

Phylogenetic Systematics of *Okenia*, *Sakishimaia*, *Hopkinsiella* and *Hopkinsia* (Nudibranchia: Goniodorididae) with Descriptions of New Species from the Tropical Indo-Pacific

Terrence M. Gosliner

Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118 U.S.A.; Email: tgosliner@calacademy.org.

The anatomy of eight species of *Okenia*, four species traditionally placed in *Hopkinsia* and one species of *Sakishimaia* was examined. The descriptions of previously described species, *Okenia pellucida*, *O. japonica*, *Hopkinsia rosacea*, *H. plana*, *H. pilosa*, *H. nakamotoensis* and *Sakishimaia kondoi* were expanded from prior morphological studies. Six new species of *Okenia* are described from the Indo-Pacific tropics. *Okenia brunneomaculata* is described from specimens collected from Indonesia and the Philippines. *Okenia purpureolineata* is known only from Okinawa in the Ryukyu Islands. *Okenia kendi* is described from specimens from Indonesia and the Philippines. *Okenia virginiae* is described from South Africa and is also known from Oman. *Okenia lambat* is described from the Philippines. *Okenia liklik* is described based on specimens from Papua New Guinea and the Philippines.

Preliminary phylogenetic studies reveal several important aspects about the relationships of these taxa. Collectively, these taxa appear to form a monophyletic clade.

Okenia mediterranea is the most basal taxon in the present analysis and is the sister group to all of the other taxa. *Hopkinsia*, *Sakishimaia* and *Hopkinsiella* are nested within *Okenia* in the analysis presented. The characteristics employed to distinguish *Sakishimaia* and *Hopkinsiella* from *Hopkinsia* are not distinctly different or represent autapomorphies or symplesiomorphies. *Hopkinsia*, when *Sakishimaia* and *Hopkinsiella* are included, constitutes a monophyletic taxon. However, maintenance of *Hopkinsia* as a distinct taxon renders *Okenia* paraphyletic. On this basis, *Hopkinsia*, *Hopkinsiella* and *Sakishimaia* are considered as synonyms of *Okenia* to preserve the monophyly of this oldest taxon.

The Indo-Pacific Goniodorididae consist of species that have been placed in the genera *Ancula* Loven, 1846; *Goniodoris* Forbes and Goodsir, 1839; *Goniodoridella* Pruvot-Fol, 1933; *Hopkinsia* MacFarland, 1905; *Hopkinsiella* Baba, 1938; *Murphydoris* Sigurdsson, 1991; *Okenia* Menke, 1830; *Sakishimaia* Hamatani, 2001; *Spahria* Risbec, 1928 and *Trapania* Pruvot-Fol, 1931. These taxa have been sporadically studied for the last 100 years with additional species described in a wide variety of faunistic and systematic treatments. Recently, Rudman's (1987) monographic study of Indo-Pacific species of *Trapania* has significantly added to our knowledge of Indo-Pacific Goniodorididae. Few taxonomic studies have focused on the distinctions between the genera *Okenia*, *Hopkinsiella*, *Hopkinsia* and *Sakishimaia*. Bouchet and Ortea (1983) revised the systematic distinctions between the former three genera and concluded that *Okenia* and *Hopkinsia* represent distinct genera, whereas *Hopkinsiella* is regarded as junior synonym of *Hopkinsia*. Most recently, Hamatani (2001) described two new species from Japan, a species of *Hopkinsia* and a member of a new genus, *Sakishimaia*.

Recent investigations of tropical coral reef ecosystems throughout the Indo-Pacific tropics from South Africa, the Philippines, Indonesia, Papua New Guinea, the Marshall Islands, and the Hawaiian Islands have yielded specimens of six new species of *Okenia*. Description of these taxa is the focus of this investigation. The discovery of additional specimens *Okenia pellucida* Burn, 1967; *O. japonica* Baba, 1949; *Hopkinsia pilosa* Bouchet and Ortea, 1983; *Hopkinsia nakamotoensis* Hamatani, 2001 and *Sakishimaia kondoi* Hamatani, 2001 has permitted the amplification of these species. Anatomical examination of these taxa and preliminary phylogenetic analyses undertaken here require systematic revision of several goniodoridid taxa. All specimens examined here are housed in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ) and the South African Museum (SAM).

SPECIES DESCRIPTIONS

Okenia Menke, 1830

Type species: *Okenia elegans* (Leuckart, 1828), by monotypy.

- Idalia* Leuckart, 1828 (type species, *Idalia elegans* (Leuckart, 1828), by original designation).
Idaliella Bergh, 1881 (type species, *Idaliella elegans* (Leuckart, 1828), by original designation).
Idalina Norman, 1890 (type species, *Idalina elegans* (Leuckart, 1828), by original designation).
Cargoa Vogel and Schultz, 1970 (type species *Cargoa cupella* Vogel and Schultz, 1970, by original designation).
Hopkinsia MacFarland, 1905 (type species: *Hopkinsia rosacea* MacFarland, 1905, by monotypy). SYN. NOV.
Hopkinsiella Baba, 1938, (type species, *H. hiroi* Baba, 1938, by original designation). SYN. NOV.
Sakishimaia Hamatani, 2001, (type species, *S. kondoi* Hamatani, 2001, by original designation). SYN. NOV.

Okenia pellucida Burn, 1967

(Figs. 1F, 2–3)

Okenia pellucida Burn, 1967:52, pls. X–XI, figs. 1–3.

MATERIAL EXAMINED.— CASIZ 078645, seven specimens, Maalena Bay, Maui, Hawaiian Islands, 6 m depth, 4 June 1991, P. Fiene Severns. CASIZ 078493, 26 specimens, 1 dissected, Marang River Mouth, 16 km s. of Kuala Terengganu, Malay Peninsula, Malaysia, intertidal zone, 26 July, 1991, T.M. Gosliner. CASIZ 168016, two specimens, Sand Island, Palmyra Atoll, Oceania, 10 m depth, 27 May 2002, T.M. Gosliner.

DISTRIBUTION.— Australia (Burn 1967), United Arab Emirates (Behrens 2001), Hawaii (Gosliner, Johnson, and Bertsch 1986), Japan (Kurihara 1999) Palmyra Atoll and Malaysia (both from present study).

NATURAL HISTORY.— *Okenia pellucida*, together with its elongate egg masses, is found commonly on large masses of the ctenostomatous bryozoan, *Zoobotryon* sp.

EXTERNAL MORPHOLOGY.— The body is elongate (7–20 mm in length) with numerous elongate, rounded papillae situated along the notal margin and on the remainder of the notum. The body (Fig. 1F) is translucent white with numerous thin brown lines that form an interconnecting network on the notum. The rhinophores also contain patches of brown pigment. The rhinophores are elongate with 11 well-spaced lamellae. The gill consists of 8 bipinnate branches.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular with a rounded buccal pump directed dorsally. Numerous small, elongate, pyriform oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buc-

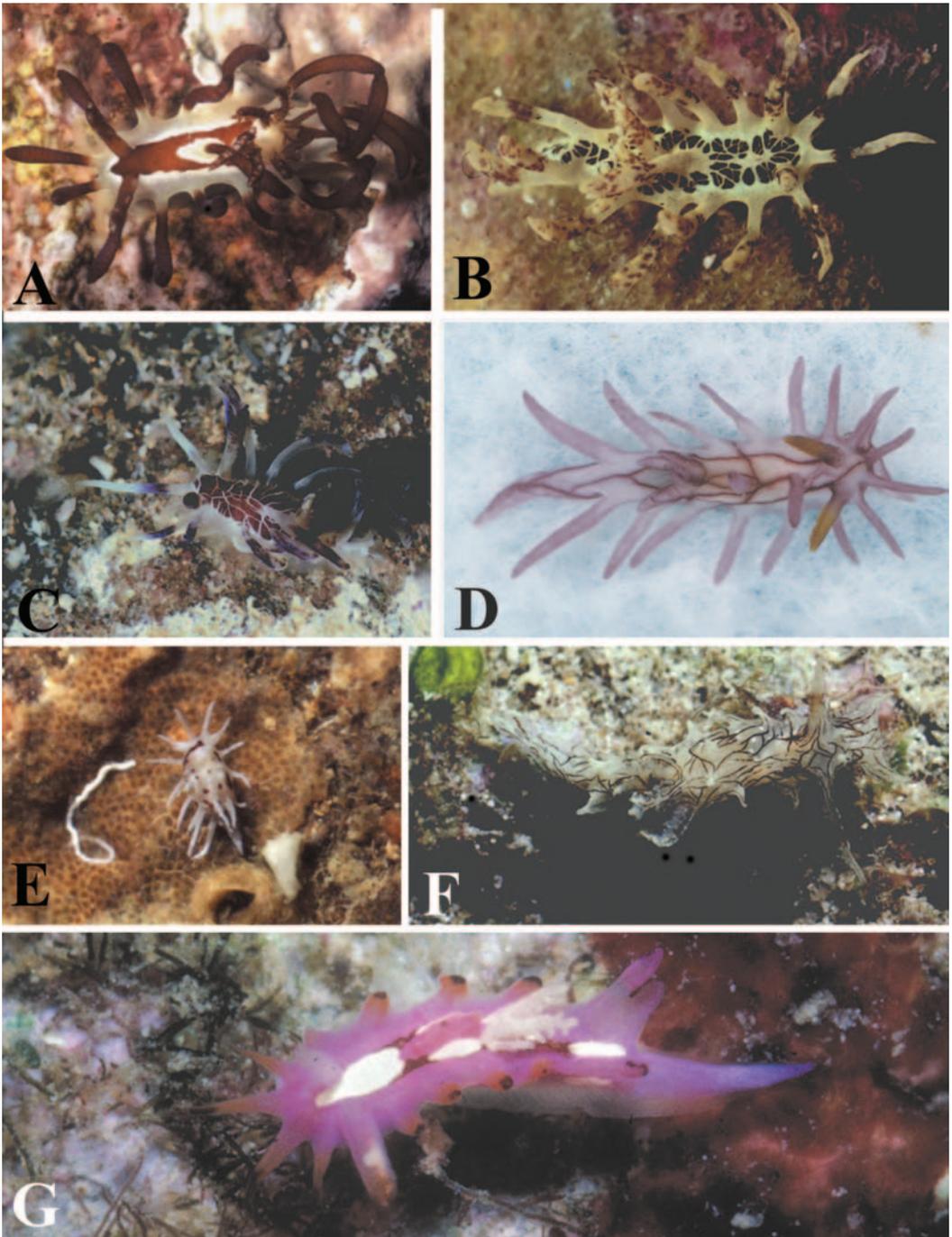


FIGURE 1. Living animals. A. *Okenia kendi* sp. nov., Sepok Point, Luzon, Philippines. B. *Okenia lambat* sp. nov. (CASIZ 084283), Devil's Point, Luzon, Philippines. C. *Okenia virginiae* sp. nov. (SAMA 35558), Vetchies Pier, Durban, South Africa. D. *Okenia purpureolineata* sp. nov., Seragaki Tombs, Okinawa, Japan, photo by R.F. Bolland. E. *Okenia brunneomaculata* sp. nov., Luzon, Philippines. F. *Okenia pellucida* Burn, 1967 (CASIZ 071398), Hawaii. G. *Okenia liklik* sp. nov., Barracuda Point, Madang, Papua New Guinea. All photos by T.M. Gosliner except as otherwise noted.

cal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates. The cuticle expands as it enters the buccal pump. The radular formula is $16 \times 1.1.0.1.1$. in one specimen examined. The inner lateral teeth (Fig. 2) are wide basally with an elongate acute bifid cusp. The masticatory margin of the inner lateral bears 17 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced (Fig. 2) with two short, blunt cusps along the outer edge.

REPRODUCTIVE SYSTEM (Fig. 3).— The preampullary duct is thin and elongate and expands into the elongate, sausage-shaped ampulla. The ampulla divides into a short oviduct that enters the female gland mass and a more elongate vas deferens. The proximal portion of the vas deferens is prostatic but relatively narrow. It curves and continues as an elongate loop that eventually widens slightly into the highly convoluted muscular, ejaculatory portion. The penial bulb is wide and conical. From it protrudes a rounded, fleshy penial papilla. The vagina is short and wide at its exit adjacent to the penis. More distally it narrows and continues as a thin duct that enters the base of the large, pyriform bursa copulatrix. From the base of the bursa is a second duct that joins with the smaller, more rounded receptaculum seminis. Near the base of the receptaculum the uterine duct separates from the duct joining the receptaculum and bursa and enters the female gland mass. The female gland mass consists of three portions, the albumen, membrane and mucous glands. The mucous gland is the largest of the nidamental glands.

DISCUSSION.— *Okenia pellucida* is immediately identifiable by its translucent white body color with a network of interconnecting thin brown lines. The present material agrees closely with that originally described by Burn (1967), with several exceptions. Burn did not describe the presence of oral glands surrounding the anterior end of the buccal mass. The original description included specimens with as many as 28



FIGURE 2. *Okenia pellucida* Burn, 1967 (CASIZ 078493). Scanning electron micrograph of radular teeth.

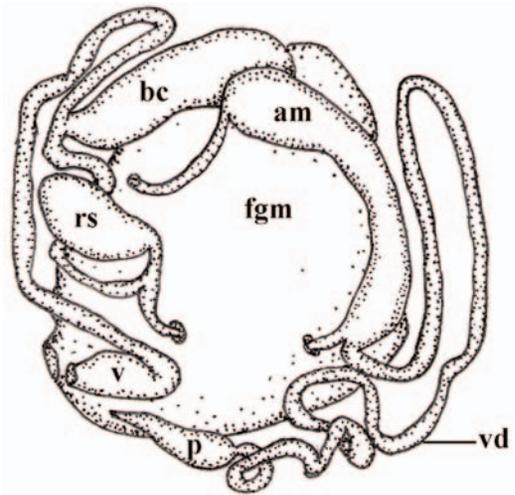


FIGURE 3. *Okenia pellucida* Burn, 1967 (CASIZ 078493). Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, rs = receptaculum seminis, v = vagina, vd = vas deferens; scale = 0.6 mm.

rows of radular teeth whereas the present material had only 16 rows. Burn also described the inner lateral teeth as having a smooth masticatory margin. The present material from Malaysia and specimens previously reported from the Hawaiian Islands (Gosliner, Johnson, and Bertsch 1986) have a series of triangular denticles along the masticatory margin. Despite these differences, the consistency in external anatomy, color pattern and reproductive anatomy suggest that all the material identified previously and from this study are conspecific. Recent records of this species support its wide ranging distribution from the United Arab Emirates to the Hawaiian Islands and Palmyra Atoll. This wide distribution of *Okenia pellucida* is not only facilitated by dispersal of planktotrophic larvae, but also by its association with the ctenostomatous bryozoan, *Zoobotryon* sp., which forms large masses carried by oceanic currents.

