*, match their prey in colour, and have small lateral papillae, which form a cluster, very similar in size and shape to the clusters of bryozoan zooids.

**Group 3 [Cheilostome, often encrusting, bryozoan prey]:** These species were previously included in the genera *Sakishimaia*, *Hopkinsiella* and *Hopkinsia*. The most striking feature is the merging of the head and the foot. Ventrally there is a lateral groove at the level of the mouth, indicating the join (Fig. 27). Two species, *O. hallucigenia* and *O. kondoi* have a pronounced oral veil which I interpret as an adaptation of the fused ‘head-foot’ caused through the change in the body shape from flattened to cylindrical. A lateral groove across the ventral surface of the oral veil (Fig. 27E) is probably homologous with the lateral groove found in the flattened species.

- *O. plana*: *Membranipora membranacea* [Membraniporidae]; *Jellyella tuberculata* [Membraniporidae]; *Cryptosula pallasiana* [Cryptosulidae]
- *O. pilosa*: *Calpensia* sp., [Microporidae]
- *O. nakamotensis*: *Tropidozoum cellariiforme* Harmer, 1957 [Euthyrisellidae]
- *O. kondoi*: *Tropidozoum cellariiforme* Harmer, 1957 [Euthyrisellidae]
- *O. stellata*: *Pleurotoichus clathratus* [Euthyrisellidae]
- *O. hallucigenia*: *Pleurotoichus clathratus* [Euthyrisellidae]
- *O. hiroi*: *Integripelta* sp. [Eurystomellidae]
- *O. rosacea*: *Integripelta bilabiata* [Eurystomellidae]

Of the four groups, this cheilostome-feeding group shows the most diversity in body shape and foregut anatomy. Some species feed on flat, encrusting colonies, a behaviour which leaves the animal much more exposed to predators than is the case for animals feeding on arborescent colonies. Two species, *O. plana* and *O. pilosa*, are extremely well camouflaged, with very flattened bodies and a colour pattern matching the colour of the colony on which they live, even to the extent of having a white reticulate pattern to match the skeleton of the prey bryozoan (Fig. 30A). Accompanying this flattening has been the fusion of the head and foot. The other six species feed on reddish bryozoans and their colour matches that of the prey. In at least one species, *O. rosacea*, the nudibranch and its prey share the same pigment, hopkinsiaxanthin (McBeth, 1971). Despite this colour simi-
larity, it is unlikely that these pink species are using colour as camouflage, as their size, shape and behaviour make them very conspicuous. *Okenia rosacea* and *O. hiroi*, for example, are often found in association with flattened, encrusting, bryozoan colonies much smaller than themselves. The other four pink species, feed on branching euthyrisellid bryozoans. Only *O. kondoi*, with a cylindrical body, similar in diameter to the branches of its prey bryozoan, could be said to be in any way cryptic. As I discuss below, it would seem most probable that this brightly coloured group of species are displaying aposematic coloration.


Group 4 [unknown bryozoan prey]: This group includes a number of relatively large species with long lateral papillae, including O. barnardi, O. mellita, O. virginiae, O. lambat Gosliner, 2004 and O. kendi Gosliner, 2004. We have no feeding information on these species except for one report (Gosliner 2004) of O. kendi being found on encrusting bryozoans. They have a relatively large inner radular tooth, with minute denticles, and at least some development of jaw elements.
Gosliner’s analysis did not take the type of bryozoan prey into account, but if we compare these four ‘feeding groups’ with the clades proposed in Gosliner’s analysis, we find considerable agreement, suggesting a close correlation between phylogenetic relationship and feeding type. In his analysis, the ascidian feeders form a clade, the cheilostome bryozoan feeders form a clade, and the three species of my Group 4 for which he had information, form a clade. The only difference is that in Gosliner’s analysis, the ctenostome bryozoan feeders were considered to be in two clades, one of which (containing \textit{O. japonica}, \textit{O. purpureolineata}) was considered to be more closely related to Group 4 than to the other ctenostome feeders.

The many ways that nudibranchs use their external shape, colour pattern, and antifeedant chemicals, often obtained from their prey, in their own defence is well known (Rudman 1991, Gosliner 2001) and although no specific studies have yet been undertaken on species of \textit{Okenia}, there are many indications that the same processes have occurred within that genus. Species such the ctenostome-feeding \textit{O. zoobotryon} and \textit{O. mija} are extremely well camouflaged, in shape and colour, as are the cheilostome-feeding \textit{O. plana} and \textit{O. pilosa}, but there are also many species which are brightly coloured and conspicuous, apparently making no attempt to hide from potential predators, highly suggestive of aposematism (Rudman, 1991). A necessary requirement for aposematism is something (molecule, sting etc) which makes the potential prey a danger to any protential predator. Most bryozoans, that we have information on, metabolise a range of bromo-alkaloids which they use in their own defence and as anti-fouling agents (Anthoni, et al. 1990, Cimino & Ghiselin 1999, Morris & Prinsep 1996, Sato & Fenical 1983). Although we have no information on any species of \textit{Okenia}, the bryozoan-feeding nembrothid nudibranchs, \textit{Tambja abdere} Farmer 1978 and \textit{T. eliora} (Marcus & Marcus, 1967), sequester antifeedant metabolites (tambjamines) from \textit{Sessibugula translucens} Osburn, 1950, in glands in their skin (Carté & Faulkner 1983, 1986, Gribble 1999) which can be exuded as defensive secretions when the animals are attacked. A third nembrothid nudibranch, \textit{Roboastra tigris} Farmer, 1978, preys on the two species of \textit{Tambja} and re-uses the tambjamines in its own defensive glands. From their conspicuous colour, behaviour, and bryozoan food, it is highly likely that at least some species of \textit{Okenia} are aposematic.