***Okenia brunneomaculata* Gosliner, sp. nov.**

(Figs. 1E, 4–5)

TYPE MATERIAL.— HOLOTYPE: CASIZ 168019, 20 m. depth, Ligpo Island, Calumpán Peninsula, Batangas Province, Luzon, Philippines, 1–2 m depth, 24 March 1993, T.M. Gosliner. PARATYPES: CASIZ 085876, 4 specimens, 2 dissected, 20 m. depth, Ligpo Island, Calumpán Peninsula, Batangas Province, Luzon, Philippines, 1–2 m depth, 24 March 1993, T.M. Gosliner. CASIZ 083853, 1 specimen, 20 m. depth, Sepok Point, Maricabán Island, Batangas Province, Luzon, Philippines, 1–2 m depth, 26 February 1992, T.M. Gosliner. CASIZ 168017, three specimens, Tulamben, Bali, Indonesia, 21 October 2001, M.D. Miller. CASIZ 168018, two specimens, Tulamben, Bali, Indonesia, 21 October 2001, M.D. Miller.

ETYMOLOGY.— The specific name, *Okenia brunneomaculata*, comes from the scattered brown spots found on the dorsal surface of the notum.

DISTRIBUTION.— This species is known only from Luzon Island, Philippines and Bali, Indonesia (present study).

NATURAL HISTORY.— This species is found on ctenostomatous bryozoans on the undersides of the large foliose sponge colonies.

EXTERNAL MORPHOLOGY.— The living animals (Fig. 1E) are small, 4–6 mm in length. The preserved specimens are 2–3 mm. long. The body is moderately short and relatively high. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly translucent white. There is a lateral band of chocolate brown and irregular spots of the same color scattered over the notum. There are 5–6 pairs of elongate notal papillae along the sides of the body. The two anteriormost pairs of papillae are situated in front of the rhinophores and are anteriorly directed. Four to seven elongate papillae are scattered mid-dorsally anterior to the gill. A single mid-dorsal papilla is present posterior to the gill. The gill consists of 3–5 unipinnate branches. The rhinophores are elongate with 10 well-spaced lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and widens anteriorly. The oral tentacles (Fig. 4A) are elongate and extend well beyond the margin of the foot.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular with a rounded buccal pump directed posteriorly. There are no obvious oral glands around the mouth. The radular sac is short and extends ventrally from the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth but no discrete jaw elements are visible. The cuticle expands as it enters the buccal pump. The radular formula is $14 \times 1.1.0.1.1.$ in one specimen examined. The inner lateral teeth (Fig. 5A) are broad basally with an acutely pointed cusp and 9–11 elongate denticles along the masticatory

margin. The outer laterals are slightly smaller and reduced (Fig. 5B) with bifid cusp with two elongate projections along the outer side.

REPRODUCTIVE SYSTEM (Fig. 4B).— The preampullary duct is short and thin and expands into sausage-shaped ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded segments. The distal end of the prostatic segment narrows into a short, curved ejaculatory portion that terminates in a narrow penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow and elongate and connects directly to the large, spherical bursa copulatrix. At the base the bursa, the receptaculum duct emerges and parallels the vagina for some distance prior to joining the large, pyriform receptaculum seminis. The uterine duct emerges from near the base of the receptaculum and enters the female gland mass.

DISCUSSION.— Several other species of *Okenia* have a whitish body color with brown markings: *O. angelensis* Lance, 1966; *O. zoobotryon* (Smallwood, 1910); *O. impexa* Marcus, 1957; *O. mija* Burn, 1967, *O. pellucida* Burn, 1967. All of these other species have much shorter notal papillae than does *O. brunneomaculata*. In *O. brunneomaculata*, the notal papillae are as long as the width of the body. The dorsal brown spots and bands of *O. brunneomaculata* are much larger than those found in the remaining species. The internal anatomy of *O. mija* remains unknown. Of the remaining species, *O. zoobotryon* and *O. angelensis* have outer lateral teeth that are short and rounded with bifid cusp (Marcus 1957; Valdés and Ortea 1995; Lance 1966). *Okenia brunneomaculata* and *O. impexa* have elongate outer laterals with a bifid cusp. In *O. impexa*, the outer lateral tooth has an additional basal denticle that is not present in *O. brunneomaculata*. *Okenia impexa* also has a single mid-dorsal papilla, whereas *O. brunneomaculata* has numerous dorsal papillae.

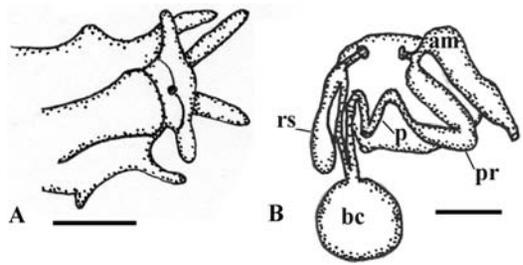


FIGURE 4. *Okenia brunneomaculata* sp. nov. (CASIZ 085876). A. Ventral surface of head; scale = 0.5 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, p = penis, pr = prostate, rs = receptaculum seminis; scale = 0.2 mm.

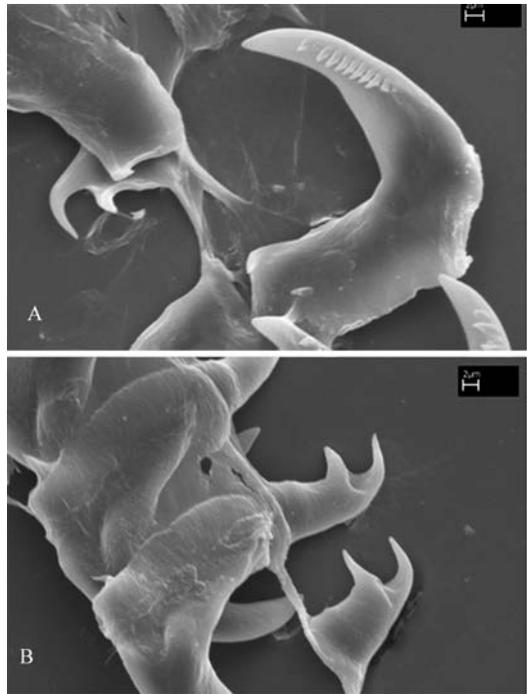


FIGURE 5. *Okenia brunneomaculata* sp. nov. (CASIZ 085876). Scanning electron micrographs of radular teeth. A. Inner lateral teeth. B. Outer lateral teeth. Scale = 2 μ m.

Okenia japonica Baba, 1949

(Figs. 6–7)

Okenia (Okenia) japonica Baba, 1949:45, fig. 45, pl. 15, fig. 52, Rudman and Darvell, 1990:39, pl. 2a.

MATERIAL EXAMINED.—CASIZ 070216, 1 specimen, 170 ft. [52 m] deep, Seragaki Beach, Okinawa, 22 April 1989, R.F. Bolland. CASIZ 099075, 1 specimen, 190 ft [58 m] deep, Seragaki Tombs, Okinawa, 12 March 1994, R.F. Bolland. CASIZ 105350, 2 specimens, 180 ft [55 m] deep, Seragaki Beach, Okinawa, 24 March 1994, R.F. Bolland. CASIZ 115378, 1 specimen, 190 ft [58 m] deep, Seragaki, Okinawa, 30 April 1989, R.F. Bolland. CASIZ 115382, 2 specimens dissected, 195 ft [59 m] deep, Seragaki, Okinawa, 11 April 1997, R.F. Bolland. RFB 2135B 180 ft [55 m] deep, Seragaki, Okinawa, 30 April 1989, R.F. Bolland.

DISTRIBUTION.—This species is known from Sagami Bay and Kii, Japan (Baba 1949) and Hong Kong (Rudman and Darvell 1990) and is here recorded from Okinawa in the Ryukyu Islands.

NATURAL HISTORY.—*Okenia japonica* was collected on erect arborescent bryozoans in 50–60 m depth (R. Bolland, pers. commun.).

EXTERNAL MORPHOLOGY.—The living animals are 10–13 mm in length. The body is moderately elongate and relatively high. There is well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly translucent white with a dense, uniform covering of opaque white. There are 6–7 pairs of elongate notal papillae along the sides of the body. The two anteriormost papillae are situated in front of the rhinophores and are anteriorly directed. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of 4–5 unipinnate branches. The anteriormost branch is frequently bifid at the base. The rhinophores are elongate with 7–8 congested lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and is wider anteriorly. The oral tentacles (Fig. 6A) are broadly triangular and extend beyond the lateral margins of the foot.

DIGESTIVE SYSTEM.—The buccal mass is thick and muscular (Fig. 6B) with a rounded buccal pump directed dorsally. Numerous, large,

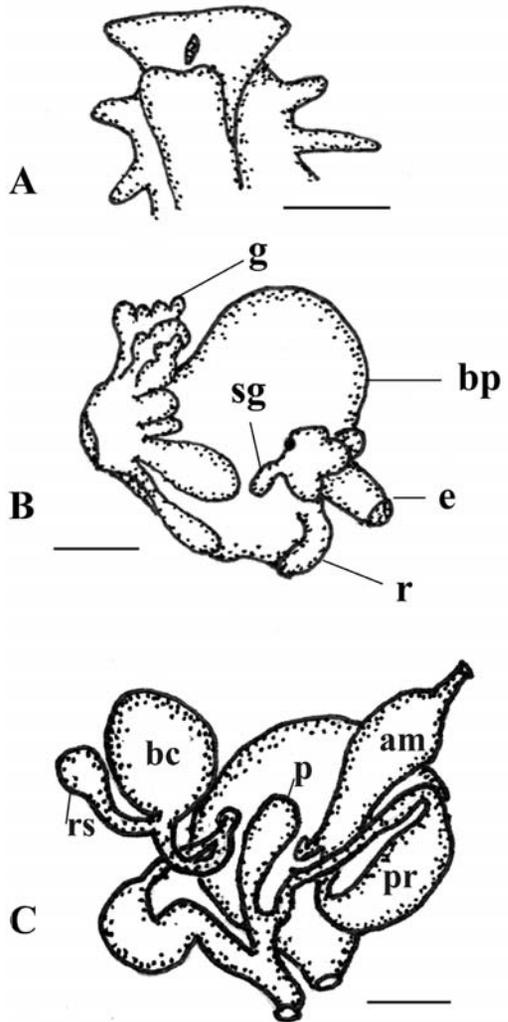


FIGURE 6. *Okenia japonica* Baba, 1949 (CASIZ115382). A. ventral view of head, scale = 1 mm. B. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland; scale = 0.25 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, p = penis, pr = prostate, rs = receptaculum seminis; scale = 0.2 mm.

elongate, pyriform oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates. The cuticle expands as it enters the buccal pump. The radular formula is $20 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 7) are wide basally with an elongate acute cusp. The masticatory margin of the inner lateral bears about 19–22 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced (Fig. 7) with a short cusp along the outer edge.

CENTRAL NERVOUS SYSTEM.— The ganglia of the central nervous system are highly concentrated and surround the esophagus, at the posterior end of the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 6C).— The preampullary duct is short and thin and expands into an ovoid ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of a single, undivided portion. The distal end of the prostatic segment narrows into an elongate, straight ejaculatory portion that terminates near the base of the wide, elongate penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and elongate basally and narrows more proximally. The narrow portion connects directly to the spherical bursa copulatrix and the smaller, pyriform receptaculum seminis. Near the middle of the narrow portion of the vagina, the uterine duct separates and enters the albumen gland.

DISCUSSION.— This species has been documented only once since its original description (Baba 1949; Rudman and Darvell 1990). The presence of a yellowish white body with fine opaque white markings is consistent between the original description and the present material. The number of notal appendages, the presence of a single medial papilla and a basally bifid anterior gill branch are also consistent between the original and present material. The denticulation and shape of the radular teeth are also very similar. The only difference noted is that Baba described 5–8 mm animals with 32–35 row of radular teeth whereas the present material (10–13 mm) has only 20 rows. The large oral glands were not noted by Baba nor was the reproductive anatomy described.



FIGURE 7. *Okenia japonica* Baba, 1949 (CASIZ 115382). Scanning electron micrograph of radular teeth; scale = 20 μ m.

There is little doubt that the present material from deep water in Okinawa represents the same species originally described by Baba.

***Okenia purpureolineata* Gosliner, sp. nov.**

(Figs. 1D, 8–9)

TYPE MATERIAL.— HOLOTYPE: CASIZ 168020, 160 ft deep, Seragaki Beach, Okinawa, 2 June 1989, R.F. Bolland. PARATYPES: CASIZ 099097, 1 specimen, 190 ft [58 m] deep, Seragaki Tombs, Okinawa 12 March 1994, R.F. Bolland. CASIZ 099085, 1 specimen, 175 ft [53 m] deep, Seragaki Tombs, Okinawa 18 February 1994, R.F. Bolland. CASIZ 070256, 1 specimen, dissected, 160 ft [49 m] deep, Seragaki Beach, Okinawa, 2 June 1989, R.F. Bolland. CASIZ 070217, 1 specimen, 180 ft. [55 m] deep, Seragaki Beach, Okinawa, 30 April 1989, R.F. Bolland.

ETYMOLOGY.— The species name, *Okenia purpureolineata*, is derived from the presence of longitudinal purple lines on the dorsal surface of the body.

DISTRIBUTION.— This species is known only from Okinawa in the Ryukyu Islands (present study).

NATURAL HISTORY.— *Okenia purpureolineata* was collected on erect arborescent bryozoans in 49–60 m depth (R. Bolland, pers. commun.).

EXTERNAL MORPHOLOGY.— The living animals (Fig. 1D) are 10–12 mm in length. The body is moderately elongate and relatively high. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly translucent purple. There is an irregular network of darker purple lines on the dorsal surface of the notum. Darker purple pigment is also present on the gill lamellae. The rhinophores are dark purple basally and red throughout most of their length. There are seven pairs of elongate notal papillae along the sides of the body. The two anteriormost pairs of papillae are situated in front of the rhinophores and are anteriorly directed. Two medial papillae are present mid-dorsally anterior to the gill. The gill consists of 4–5 unipinnate branches. The rhinophores are elongate with 18–21 congested lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and is wider anteriorly. The oral tentacles are broadly triangular and extend beyond the lateral margins of the foot.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular (Fig. 8A) with a rounded buccal pump directed posterodorsally. Numerous large, elongate, pyriform oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and

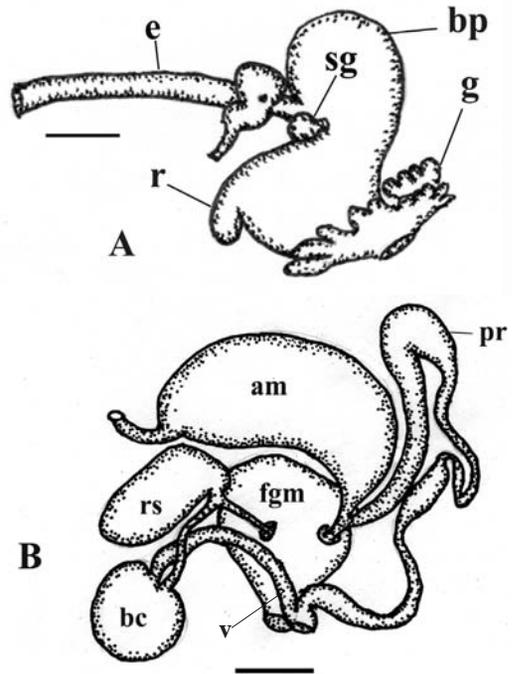


FIGURE 8. *Okenia purpureolineata* sp. nov. (CASIZ 070256). A. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland; scale = 0.25 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.35 mm.

extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is $28 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 9A) are wide basally with an elongate acute cusp. The masticatory margin of the inner lateral bears 9–12 coarse, triangular denticles. The outer laterals are small and reduced (Fig. 9B) and quadrangular.

CENTRAL NERVOUS SYSTEM.— The ganglia of the central nervous system are highly concentrated and surround the esophagus, at the posterior end of the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 8B).— The preampullary duct is short and thin and expands into a large sausage-shaped ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and bilobed. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates at the top of the widest portion of the elongate penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is narrow and elongate throughout its length. The proximal end of the vagina enters the spherical bursa copulatrix. At the base of the bursa another duct connects the large, pyriform receptaculum seminis. At the base of the receptaculum, the short uterine duct separates and enters the albumen gland.

DISCUSSION.— *Okenia purpureolineata* is similar to *O. japonica* in its external body shape. Both species occur sympatrically in relatively deep water from Okinawa. Although *O. japonica* is uniformly white in color, *O. purpureolineata* is purple with darker purple lines on the notum and red rhinophores. *Okenia purpureolineata* has two mid-dorsal papillae but only one is present in *O. japonica*. Both species have large oral glands surrounding the anterior end of the buccal mass, but

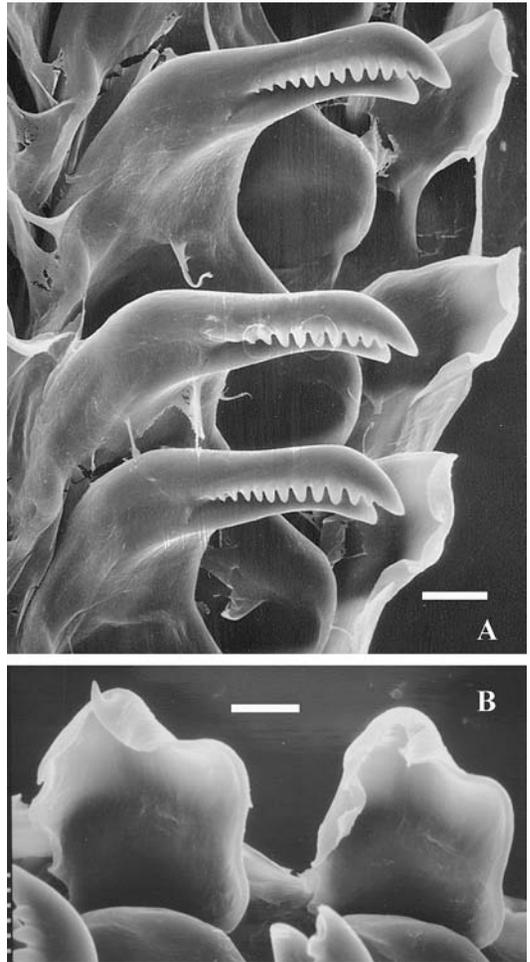


FIGURE 9. *Okenia purpureolineata* sp. nov. (CASIZ 070256). Scanning electron micrographs of radular teeth. A. View of half row of radular teeth; scale = 19 μ m. B. Outer lateral teeth; scale = 12 μ m.

there are more numerous glands in *O. purpureolineata*, that are smaller in size. The inner lateral teeth of *O. purpureolineata* have 9–12 large denticles along the masticatory border whereas there are 19–22 finer denticles on the inner laterals of *O. japonica*. In the reproductive system of *O. purpureolineata*, the receptaculum seminis and bursa copulatrix are well separated from each other whereas in *O. japonica* they are immediately adjacent to each other.

***Okenia kendi* Gosliner, sp. nov.**

(Figs. 1A, 10–11)

Okenia sp. 2 Gosliner, Behrens and Williams, 1996:171, fig. 605.

TYPE MATERIAL.—**HOLOTYPE:** CASIZ 110451, 1 specimen, Bethlehem, Caban Island, Batangas Province, Luzon, Philippines, 10 m depth, 24 April 1997, T.M. Gosliner. **PARATYPES:** CASIZ 085880, 2 specimens, Babbit, Calumpan Peninsula, Batangas Province, Luzon, Philippines 25 March 1993, T.M. Gosliner. CASIZ 085892, 2 specimens, Layalayag, Maricaban Island, Batangas Province, Luzon, Philippines, 22 March 1993, T.M. Gosliner. CASIZ 085877, 2 specimens, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 23 March 1993, T.M. Gosliner. CASIZ 085883, 2 specimens dissected, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 26 March 1993, T.M. Gosliner. CASIZ 097397, 1 specimen, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 13 March 1994, T.M. Gosliner. CASIZ 105681, 1 specimen, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 26 February 1995, T.M. Gosliner. CASIZ 106593, 1 specimen, Bethlehem, Caban Island, Batangas Province, Luzon, Philippines, 15 m depth, 19 April 1996, T.M. Gosliner. CASIZ 093923, 2 specimens, Tandarusa Wreck and Pulau Kecil, Lembeh Strait, Manado, Sulawesi, Indonesia, 5–6 November 1993, P. Fiene Severns.

ETYMOLOGY.— The specific epithet *kendi* is the Filipino word for candy, in reference to its appearance to a sweet confection.

DISTRIBUTION.— This species is known from the Luzon Island, Philippines (Gosliner, Behrens, and Williams 1996) and Sulawesi, Indonesia (present study).

NATURAL HISTORY.— *Okenia kendi* is found on the underside of the large brown leafy sponge *Phyllospongia lamellosa* (Esper, 1799), on shallow reefs in 5–15 meters of water, where it feeds upon encrusting bryozoans (Gosliner, Behrens, and Williams, 1996).

EXTERNAL MORPHOLOGY.— The living animals (Fig. 1A) attain 30 mm in length. Preserved specimens range in size from 15–25 mm. The body is wide and dorso–ventrally flattened. There is a well–developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The general body color is translucent yellowish white. There is a broad mid-dorsal band of maroon pigment that runs from anterior to the rhinophores to the posterior end of the foot. The band divides around the mid-dorsal papillae and the two bifurcations rejoin each other posterior to the gills. The rhinophores and gill also have maroon pigment but also possess opaque white markings along their lengths. The medial and marginal papillae are maroon at the base and possess purple pigment more distally. There is a lateral line of maroon present on either side of the body between the notum and the foot. There are eight pairs of elongate notal papillae along the sides of the body. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of three unipinnate branches that are bifid or trifid at the base. The rhinophores are elongate with 31 congested lamellae. The anterior end of the foot contains two elongate rounded lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is broad and is divided anteriorly. A groove separates the foot from the mouth and oral tentacles (Fig. 10A).

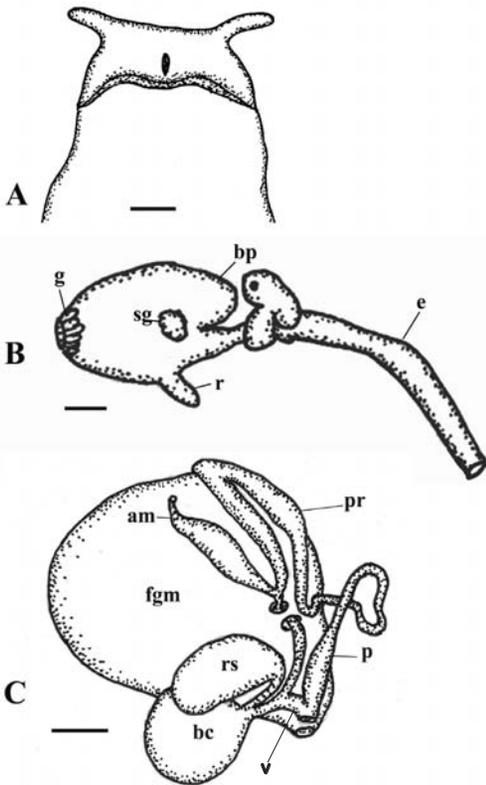


FIGURE 10. *Okenia kendi* sp. nov. (CSIZ 085883). A. ventral view of head; scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland, scale = 0.5 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.4 mm.

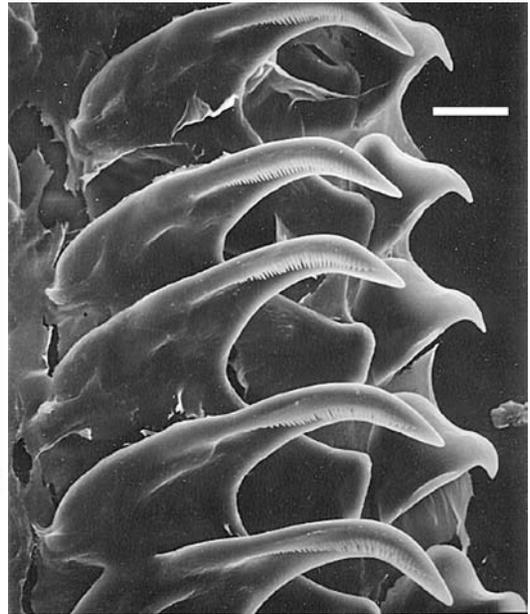


FIGURE 11. *Okenia kendi* sp. nov. (CASIZ 085883). Scanning electron micrograph of radular teeth; scale = 23 μ m.

the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is $26 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 11) are broad basally with an acutely pointed cusp and 35–38 elongate denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 11) with an elongate cusp along their outer side.

CENTRAL NERVOUS SYSTEM.—The ganglia of the central nervous system are highly concentrated and surround the esophagus, immediately posterior to the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 10C).—The preampullary duct is short and thin and expands into an elongate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamen-

DIGESTIVE SYSTEM.—The buccal mass is thick and muscular (Fig. 10B) with a rounded buccal pump directed posteriorly. There are a few elongate oral glands around the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of

tal glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates in a wide, elongate penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and short and connects directly to the spherical bursa copulatrix. Near the base of the vagina, the uterine duct separates and enters the albumen gland. From the base of the bursa copulatrix, a narrow duct connects the bursa with the large, pyriform receptaculum seminis.

DISCUSSION.— Two described species of Indo-Pacific species of *Okenia* are similar in external appearance to *O. kendi*. *Okenia plebeia* (Bergh, 1902) and *Okenia barnardi* Baba, 1937, have a series elongate appendages along the notal margins and possess a single elongate mid-dorsal papilla. The color pattern of living specimens of *O. plebeia* is unknown. The radula of *O. plebeia* has a similar formula to that of *O. kendi*. with 27–28 rows of teeth. The inner lateral teeth of *O. plebeia* have approximately 30 denticles along the masticatory margin whereas *O. kendi* has 35–38 denticles. The outer lateral teeth of *O. plebeia* are rounded but those of *O. kendi* have a sharply pointed apical extension. The reproductive system of *O. plebeia* has a short prostate with a muscular portion that is four times the length of the penis. In *O. kendi*, the prostate is long and the muscular portion of the vas deferens is only about twice the length of the penis.

Okenia barnardi has a markedly different color pattern to that of *O. kendi*. It is light brown with a darker brown band near the notal margin that is punctuated by opaque white spots. An opaque white line is present dorsally on the posterior end of the foot. In contrast, *O. kendi* has a pattern of maroon blotches located on the notum. The anatomy of *O. barnardi* is largely undescribed. The radula was depicted in the original description (Baba 1937). The outer lateral teeth of *O. barnardi* have a rounded apex whereas there is a pronounced apical denticle on the outer laterals of *O. kendi*.

***Okenia virginiae* Gosliner, sp. nov.**

(Figs. 1C, 12–13)

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

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

TYPE MATERIAL.— HOLOTYPE: SAM A35558, one specimen, dissected, Vetchies Pier, Durban, South Africa, 28 April 1982, T.M. Gosliner.

ETYMOLOGY.— *Okenia virginiae* is named for my mother, Virginia Malaney Gosliner, in recognition of her nurturing my earliest interest in natural history.

DISTRIBUTION.— This species is known from the Natal, South Africa (Gosliner 1987) and Oman (Debelius 1996).

NATURAL HISTORY.— *Okenia virginiae* was found on the underside of a small rock in 2 meters of water. The specimen when dissected was found to be parasitized by three trematodes.

EXTERNAL MORPHOLOGY.— The living animal (Fig. 1C) was 10 mm in length. It is 8 mm long in the preserved state. The body is wide and dorsoventrally flattened. There is well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The general body color is translucent white. There is a broad mid-dorsal band of brown pigment that runs from anterior to the rhinophores to the posterior end of the foot. It is interrupted by an irregular network of white pigment. The notal papillae, rhinophores and gill have irregular maroon bands along their length. There are 8 pairs of elongate notal papillae along the sides of the body. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of three unipinnate branches that are bifid or trifid at the base. The rhinophores are elongate with 21 congested lamellae. The

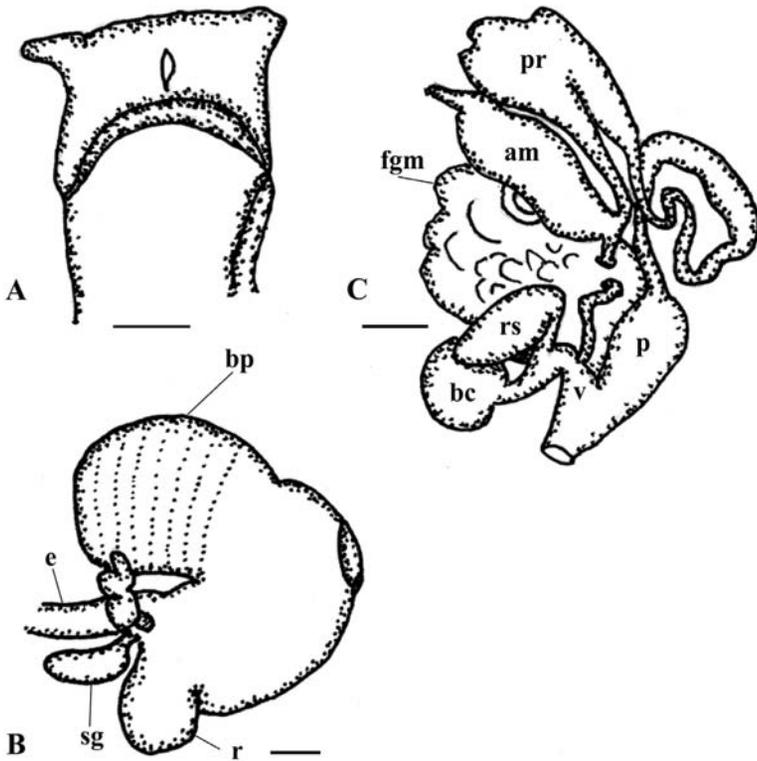


FIGURE 12. *Okenia virginiae* sp. nov. (SAMA 35558). A. ventral view of head scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, g = oral glands, r = radula sac, sg = salivary gland; scale = 0.1 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.2 mm.

anterior end of the foot contains two elongate rounded lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is broad and is divided anteriorly. A groove separates the foot from the mouth and elongate, triangular oral tentacles (Fig. 12A).