The pink ‘\textit{Hopkinsia}-group’ forms an interesting subset of species. In Gosliner’s analysis of some of these species, \textit{O. hiroi} is separated from the others on the size of the receptaculum seminis, while the others are separated from each other on features of the radular morphology. If we consider the actual bryozoans being eaten by each species, serious consideration needs to be given to the possibility that two closely related species could have quite differently shaped teeth. For example, \textit{O. hiroi} from the northwestern temperate Pacific and \textit{O. rosacea}, from the northeastern temperate Pacific, show considerable similarity in external shape, they both feed on eurystomellid bryozoans of the genus \textit{Integripelta}, and they have a contiguous geographic distribution on either side of the temperate northern Pacific. One major difference is the shape and size of the radular teeth.
In *O. rosacea*, the inner teeth are extremely elongate, approximately 800 micrometers long, and have a recurved tip (Gosliner 2004). The inner teeth of *O. hiroi*, on the other hand, are denticulate, have a bifid tip, and are approximately 120 micrometers long (Fig. 21). These differences do not necessarily mean they are not closely related. As the other pink species show, it could just be that the two species have evolved a different way of feeding on similar foods. The other four species, all from the tropical Pacific, feed on branching, erect species of euthyrisellid bryozoans, and have a few prominent papillae which are often held erect. As I have discussed earlier, these four species form two similar pairs of species, each pair feeding on a different species of bryozoan. The species in each pair feed on the same bryozoan and each pair consists of a relatively flattened species and an upright cylindrical species. In these pairs, we find the most atypical radular morphology for the genus *Okenia*, and in each case, the radular morphology of the species within a pair is quite different (Figs 17, 19). This could suggest that form and function have no relationship, but as I have shown in coral-eating aeolids, (Rudman, 1981), different species can approach the same problem in different ways. The inner teeth of *O. stellata* and *O. nakamotoensis* appear to have evolved from a tooth similar to that of *O. rosacea*. The dorsal groove is also found in *O. hiroi* (Fig. 21) which has teeth much more typical of the genus.

How the blunt, rod-like teeth of *O. stellata* function is unknown. However, the inner teeth of *O. hallucigenia*, which feeds on the same bryozoan as *O. stellata*, are quite different in shape (Fig. 19) with greatly developed fine denticles. Of particular interest is the difference in size of the inner teeth in animals of similar size. In *O. stellata*, the rod-like teeth are approximately 800 micrometers long, while in *O. hallucigenia* they are only 30–40 micrometers, a difference in size of considerable magnitude. Obviously the teeth in the two species are being used in a different way. The foregut of *O. hallucigenia* is also unique, being the only species of the genus reported to have an oral tube. The possession of a long oral tube like this suggests that the teeth are everted some distance out of the mouth during feeding. I would suspect *O. hallucigenia* feeds on individual bryozoan zooids, one at a time, by inserting its tiny teeth into the individual chambers. If this is so, it would be a remarkable parallel to the situation found amongst the *Porites*-feeding aeolids, where the teeth of *Phestilla lugubris* (Bergh, 1870) are relatively large, while the teeth of *Cuthona poritophages* (Rudman, 1979) and *Phestilla minor* (Rudman, 1981) are relatively small for their respective genera. This reflects their different feeding techniques, with *P. lugubris* scraping large sheets of tissue from the coral colony, while *P. minor* and *C. poritophages* are picking individual polyps. From the tooth sizes shown in Gosliner’s review, *O. nakamotoensis* and *O. kondoi* would appear to show the same great difference in the tooth size. *Okenia rosacea* and *O. hiroi* can possibly be considered a third pair of species. Although not sympatric, their distributions are contiguous, they feed on closely related bryozoans, and there is the same great disparity in tooth size.

In most nudibranch groups, the radular morphology has proved to be a good indicator of phylogenetic relationships. In an ideal world, we would have multiple characters across
many organ systems to use in such an analysis, but in the case of *Okenia*, much of the anatomy shows little variation within the genus. Of the 21 characters used by Gosliner (2004), nine refer directly to the gut and seven to aspects of the body shape, all of which are directly associated with the food the particular species is feeding on. For example, it is possible that *O. stellata* and *O. hallucigenia* are a species pair descended from a common ancestor which have evolved separate solutions to feeding on *Pleurotoichus clathratus*, and similarly, perhaps *O. nakamutoensis* and *O. kondoi* have done the same on *Tropidozoum cellaiforme*, and *O. kondoi* and *O. hiroi* on eurystromellid bryozoans. Alternatively, perhaps *O. stellata*, *O. nakamutoensis* and *O. rosacea* have a common origin, and similarly *O. hallucigenia*, *O. kondoi* and *O. hiroi*. If this were the case, we would have the improbable coincidence of each bryozoan independently becoming the food of two unrelated species of *Okenia*, one with a large inner radular tooth and one with a very small radular tooth. Although it is essential to understand the anatomy of these species before hypothesising on their evolutionary relationships, it is probably impossible to adequately test these evolutionary hypotheses until we have a better knowledge of their biology.

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