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular (Fig. 12B) with a rounded buccal pump directed posteriorly. There are a few elongate oral glands around the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates with a denticulate margin (Fig. 13B). The cuticle expands as it enters the buccal pump. The radular formula is $24 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 13A) are broad basally with an acutely pointed cusp and 22–33 small, irregular denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 13A). They have a short cusp along their outer side.

CENTRAL NERVOUS SYSTEM.— The ganglia of the central nervous system are highly concentrated and surround the esophagus, immediately posterior to the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure.

Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 12C).— The preampullary duct is short and thin and expands into an elongate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and short and connects directly to the spherical bursa copulatrix. Near the base of the vagina, the uterine duct separates and enters the albumen gland. Distal from the base of the bursa copulatrix, a narrow duct connects the bursa with the large, pyriform receptaculum seminis.

DISCUSSION.— This species has been recently erroneously identified as *Okenia barnardi* (Debelius, 1996:196, upper photo). *Okenia virginiae* differs from *O. barnardi* in its color pattern by having dark brown pigment located in the center of the notum rather than submarginally and in having a network of white lines rather than opaque white spots. The outer lateral teeth are broad basally with a rounded apex in both *O. barnardi* and *O. virginiae*, in contrast to *O. kendi*, where the outer lateral teeth each have a pointed cusp. The reproductive anatomy of *O. barnardi* has not been described. *Okenia virginiae* has a reproductive system with a short vagina with the uterine duct entering the vagina near its base. This arrangement has not been described for any other member of the genus.

***Okenia lambat* Gosliner, sp. nov.**

(Figs. 1B, 14–15)

TYPE MATERIAL.— Holotype: CASIZ 084283, 1 specimen, dissected, Devil's Pt., Maricaban Island, Batangas Province, Luzon, Philippines, 10 m depth, 23 February 1992, T.M. Gosliner.

ETYMOLOGY.— The specific epithet *lambat* is derived from the Filipino word for net, referring to the network of white markings that is visible through the brown notal pigment.

DISTRIBUTION.— This species is known from the Luzon Island, Philippines (present study).

NATURAL HISTORY.— *Okenia lambat* has been found under a small stone in 10 meters of water.

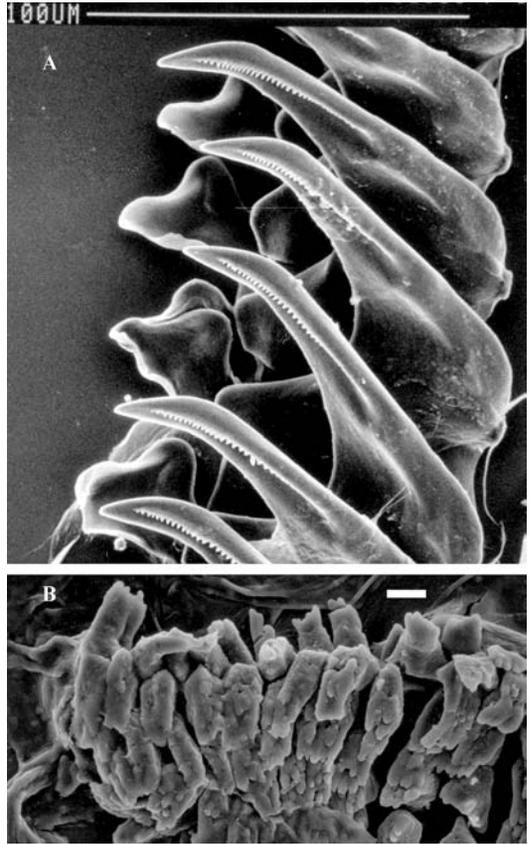


FIGURE 13. *Okenia virginiae* sp. nov. (SAMA 35558). Scanning electron micrographs. A. Half-row of radular teeth; scale = 100 μ m. B. Jaw rodlets; scale = 6 μ m.

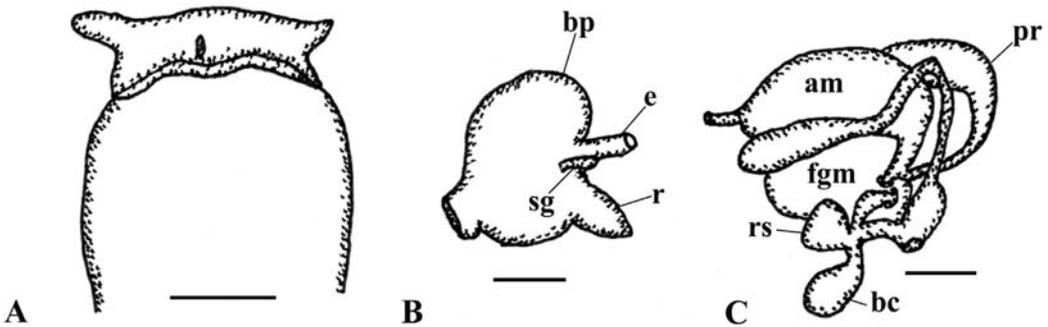


FIGURE 14. *Okenia lambat* sp. nov. (CASIZ 084283). A. ventral view of head, scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac, sg = salivary gland; 0.2 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis; scale = 0.1 mm.

EXTERNAL MORPHOLOGY.— The living animal (Fig. 1B) was 7 mm in length. Preserved, the specimen is 6 mm long. The body is wide and dorsoventrally flattened. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The general body color is opaque yellowish white. There is a broad mid-dorsal band of brown pigment that runs from anterior to the rhinophores to the posterior end of the foot. It is interrupted by an irregular network of white pigment. The notal papillae, rhinophores and gill have irregular maroon spots along their length. There are 8 pairs of elongate notal papillae along the sides of the body. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of three elongate, unipinnate branches. The two lateral branches are undivided and the anterior one is bifid to the base. The rhinophores are elongate with 18 congested lamellae. The anterior end of the foot contains two elongate rounded lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is broad and is divided anteriorly. A groove separates the foot from the mouth and oral tentacles (Fig. 14A).

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular (Fig. 14B) with a massive rounded buccal pump directed posteriorly. There are a few elongate oral glands around the mouth. The radular sac is relatively short and extends posteroventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded rods. The cuticle expands as it enters the buccal pump. The radular formula is $18 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 15A) are broad basally with an acutely pointed cusp and 18–19 denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 15B). They have an elongate cusp along their upper margin of the outer side and a rounded lobe basally.

REPRODUCTIVE SYSTEM (Fig. 14C).— The preampullary duct is short and thin and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is relatively narrow and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, curved ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is wide and short and connects directly to the spherical bursa copulatrix. Near the base

of the bursa, the uterine duct separates from the vagina and enters the albumen gland. Also from the base of the bursa copulatrix, an additional narrow duct connects the bursa with the small, rounded receptaculum seminis.

DISCUSSION.— *Okenia lambat* is very similar in its external appearance to *O. virginiae*. Both species have a series of lateral papillae with a single medial one and have dark brown dorsomedial pigment interrupted by a network of white lines. The general body color of *O. virginiae* is translucent white to cream whereas that of *O. lambat* is opaque yellowish white. Internally there are other differences that distinguish these taxa. In *O. lambat*, the masticatory margin-bearing denticles extend virtually to the apex of the primary cusp, in *O. virginiae* whereas the denticles terminate well short of the apex. The outer lateral teeth of *O. lambat* each bear an extended, acutely-pointed cusp, but in *O. virginiae* the cusp is much shorter and more rounded. Despite the fact that both *O. lambat* and *O. virginiae* are unique in having a much-shortened vagina, there are differences in the reproductive anatomy of the two species. In *O. lambat* the ejaculatory portion of the vas deferens is relatively short and is of uniform diameter throughout its length. In contrast, the elongate ejaculatory vas deferens of *O. virginiae* consists of a thin distal portion that expands into a wider portion that enters the penial bulb. In *O. lambat*, the uterine duct joins the vagina at the base of the receptaculum seminis whereas in *O. virginiae* it enters the genital atrium at the base of the vagina.

***Okenia liklik* Gosliner, sp. nov.**

(Figs. 1G, 16–17)

TYPE MATERIAL.— **HOLOTYPE:** CASIZ 168021, one specimen, Barracuda Pt., Tab Island, Madang Lagoon, Madang, Papua New Guinea, 7 February 1988, R.C. Willan. **PARATYPES:** CASIZ 168022, one specimen, Barracuda Pt., Tab Island, Madang Lagoon, Madang, Papua New Guinea, 7 February 1988, R.C. Willan. CASIZ 168023, one specimen, dissected, Bus Stop, Balayan Bay, Batangas, Luzon Island, Philippines, 10 m depth, 9 May 2001, Á. Valdés.

Etymology.— The specific epithet *liklik* is the Papuan pidgin word for small, in reference to the tiny body size of the mature specimens of this species.

DISTRIBUTION.— This species has been found from Papua New Guinea and Luzon Island in the Philippines (present study).

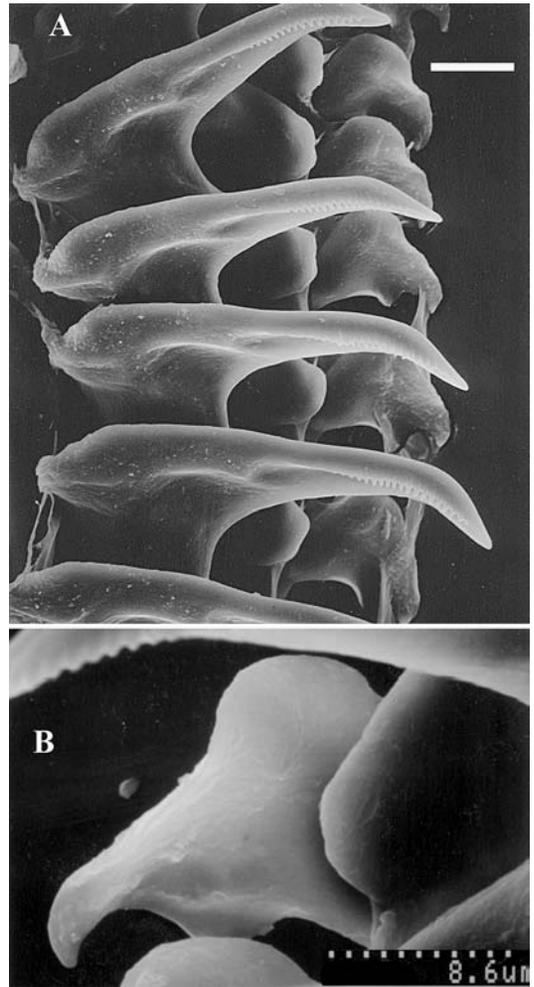


FIGURE 15. *Okenia lambat* sp. nov. (CASIZ 084283). Scanning electron micrograph of radular teeth. A. View of half row of radular teeth; scale = 13 μm . B. Outer lateral tooth; scale = 8.6 μm .

EXTERNAL MORPHOLOGY.— The living animals (Fig. 1G) are small, 3–4 mm in length. The body is elongate and relatively high. There is a well-developed, continuous notal border. Immediately ventral to the notum is a series of small subdermal mantle glands situated in the posterior half of the body (Fig. 16A). The foot extends posteriorly and is devoid of notal papillae. The body color is uniformly purplish pink. There is mid-dorsal band of chocolate brown that is interrupted by connected or three interrupted, irregular opaque white markings. The gill is uniformly opaque white. All but the posterior pair of papillae are tipped with an orange subapical marking and, in some cases, a chocolate brown apex. The posterior pair and the single medial papilla are purple with chocolate brown, but lack orange pigment. There are 8–9 pairs of elongate notal papillae along the sides of the body. The two anteriormost pairs of papillae are situated in front of the rhinophores and are anteriorly directed. A single mid-dorsal papilla is present anterior to the gill. It has the form of a crenulate crest rather than a more typical digitiform papilla. The gill consists of 3 unipinnate branches. The rhinophores are elongate with 17–18 congested lamellae. The anterior end of the foot contains two elongate triangular lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and is divided anteriorly.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular (Fig. 16B) with a large rounded, elongate buccal pump directed posteriorly. There are a several elongate oral glands around the

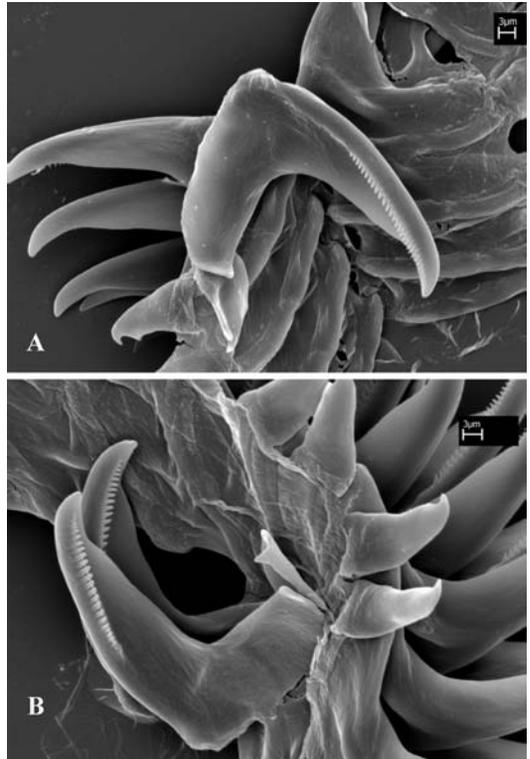
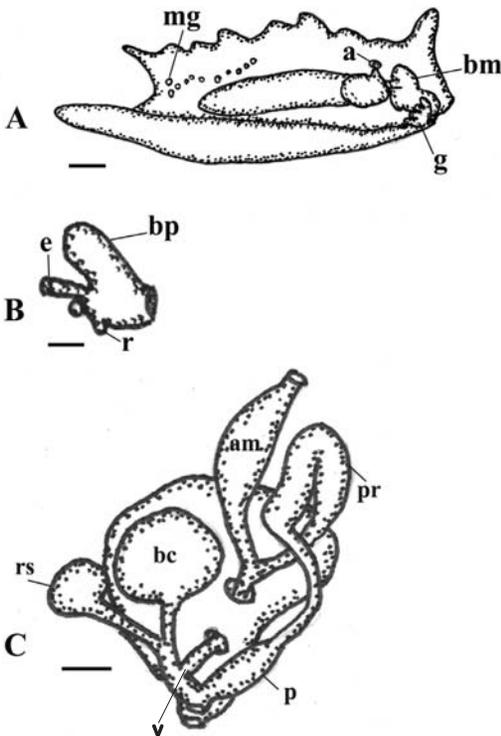


FIGURE 16 (left). *Okenia liklik* sp. nov. (CASIS 168023). A. Lateral view of preserved specimen, a = anus, bm = buccal mass, g = oral glands, mg = mantle glands; scale = 0.2 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac; scale = 0.1 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.1 mm.

FIGURE 17 (right). *Okenia liklik* sp. nov. (CASIS 168023). Scanning electron micrograph of radular teeth. A. Inner lateral teeth; scale = 3µm. B. Inner and outer lateral teeth; scale = 3µm.

mouth. The radular sac is relatively short and extends posteroventrally from the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. No distinct rodlets are evident around the opening of the buccal cuticle. The radular formula is $12 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 17A, B) are broad basally with an acutely pointed cusp and 24–26 fine denticles along the masticatory margin. The outer laterals are smaller and reduced (Fig. 17B) with a single acute cusp.

REPRODUCTIVE SYSTEM (Fig. 16C).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic segment of the vas deferens is relatively narrow and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, curved ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is wide and short and connects directly to the small, triangular bursa copulatrix. Near the base of the vagina, the short uterine duct separates from the vagina and enters the albumen gland. Also from the middle of the vaginal duct, an additional narrow duct connects the bursa with the large, rounded receptaculum seminis.

DISCUSSION.— *Okenia liklik* has a distinctive purplish pink body color with orange, brown and opaque white markings. No other described species has been described as having glands situated near the posterior margin of the mantle. As in some other species of *Okenia*, such as *O. japonica* and *O. purpureolineata*, the body is elongate and narrow and large oral glands are present surrounding the mouth. The relatively large, unifid outer lateral teeth are more elongate than those found in other described species.

Okenia rosacea (MacFarland, 1905)

(Figs. 18–19)

Hopkinsia rosacea MacFarland, 1905:53; 1906:149, pl. 31, figs. 24,25, pl. 21, figs. 97–103.

Okenia rosacea (MacFarland, 1905) **comb. nov.**

MATERIAL EXAMINED.— CASIZ 072075, specimens, one dissected, Great Tide Pool, Pacific Grove, California, 1 June 1973, Gary McDonald.

DISTRIBUTION.— This species was originally described from Monterey Bay, California (MacFarland 1905) has been found from Coos Bay, Oregon to Isla San Martin, Baja California (Behrens 1991).

NATURAL HISTORY.— This species feeds upon the cheilostomatous bryozoan, *Eurystomella* sp. (Behrens 1991).

DIGESTIVE SYSTEM.— The buccal mass is large and the radular sac is elongate, extending well behind the posterior end of the muscular mass. The radular teeth of *Okenia rosacea* are distinctive. The inner laterals (Fig. 18) are elongate with a recurved apex forming a distinctive hook. The outer laterals are reduced to a small vestigial plate.

REPRODUCTIVE SYSTEM (Fig. 19).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the much wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental



FIGURE 18. *Okenia rosacea* (MacFarland, 1905). (CASIZ 072075) Scanning electron micrograph of inner lateral tooth; scale = 200 μ m.

glands exit ventrally to the vagina and penis. The prostatic segment of the vas deferens is relatively wide and consists of two folded portions. The distal end of the prostatic segment narrows into an elongate, convoluted ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow and elongate and connects directly to the large, saccate bursa copulatrix. Near the distal end of the vagina, the long uterine duct separates from the vagina and enters the albumen gland. Also from the distal end of the vaginal duct, an additional narrow duct connects to the small, saccate receptaculum seminis. Penial hooks were not observed.

DISCUSSION.— *Okenia rosacea* is similar to *O. hiroi* (Baba, 1938) in its external anatomy and uniform pink coloration. The two species differ markedly in their radular anatomy: whereas *O. rosacea* has elongate, curved inner lateral teeth, those of *O. hiroi* are denticulate and hamate in shape. Only *O. rosacea* and *O. nakamotoensis* have elongate inner lateral radular teeth that terminate in a sharply curved apex. Those of *O. nakamotoensis* are even thinner and more elongate than those found in *O. rosacea*. Subsequent phylogenetic analysis shows that *Hopkinsia* is nested within *Okenia* and is therefore regarded as a synonym of the older taxon, *Okenia*.

Okenia plana Baba, 1960

(Figs. 20B, 21–22)

Okenia plana Baba, 1960:80, pl.7, figs 2a–d).

Hopkinsia plana (Baba, 1960), Bouchet and Ortea, 1983:231; Rudman and Darvell, 1990:37, pl.1f.

MATERIAL EXAMINED.— CASIZ 001026, six specimens, two dissected. Cooley's Landing, East Palo Alto, San Francisco Bay, California, 2 February 1977, D. Chivers. CASIZ 101373, five specimens, two dissected, Berkeley Fishing Pier, San Francisco Bay, California, 6 March 1963, L. Andrews. CASIZ 083837, 1 specimen, dissected, Seafari, Calumpán Peninsula, Batangas Province, Luzon, Philippines, 1–2 m depth, 17 February 1992, T.M. Gosliner.

DISTRIBUTION.— This species was originally described from Japan (Baba, 1960) and later recorded from Hong Kong (Rudman and Darvell 1990), California (Steinberg 1963; Behrens 1991), New Zealand and Australia (Rudman 1998). The present specimen extends the range to the Philippines. The specimens from California represents a human introduction (Behrens 1991).

NATURAL HISTORY.— In the Philippines this species was found under coral rubble in about 6 meters of water. Specimens introduced into San Francisco Bay have been observed on the encrusting cheilostomatous bryozoan, *Membranipora* sp., growing on arborescent algae (present study).

EXTERNAL MORPHOLOGY.— The living animals (Fig. 20B) attain 10–15 mm in length. Preserved specimens were 4–9 mm long. The body is broad and ovoid. There is no distinct notal border. The foot is short and does not extend beyond the oval of the general body. The body is uni-

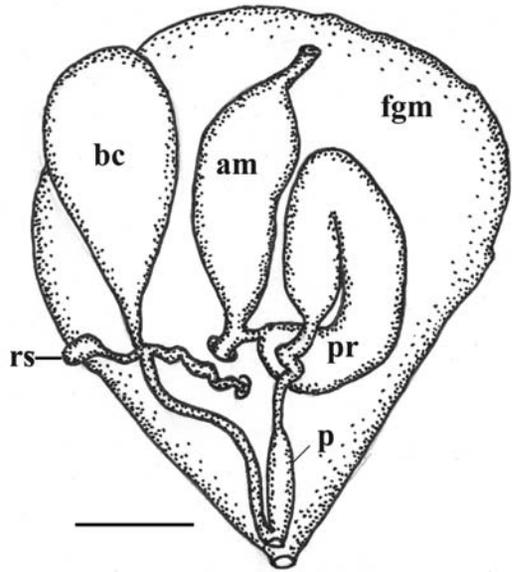


FIGURE 19. *Okenia rosacea* (MacFarland, 1905). (CASIZ 072075). Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis; scale = 1.0 mm.

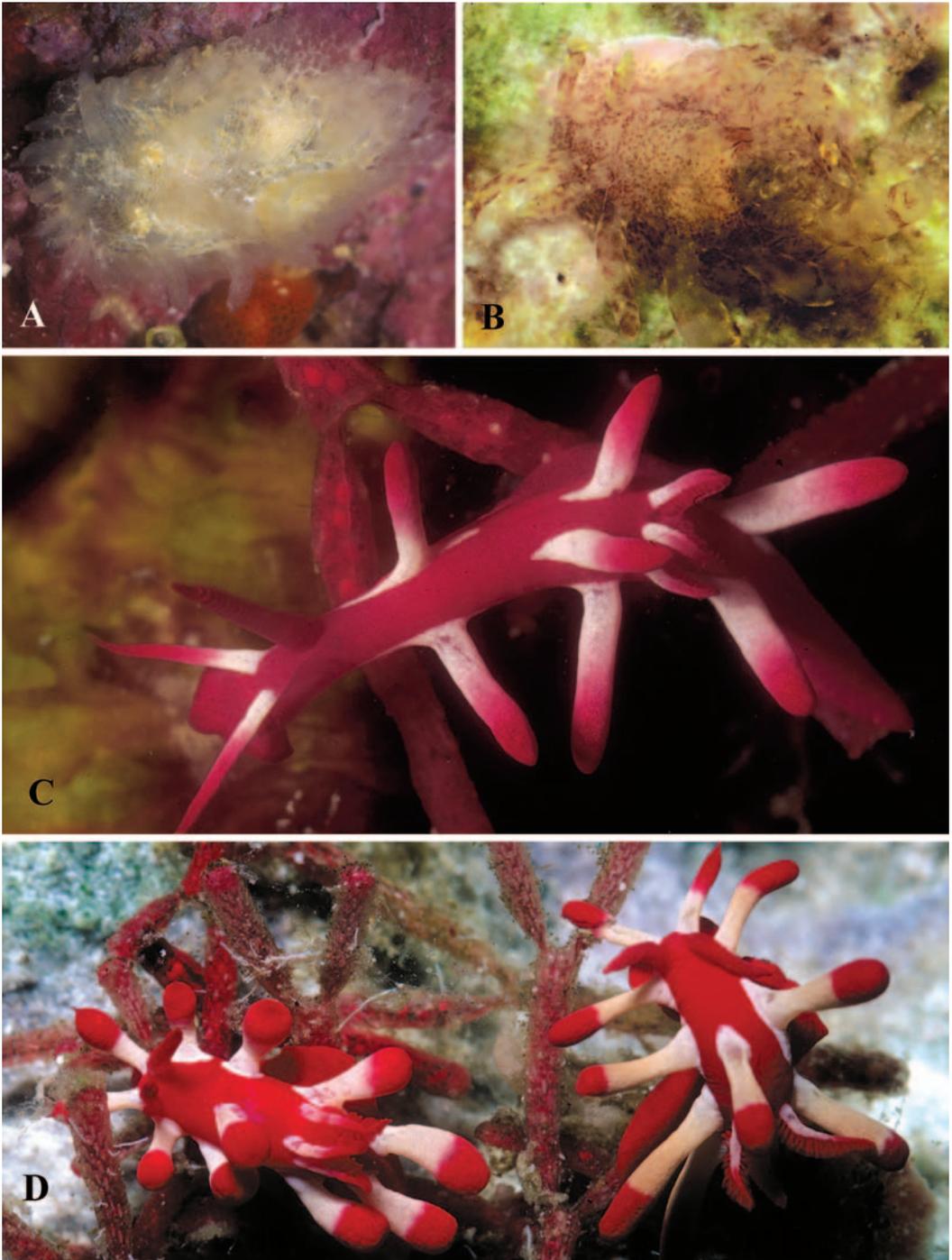


FIGURE 20. Living animals. A. *Okenia pilosa* (Bouchet and Ortea), 1983 (CASIZ 109784), Barracuda Point, Madang, Papua New Guinea. B. *Okenia plana* Baba, 1960 (CASIZ 083837), Anilao, Luzon, Philippines. C. *Okenia kondoi* (Hamatani, 2001), Balicasag Island, Bohol, Philippines. D. *Okenia nakamotoensis* (Hamatani, 2001), Balicasag Island, Bohol, Philippines, photo by G. Williams. All photos by T.M. Gosliner except as otherwise noted.

formly translucent yellowish white with the exception of small brown spots scattered over the surface of the notum and occasional opaque white spots. The notal papillae, rhinophores and gill all possess larger brown and yellow blotches. There are 5 pairs of elongate papillae scattered on either side of the dorsal surface of the body. A single medial papillae is present mid-dorsally anterior to the gill. The gill consists of 9–11 unipinnate branches. The rhinophores are relatively short with 12–15 congested lamellae. The anterior end of the foot is deeply indented anteriorly forming a v-shaped edge that encloses the mouth (Fig. 21A). The oral tentacles are indistinct but are separated from the foot by a groove. The genital aperture is situated on the right side of the dorsal surface of the body approximately a third of the length of the body posterior to the head.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular with a rounded buccal pump situated anteriorly. The radular sac is relatively short. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is $21-29 \times 1.1.0.1.1$ in two specimens examined. The inner lateral teeth (Fig. 22) are thin and elongate and with a straight apex. They are devoid of denticles. The outer laterals are small and reduced with two pointed denticles along the outer margin, occasionally with 2–3 smaller denticles along the edge.

REPRODUCTIVE SYSTEM (Fig. 21B).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the narrow vas deferens that expands into a massive, lobate prostatic portion. The oviduct enters the highly folded female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. More distally the lobate prostatic segment of the vas deferens narrows somewhat into a second glandular section that is relatively wide and consists of two folded sections. The distal end of the prostatic segment narrows into an elongate, thin, curved ejaculatory portion that terminates in a narrow penis. There is no distinct penial papilla. The thin vaginal duct exits adjacent to the penis. It is elongate and narrow and connects directly to the large, spherical bursa copulatrix. Near the base of the bursa, another elongate duct enters the small pyriform receptaculum seminis. Also from the base of the receptaculum, the short uterine duct enters the large female gland mass.

DISCUSSION.— *Okenia plana* lacks the pink color of *O. rosacea* and *O. hiroi* and is uniformly

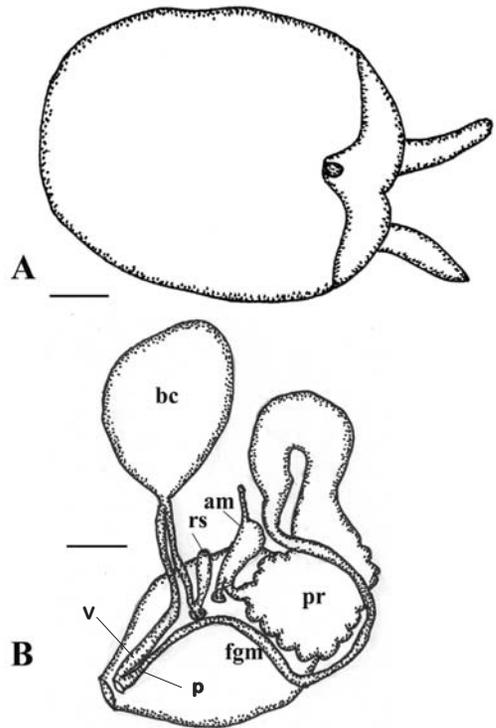


FIGURE 21. *Okenia plana* Baba, 1960. A. Ventral view of preserved specimen, (CASIZ 083837); scale = 0.6 mm. B. Reproductive system, (CASIZ 001026), am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.5 mm.

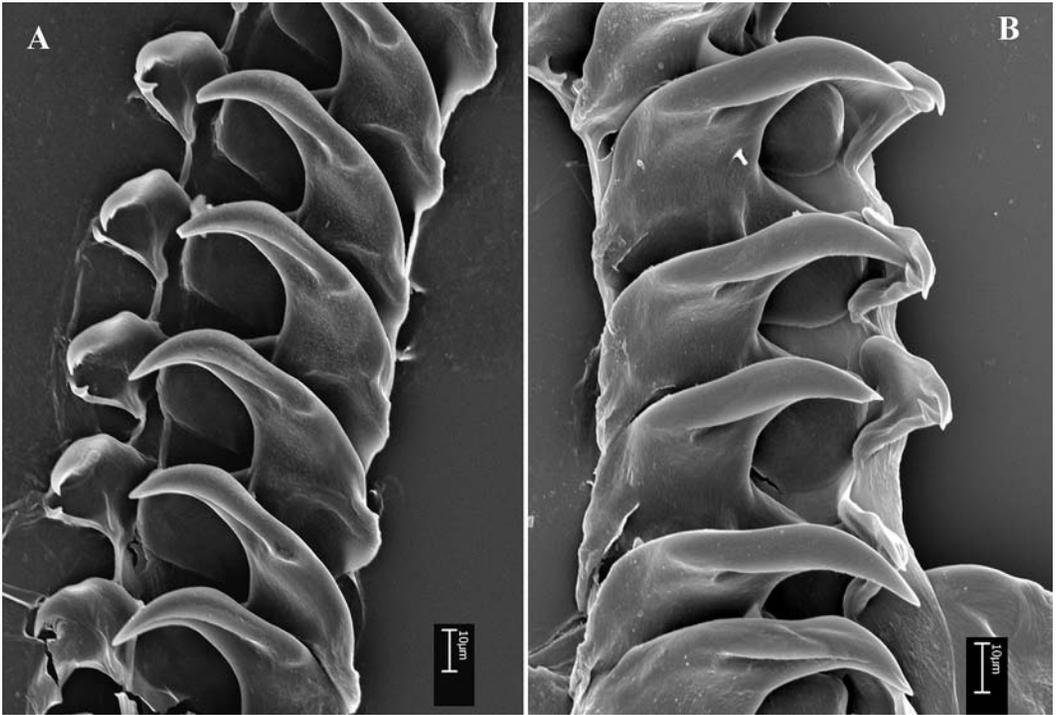


FIGURE 22. *Okenia plana* (Baba, 1960). Scanning electron micrographs of radular teeth. A. Half row of radular teeth of specimen from San Francisco Bay (CASIZ 001026); scale = 10µm. B. Half row of radular teeth of specimen from the Philippines (CASIZ 083837); scale = 10µm

yellowish white with black spots and opaque white markings on the notum and notal papillae. Its color pattern is similar to that found in *O. pilosa* Bouchet and Ortea, 1983. The two species differ in the arrangement of the notal papillae and in their radular anatomy. In *O. plana* there are almost always five pairs of marginal notal papillae and a single mid-dorsal papilla, whereas in *O. pilosa* there are 35–40 scattered papillae over the surface of the notum. In *O. plana* the inner lateral teeth are short and evenly arched, whereas in *O. pilosa* the primary cusp is far more elongate. In *O. plana*, the outer lateral tooth has two primary denticles with occasional 2–3 smaller denticles. In *O. pilosa* the outer lateral teeth have up to 14 denticles along their outer margin.

There is little anatomical difference in the Californian and Philippine specimens examined here. The primary difference is in the color pattern. The specimens from California have larger, darker brown spots that are more regularly distributed over the surface of the notum and notal papillae. There is little difference in the shape and denticulation of the radular teeth. The reproductive anatomy of this species has not previously been described. The most distinctive features of the reproductive anatomy are the lobed prostate, the extremely narrow ejaculatory portion of the vas deferens and the thin vagina.

Okenia pilosa (Bouchet and Ortea, 1983)

(Figs. 20A, 23–24)

Hopkinsia pilosa Bouchet and Ortea, 1983:227, figs 1–7; Rudman and Darvell, 1990:36, pl. 1.e.

Okenia pilosa (Bouchet and Ortea, 1983) **comb. nov.**

MATERIAL EXAMINED.— CASIZ 109784, 10 m depth, Barracuda Point, Tab Island, Madang

Lagoon, Madang, Papua New Guinea, 4 November 1996, T. M. Gosliner.

DISTRIBUTION.— This species was originally described from New Caledonia (Bouchet and Ortea 1983) and later recorded from Hong Kong (Rudman and Darvell 1990). The present specimen extends the range to Papua New Guinea.

NATURAL HISTORY.— This species is found under coral rubble in about 6 meters of water.

EXTERNAL MORPHOLOGY.— The living animals (Fig. 20A) reach 13 mm in length. The preserved specimen was 11 mm long. The body is broad and ovoid. There is no distinct notal border. The foot is short and does not extend beyond the oval of the general body. The body is uniformly translucent white with the exceptions of a network of opaque white and yellow pigment on the notum and rhinophores. The gill rachises are also translucent yellow. Scattered brown spots are present on the notum. There are 35–40 elongate papillae scattered over the dorsal surface of the body. A single medial papilla is present mid-dorsally and is situated immediately anterior to the gill. The gill consists of 12 bipinnate branches. The rhinophores are relatively short with 7–8 congested lamellae. The anterior end of the foot is deeply indented anteriorly forming a v-shaped edge that

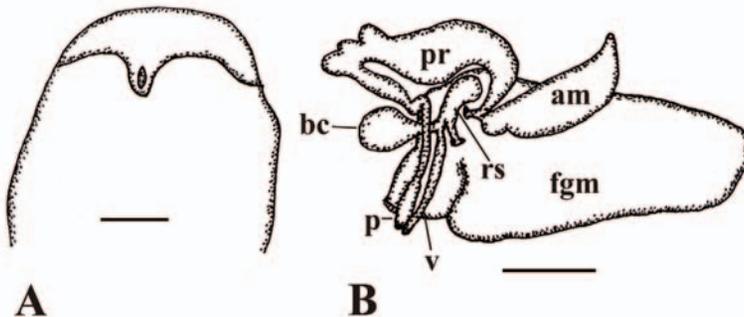


FIGURE 23 *Okenia pilosa* (Bouchet and Ortea, 1983) (CASIZ 109784). A. Ventral view of preserved specimen; scale = 1.0 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.4 mm.

encloses the mouth (Fig. 23A). The oral tentacles are indistinct but are separated from the foot by a groove. The genital aperture is situated on the right side of the dorsal surface of the body approximately a third of the length of the body posterior to the head.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular with a rounded buccal pump situated anteriorly. The radular sac is relatively short. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is $19 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 24) are thin and elongate and with a straight apex. They are devoid of denticles. The outer laterals are small and reduced with an approximately 14 denticles along the masticatory margin.

REPRODUCTIVE SYSTEM (Fig. 23B).— The preampullary duct is short and expands into a wide saccate ampulla. The ampulla divides into a short, narrow oviduct and the wide prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic segment of the vas deferens is relatively wide and consists of two convoluted, folded portions. The distal end of the prostatic segment narrows

into an elongate, curved ejaculatory portion that terminates in a short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is elongate and narrow and connects directly to the small, spherical bursa copulatrix. Near the base of the bursa, a short duct enters the pyriform receptaculum seminis. Also from the base of the receptaculum, the short uterine duct enters the large female gland mass.

DISCUSSION.— As in *Okenia plana*, a translucent body color with mottled brown spots and opaque white pigment makes the living animals of *O. pilosa* exceedingly cryptic when encountered on their host bryozoans. The anatomical distinctions between these two taxa are reviewed in the discussion following *O. plana*.

In their original description of *H. pilosa*, Bouchet and Ortea (1983) revised the systematics of taxa included in *Hopkinsia*. They transferred *Okenia plana* Baba, 1960 and *Hopkinsiella*, with its monotypic species, *H. hiroi*, to *Hopkinsia*. They noted that radular differences between *Hopkinsia rosacea* and *Hopkinsiella hiroi* were of specific value rather than generic value. They noted that the primary feature that distinguishes *Hopkinsia* from *Okenia* is the absence of a distinct pallial ridge in the former. Bouchet and Ortea stated that members of the two genera feed on different prey with species of *Hopkinsia* feeding on Bryozoa whereas species of *Okenia* feed on tunicates. However, it is evident from many studies, including the present work, that several species of *Okenia* are also specialists on bryozoans rather than tunicates (Burn 1967; Rudman and Darvell 1990; present study). Subsequent phylogenetic analysis supports the inclusion of all of these taxa within a single monophyletic taxon, *Okenia*.

***Okenia nakamotoensis* (Hamatani, 2001)**

(Figs. 20D, 25–26)

Okenia sp. 1 Gosliner, Behrens and Williams, 1996: 171, fig. 604.

Hopkinsia nakamotoensis Hamatani, 2001:151, fig. 1 A–E.

Okenia nakamotoensis (Hamatani, 2001) **comb. nov.**

MATERIAL EXAMINED.— CASIZ 096238, 5 specimens, 2 dissected, Balacasag Island, Bohol, Philippines, 29 m. depth, 21 March 1994, T. M. Gosliner. CASIZ 096244, 2 specimens, Balacasag Island, Bohol, Philippines, 34 m. depth, 22 March 1994, T. M. Gosliner. CASIZ 117028, 1 specimen, 20 m depth, R. Buoy Pinnacle, Kwajalein Atoll, Marshall Islands, 28 March 1992, S. Johnson. CASIZ 120736, 3 specimens, Cement Ship Pinnacle, Enewetak Atoll, Marshall Islands, 21 August 1983, S. Johnson. CASIZ 120732, 4 specimens, 1 dissected, Enewetak Atoll, Marshall Islands, 5 June 1983, S. Johnson. CASIZ 120733, 5 specimens, 15 m depth, R. Buoy Pinnacle, Kwajalein

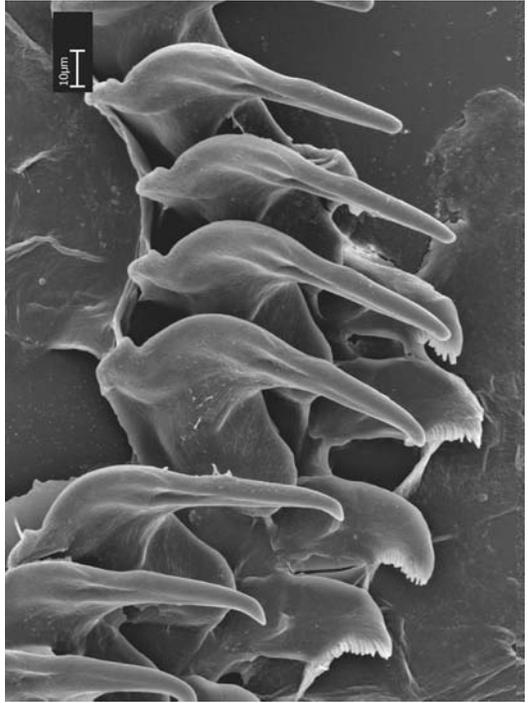


FIGURE 24. *Okenia pilosa* (Bouchet and Ortea), 1983 (CASIZ 109784). Scanning electron micrograph of radular teeth; scale = 10 μ m.

Atoll, Marshall Islands, 18 June 1982, S. Johnson. CASIZ 120734, 5 specimens, R. Buoy Pinnacle, Kwajalein Atoll, Marshall Islands, 22 June 1982, S. Johnson. CASIZ 120735, 7 specimens, 1–20 m depth, R. Buoy Pinnacle, Kwajalein Atoll, Marshall Islands, J. Johnson. CASIZ 093922, 5 specimens, unnamed reef near Koon Island, East Banda Sea, Indonesia, 17–30 m depth, 14 November 1993, P. Fiene Severns.

DISTRIBUTION.— This species is known from the Kuroshima Island, Japan (Hamatani 2001) Indonesia, Bohol and Cebu Islands (Philippines) and Enewetak and Kwajalein Atolls (Marshall Islands) (Gosliner, Behrens, and Williams 1996; present study).

NATURAL HISTORY.— This species is found on outer reef faces in 10–30 meters of water, where it feeds upon the bright red bryozoan, *Tropidozoum cellariforme* Harmer, 1957 (Gosliner, Behrens, and Williams 1996).

EXTERNAL MORPHOLOGY.— The living animals (Fig. 20D) attain 20 mm in length. Preserved specimens range in size from 3–13 mm. The body is elongate and wide. There is no distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body is uniformly red with the exceptions of the gill rachises and the base of the notal papillae, which are pinkish white. The gill lamellae and apices of the notal papillae are the same color as the remainder of the body. There are five pairs of elongate notal papillae along the sides of the body. Two of these are situated anterior to the rhinophores. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of 3–4 unipinnate branches. The rhinophores are elongate with 13–20 congested lamellae. The anterior end of the foot is rounded and forms a projection anterior to the mouth. The oral tentacles are fused to form an oral veil. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head.

DIGESTIVE SYSTEM.— The buccal mass is thick and muscular (Fig. 25A) with a rounded buccal pump situated anteriorly. The radular sac is elongate and is approximately equal in length to the rest of the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular rounded plates. The cuticle expands as it enters the buccal pump. The radular formula is $16 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 26A) are extremely thin and elongate and with a hooked apex (Fig. 26B). They are devoid of denticles. Some of the older teeth are eroded and have a simple rounded or irregularly fractured apex. The outer laterals are small and reduced (Fig. 26C) with an anteriorly directed cusp.

CENTRAL NERVOUS SYSTEM.— The ganglia of the central nervous system are highly concentrated and surround the esophagus. The cerebral and pleural ganglia are largely fused. A sessile eye

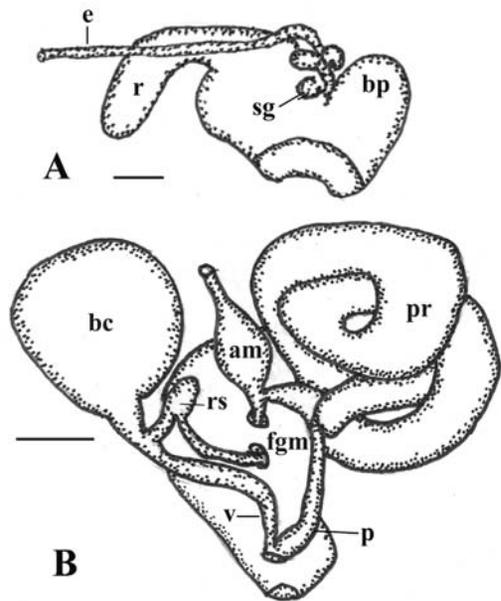


FIGURE 25. *Okenia nakamotoensis* (Hamatani, 2001) (CASIZ 096238). A. Buccal mass, bp = buccal pump, e = esophagus, sg = salivary gland, r = radular sac; scale = 1.0 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.5 mm.

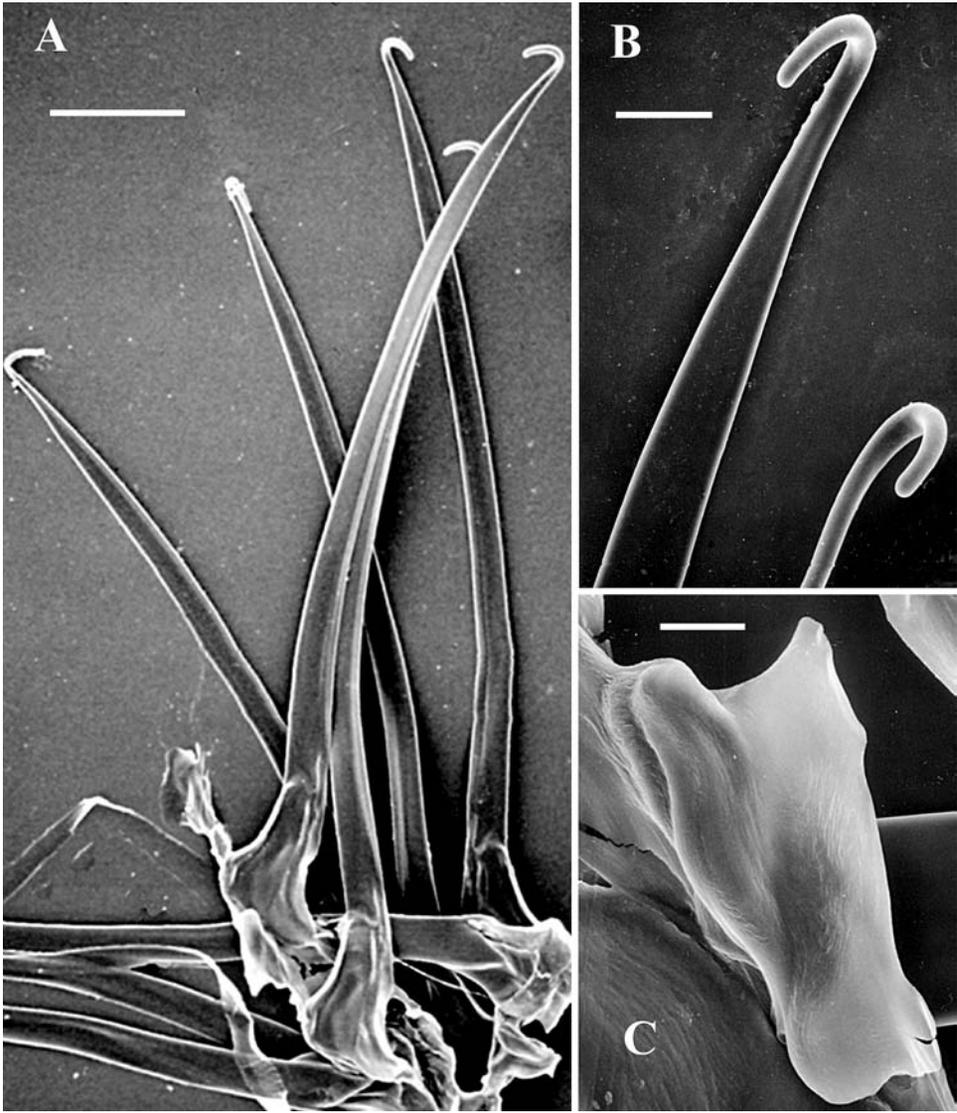


FIGURE 26. *Okenia nakamotoensis* (Hamatani, 2001) (CASIZ 096238). Scanning electron micrographs. A. Inner lateral teeth, scale = 150 μm . B. Apices of inner lateral teeth; scale = 34 μm . C. Outer lateral tooth; scale = 20 μm .

is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

REPRODUCTIVE SYSTEM (Fig. 25B).— The preampullary duct is short and thin and expands into an ovoid ampulla. The ampulla divides into a short, narrow oviduct and the wide prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of approximately three coils. The distal end of the prostatic segment narrows into a short, straight ejaculatory portion that terminates in an indistinct, but slightly wider penis. There is no dis-

tinct penial papilla. Inside the distal end of the penis are penial spines. The thin elongate vagina exits adjacent to the penis. It connects to the large, spheroid bursa copulatrix. From the base of the bursa a short duct connects to the small, serial receptaculum seminis. From the proximal end of the receptaculum the uterine duct joins with the female gland mass.

DISCUSSION.— The original description of *O. nakamotoensis* (Hamatani, 2001) includes illustrations of the external anatomy, the buccal mass and the radular teeth. All of these features, as originally described, are consistent with the present material from the Marshall Islands and the Philippines. The shape of the inner lateral teeth closely resembles that described for the type species of the genus *Hopkinsia*, *O. rosacea*. In both taxa, the inner laterals are thin and elongate with a hook-shaped apex, although the teeth are thinner and more elongate in *O. nakamotoensis* than in *O. rosacea*. *Okenia nakamotoensis* differs externally from *O. rosacea*. It is bright red with white pigment situated basally on the notal appendages and red apices whereas *O. rosacea* is uniformly pink in color. Also, *O. rosacea* has more numerous randomly distributed notal appendages while *O. nakamotoensis* has five pairs of lateral appendages and a single mid-dorsal appendage anterior to the gill. The reproductive systems of the two species are similar in configuration with several notable differences. Although the ampulla of *O. rosacea* is larger than that found in *O. nakamotoensis*, the prostatic portion of the vas deferens of *O. nakamotoensis* is more highly convoluted, consisting of several loops, than that of *O. rosacea*.

***Okenia kondoi* (Hamatani, 2001)**

(Figs. 20C, 27–28)

Sakishimaia kondoi Hamatani, 2001:153, Fig 2a–e.

Okenia kondoi (Hamatani, 2001) **comb. nov.**

MATERIAL EXAMINED.— CASIZ 158272, 5 specimens, Balacasag Island, Bohol, Philippines, 29 m. depth, 21 March 1994, T.M. Gosliner. CASIZ 106551, 7 specimens, 1 dissected, Agus Point, Mactan Island, Cebu, Philippines, 20 m. depth, 27 April 1996, M. Miller and T.M. Gosliner. CASIZ 158273, 4 specimens, CASIZ 120732, 4 specimens, Enewetak Atoll, Marshall Islands, 5 June 1983, S. Johnson.

DISTRIBUTION.— This species is known from the Kuroshima Islands, Japan (Hamatani, 2001), Bohol and Cebu Islands (Philippines) and Enewetak and Kwajalein Atolls (Marshall Islands) (Gosliner, Behrens, and Williams 1996; present study).

NATURAL HISTORY.— This species is found together with *O. nakamotoensis* on outer reef faces in 10–30 meters of water, where it feeds upon the bright red bryozoan, *Tropidozoum cellariforme* Harmer, 1957.

EXTERNAL MORPHOLOGY.— The living animals (Fig. 20C) attain 20 mm in length. Preserved specimens range in size from 3–13 mm. The body is elongate and narrow. There is no distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body is uniformly red with the exceptions of the gill rachises and the base of the notal papillae, which are pinkish white. The gill lamellae and apices of the notal papillae are the same color as the remainder of the body. There are four pairs of elongate notal papillae along the sides of the body. Two of these are situated anterior to the rhinophores and are more thin and elongate than the more lateral ones. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of 3–5 unipinnate branches. The rhinophores are elongate with 10–20 congested lamellae. The anterior end of the foot expands into two rounded lobes that are united as a small hood that surrounds the mouth (Fig. 27A). The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head.

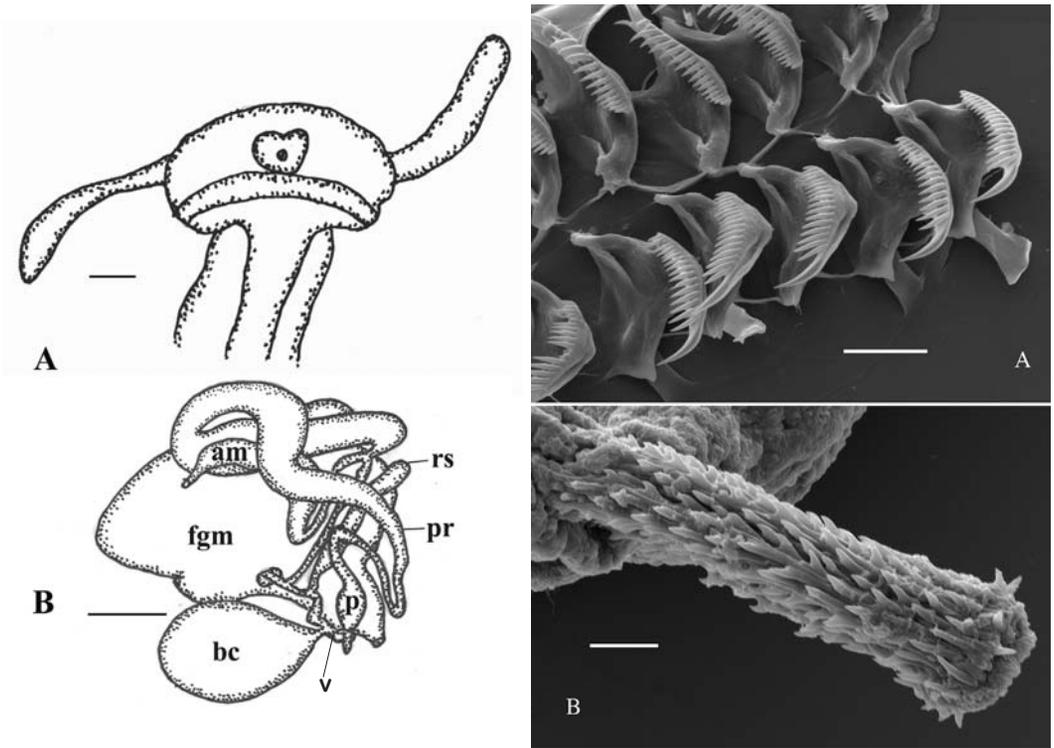


FIGURE 27 (left). *Okenia kondoi* (Hamatani, 2001) (CASIZ 106551). A. ventral view of head; scale = 0.2 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina; scale = 0.3 mm.

FIGURE 28 (right). *Okenia kondoi* (Hamatani, 2001) (CASIZ 106551). Scanning electron micrographs. A. Radular teeth; scale = 35 μ m. B. Penial armature; scale = 100 μ m.

DIGESTIVE SYSTEM.—The buccal mass is thick and muscular with a rounded buccal pump situated anteriorly. The radular sac is short and protrudes only slightly from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately dorsal and anterior to the entrance of the radular sac. A rounded, lobate salivary gland is present on either side of the buccal mass at the point where the esophagus enters the mass. Lobate oral glands are present at the anterior end of the buccal mass around the mouth. The radular formula is $25 \times 1.1.0.1.1$. The inner lateral teeth (Fig. 28A) are truncate with a broad base and an elongate masticatory margin. The tooth contains 16–17 elongate denticles. The outer laterals are small and reduced to elongate, fan-shaped, quadrangular plates.

REPRODUCTIVE SYSTEM (Fig. 27B).—The preampullary duct is short and thin and expands into an elongate, cylindrical ampulla. The ampulla is curved and divides into an elongate, narrow oviduct and the wide prostatic portion of the vas deferens. The oviduct enters the rounded, elongate receptaculum seminis. The lobate female gland mass consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded adjacent portions. The distal end of the prostatic segment narrows into a long, curved ejaculatory portion that terminates in a distinct conical penis. Protruding from the penial bulb is a cuticular portion bearing rows of chitinous hooks (Fig. 28B). The thick short base of the massive bursa

copulatrix functions as the vagina. Near its base is a short duct that bifurcates and joins the albumen gland and the elongate receptaculum seminis.

DISCUSSION.— Hamatani (2001) described *Sakishimaia* as a distinct genus based on the presence of a cylindrical slender body, absence of a pallial margin and velum and the absence of second (outer) lateral teeth. Scanning electron micrographs of the radula of *O. kondoi* (Fig. 28A) clearly show the presence of outer lateral teeth. The only characteristic unique to *O. kondoi* is the more body shape that is more elongate than species of *Hopkinsia*. This feature is shown to represent an autapomorphy for this taxon. The phylogeny presented here indicates that *O. kondoi* is nested within *Hopkinsia*, which in turn is nested within *Okenia*. Consideration of *Sakishimaia* as a distinct genus renders *Hopkinsia* paraphyletic. Similarly maintaining *Hopkinsia* makes *Okenia* paraphyletic. Thus, I consider it more prudent to consider *Sakishimaia* as a synonym of *Okenia* to maintain the monophyly of this taxon.

PHYLOGENETICS

To date, no phylogenetic analysis has been undertaken for members of the genera *Okenia*, *Hopkinsia*, *Hopkinsiella* and *Sakishimaia*. In the absence of phylogenetic studies there has been no objective test of the monophyly of these taxa. Recent works including these taxa (Bouchet and Ortea 1983; Hamatani 2001) have based systematic revisions exclusively on traditional rather than phylogenetic criteria. It is therefore important to conduct a preliminary phylogenetic analysis of members of these taxa. To facilitate such an analysis, morphological and anatomical studies were undertaken. Most data used to construct the matrix for phylogenetic analysis are derived from the morphological studies presented here. In addition to the species specifically discussed here, specimens of *Okenia angelensis* Lance, 1966 were examined (CASIZ 072351, 4 specimens, one dissected, Morro Bay, California, May-June 1981, David Behrens). Morphological description for other species were taken from the literature to represent morphological variation and geographical breadth. Specifically, anatomical details for the following taxa were derived from the following morphological studies: *Diaphorodoris luteocincta* (Schmekel and Portmann, 1982), *Goniodoris nodosa* (Thompson and Brown, 1984), *Okenia impexa* (Marcus, 1958; Schmekel and Portmann 1982), *O. zoobotryon* (Marcus, 1957, as *O. evelinae*; Valdés and Ortea 1995), *O. quadricornis* (Valdés and Ortea, 1995), *O. elegans* (Valdés and Ortea, 1995), *O. aspersa* (Schmekel and Portmann, 1982), *O. mediterranea* (Valdés and Ortea, 1995) and *O. hiroi* (Baba, 1938).

To determine the phylogenetic relationships of species of *Okenia*, *Hopkinsia*, *Hopkinsiella* and *Sakishimaia*, twenty morphological characters and one biological character were examined for 23 taxa, including *Diaphorodoris luteocincta* and *Goniodoris nodosa* as outgroup taxa. These taxa were chosen primarily because their anatomy is reasonably well described. These taxa also represent an excellent sample of the morphological variation that is known to exist in these taxa and also represent global geographical coverage of the known distribution of the Goniodorididae. All characters were treated as unordered. The following characters were considered:

1. *Body shape*: In the outgroup taxa and in many species of *Okenia* and *Hopkinsia* the body is short and ovoid (0). In some species of *Okenia* and *Sakishimaia kondoi* the body is narrow and elongate (1).
2. *Mantle between notum and foot*: In the outgroup and species of *Okenia*, the lateral margins of the body provide a surface distinct from the notum and foot (0). In these taxa, the genital opening is situated on this lateral surface of the right side of the body. In species of *Hopkinsia* and *Sakishimaia*, there is no distinct lateral surface and the notum slopes to the foot (1). In these taxa, the genital opening is on or near the lateral margin of the notum.
3. *Notal ridge*: In the outgroup taxa the notal edge is demarcated by a distinct thickening of tissue around its

- entire margin (0), whereas all of the ingroup taxa lack any thickening around the mantle margin (1).
4. *Mid-dorsal crest*: In the outgroup taxa and *Okenia mediterranea*, there is a distinct mid-dorsal longitudinal crest that extends between the rhinophores and gill (0). In the remaining taxa, no thickening of tissue is present (1).
 5. *Caudal crest*: The outgroup taxa, *O. mediterranea* and *O. quadricornis* have a caudal crest extending along the middle of posterior portion of the foot (0). This feature is absent in the remaining taxa studied here (1).
 6. *Oral tentacle shape*: In *Diaphorodoris luteocincta* and several species of *Okenia*, the oral tentacles are rounded in shape (0). In other species, including *Goniodoris nodosa* and most species of *Okenia*, the oral tentacles are triangular and tentacular (1), whereas in species of *Hopkinsia* and *Sakishimaia*, the oral tentacles are fused with the mouth region to form an oral veil (2).
 7. *Buccal pump*: In most species examined here, including the outgroup taxa and most of the ingroup taxa, the buccal pump portion of the buccal mass is moderately expanded (0), whereas in *Okenia virginiae* and *O. lambat* it is greatly expanded into a massive structure (1).
 8. *Radular sac*: In the outgroup and vast majority of the ingroup taxa, the radular sac is much shorter than the rest of the buccal mass (0) whereas in *Hopkinsia rosacea* and *H. nakamotoensis* it is almost as long or longer than the buccal mass (1).
 9. *Marginal papillae*: In the outgroup taxa, the margin of the notum may be undulate or irregular, but distinct lateral papillae are absent (0). In all of the ingroup taxa, elongate lateral papillae extend outward from the sides of the body (1).
 10. *Mid-dorsal papillae*: In the ingroup taxa there are numerous conical papillae evenly distributed over the surface of the notum. This arrangement is also found in some species of *Okenia* and *Hopkinsia pilosa*. Mid-dorsal papillae are absent in *O. aspersa* and *O. quadricornis* (1). *Okenia purpureolineata* is unique in having two mid-dorsal papillae anterior to the gill (2). In many species of *Okenia*, *Hopkinsia* and *Sakishimaia*, there is a single mid-dorsal papillae anterior to the gill (3).
 11. *Rhinophoral lamellae*: In the outgroup taxa and the vast majority of ingroup taxa, the rhinophores are characterized by having crowded lamellae along most of their length (0). In *Okenia angelensis*, *O. impexa*, *O. pellucida*, *O. zoobotryon* and *O. brunneomaculata* the rhinophoral lamellae are well separated from each other (1).
 12. *Inner lateral tooth shape*: In the outgroup and most ingroup taxa the inner lateral teeth have a broad shape with a thick pointed cusp (0). In *Hopkinsia rosacea* and *H. nakamotoensis* the inner lateral teeth are highly modified and much elongated (1).
 13. *Inner lateral tooth denticulation*: The ingroup taxa, *Hopkinsia hiroi*, and many species of *Okenia* the masticatory margin of the inner lateral tooth bears numerous fine teeth (0). Some species of *Okenia* and *Sakishimaia* (*O. impexa*, *O. pellucida*, *O. zoobotryon*, *O. brunneomaculata*, *S. kondoi*) have inner lateral teeth with fewer, coarser denticles (1). In *Hopkinsia rosacea*, *H. pilosa*, *H. plana* and *H. nakamotoensis* the inner lateral teeth entirely lack denticles (2).
 14. *Inner lateral tooth apex*: In the outgroup taxa and the vast majority of ingroup taxa the apex of the inner lateral tooth is gently curved with an acute apex (0). In *Hopkinsia rosacea* and *H. nakamotoensis*, the apex of the inner laterals are sharply curved with a rounded apex (1).
 15. *Outer lateral tooth*: The shape of the outer lateral teeth varies considerably in the taxa considered. In the outgroup and most of the ingroup taxa the outer laterals have a single apex (0). In *Okenia impexa* and *O. brunneomaculata* the outer lateral teeth have a deeply divided tooth with two sharp projections (1). The outer lateral tooth of *Hopkinsia rosacea* and *H. nakamotoensis* is greatly reduced in size to a tiny plate (2). The outer lateral tooth of *Sakishimaia kondoi* is flat and quadrangular in shape (3). The outer lateral tooth of *Hopkinsia plana* and *H. pilosa* is multidentulate (4).
 16. *Oral glands*: In the outgroup taxa and the vast majority of ingroup taxa studied here, there are minute oral glands at the anterior base of the buccal mass, adjacent to the mouth (0). Large oral glands are present in *Okenia japonica*, *O. liklik* and *O. purpureolineata* (1). The development of oral glands remains unknown for *Okenia aspersa*, *O. zoobotryon* and *Hopkinsia hiroi* (?).
 17. *Ampulla length*: The ampulla provides the hermaphroditic duct from the ovotestis to the genital aperture. It also serves as an endogenous sperm storage organ. In the outgroup taxa and many ingroup taxa, the ampulla is elongate (0). In *Okenia japonica*, *O. virginiae*, *O. impexa*, *O. brunneomaculata*, *O. lambat*, *O.*

- purpureolineata*, *H. pilosa*, *H. plana*, *H. rosacea*, *H. nakamotoensis* and *Sakishimaia kondoi*, it is short (1). The form of the ampulla is not known for *O. aspersa* or *O. quadricornis* (?).
18. *Receptaculum seminis*: In the outgroup and the vast majority of ingroup taxa the diameter of the receptaculum seminis is about the same size as the bursa copulatrix (0) whereas in species of *Hopkinsia* and *Sakishimaia kondoi*, the diameter of the receptaculum seminis is much smaller than the bursa copulatrix (1). The form of the receptaculum seminis is not known in *Okenia quadricornis*, *O. aspersa*, *O. zoobotryon* or *Hopkinsia hiroi* (?).
 19. *Uterine duct*: In the outgroup taxa and the majority of ingroup taxa the uterine duct is proximal to the receptaculum seminis (0). In *O. japonica*, *O. virginiae*, *O. lambat*, *O. kendi* and *O. liklik*, the uterine duct emerges from the vagina (1). The uterine duct position is unknown for *Okenia quadricornis*, *O. aspersa* or *Hopkinsia hiroi* (?).
 20. In the outgroup taxa and the vast majority of the ingroup taxa, the vagina is long (0). In *Okenia virginiae*, *O. lambat* and *O. kendi*, the vagina is short (1). The length of the vagina is unknown for *Okenia quadricornis*, *O. aspersa*, *O. zoobotryon* or *Hopkinsia hiroi* (?).
 21. Members of the taxa studied either feed on bryozoans (0) or tunicates (1). Food associations are unknown for *Okenia liklik* (?).

In order to determine phylogenetic relationships, the following data were entered into a data matrix using MacClade 3.01 (Table 1). This analysis was performed using PAUP 3.1.1, for the data matrix. All characters were treated as un-ordered and unweighted. A Heuristic search using stepwise addition from 1000 random starting trees was undertaken using the DELTRAN option, resulting in 200 trees with a length of 41, a consistency index of 0.683 and retention index of 0.824. The strict consensus of these trees is shown in Figure 29. Bremer support analysis was conducted to test the robustness of the tree.

DISCUSSION

The preliminary phylogeny presented here is moderately well supported, given the number of characters. Bremer support values are included in Figure 29. Most nodes have a Bremer support value of 1. The two most basal nodes have a Bremer support value of at least 2. Additionally, the clade that contains *Hopkinsia rosacea* and *H. nakamotoensis* also has a value of at least 2. Further analysis was not possible, owing to the large number of trees that were produced (more than 60,000) after adding trees with two more steps. Adding a third step to the tree lengths far exceeded the computing ability of the computer dedicated to phylogenetic analysis. The greater robustness of these basal clades is especially important for the subsequent systematic conclusions that are discussed.

The phylogenetic hypothesis presented in Figure 29 suggests several important aspects regarding the phylogeny of *Okenia*, *Hopkinsia*, *Hopkinsiella* and *Sakishimaia*. These taxa collectively form a monophyletic taxon characterized by two synapomorphies (presence of marginal papillae and absence of a notal ridge). *Okenia mediterranea* is the sister taxon to all the remaining members of the ingroup. Several large monophyletic clades are formed by species traditionally included in *Okenia*. This first clade contains the European Atlantic taxa, *O. elegans*, *O. aspersa* and *O. quadricornis* and is the sister group to all the remaining taxa. This clade is supported by an ecological synapomorphy, that all these taxa feed on tunicates rather than bryozoans. It is also interesting to note that Valdés and Ortea (1995) considered *O. aspersa* and *O. quadricornis* as the same species. This issue needs to be more fully studied with comparative material from Atlantic and Mediterranean waters. Members of this clade have short, rounded oral tentacles, as in the outgroup taxon *Diaphorodoris luteocincta*. *Okenia leachi* (Alder and Hancock, 1854) may also be a member of this clade. It also has rounded oral tentacles and feeds upon tunicates, but its anatomy remains largely unknown.

TABLE 1. Data matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
	body	mant	notal	mid-caud	oral	bucc	radul	maro	mid	rhind	inner	inner	inner	inner	seco	oral	lampl	recef	uteri	vagif	feedi	
<i>Diaphorodoris luteocincta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Goniodoris nodosa</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1
<i>Okenia angelensis</i>	1	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Okenia quadricornis</i>	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	?	?	?	?	?	1
<i>Okenia elegans</i>	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Hopkinsiella hiroi</i>	0	1	1	1	1	2	?	?	1	0	0	0	0	0	0	?	?	?	?	?	?	0
<i>Okenia impexa</i>	0	0	1	1	1	1	0	0	1	3	1	0	1	0	1	0	1	0	0	0	0	0
<i>Okenia japonica</i>	1	0	1	1	1	1	0	0	1	3	0	0	0	0	0	1	1	0	1	0	0	0
<i>Okenia mediterranea</i>	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Okenia pellucida</i>	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Hopkinsia pilosa</i>	0	1	1	1	1	2	0	0	1	0	0	0	2	0	4	0	1	1	0	0	0	0
<i>Hopkinsia plana</i>	0	1	1	1	1	2	0	0	1	3	0	0	2	0	4	0	1	1	0	0	0	0
<i>Okenia aspersa</i>	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	?	?	?	?	?	?	?
<i>Hopkinsia rosacea</i>	0	1	1	1	1	2	0	1	1	0	0	1	2	1	2	0	1	1	0	0	0	0
<i>Okenia zoobotryon</i>	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Okenia virginiae</i>	0	0	1	1	1	1	1	0	1	3	0	0	0	0	0	0	1	0	1	1	0	0
<i>Okenia lambat</i>	0	0	1	1	1	1	1	0	1	3	0	0	0	0	0	0	1	0	1	1	0	0
<i>Okenia kendi</i>	0	0	1	1	1	1	0	0	1	3	0	0	0	0	0	0	0	0	1	1	0	0
<i>Okenia liklik</i>	1	0	1	1	1	1	0	0	1	3	0	0	0	0	0	1	1	0	1	0	0	?
<i>Okenia brunneomaculata</i>	0	0	1	1	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0
<i>Hopkinsia nakamotoensis</i>	0	1	1	1	1	2	0	1	1	3	0	1	2	1	2	0	1	1	0	0	0	0
<i>Sakashimaia kondoi</i>	1	1	1	1	1	2	0	0	1	3	0	0	1	0	3	0	1	1	0	0	0	0
<i>Okenia purpureolineata</i>	1	0	1	1	1	1	0	0	1	2	0	0	0	0	0	1	1	0	0	0	0	0

The sister group of these three species contain three distinct clades. The first of these, supported by two apomorphies (tentacular oral tentacles, sparse rhinophoral lamellae) contains *O. angelensis*, *O. zoobotryon*, *O. pellucida* and the sister species, *O. impexa* and *O. brunneomaculata*. *Okenia impexa* and *O. brunneomaculata* share two synapomorphies, coarse denticles on the inner lateral tooth and a bifid outer lateral tooth. Additionally, all of these taxa have a translucent white body color with varied brown markings. They also all appear to feed upon ctenostomatous bryozoans. It appears that *O. mija* Burn, 1967 may also be a member of this clade. Its internal anatomy remains largely unknown, but it has a similar color pattern, feeds on ctenostomatous bryozoans and has sparse rhinophoral lamellae. Collectively members of this clade inhabit a wide geographical area and include subtropical and tropical Atlantic, Eastern Pacific and Indo-Pacific taxa. Understanding the detailed phylogeny of this clade may also shed some additional light on the historical biogeography of this taxon.

The second clade is supported by three synapomorphies (absence of a distinct lateral surface of the body, oral tentacles fused with the mouth region to form an oral veil and the presence of a short ampulla). *Sakishimaia kondoi* is nested within the species traditionally placed within *Hopkinsia*. *Hopkinsiella hiroi* is basal within this clade, but lacks any autapomorphies. *Hopkinsia rosacea* and *H. nakamotoensis* are sister species, a relationship that is supported by five synapomorphies. These taxa are all Pacific in their distributions, from the Indo-Pacific tropics and subtropics and temperate Japan and California.

The third clade is restricted to the Indo-Pacific tropics and adjacent subtropical waters of Japan. It is supported by three synapomorphies, the presence of tentacular oral tentacles, the presence of a single mid-dorsal papillae and the presence of short ampulla. This clade is divided into two sister clades. One of these, contains *Okenia liklik*, *O. purpureolineata* and *O. japonica*. These three species have an elongate body and large oral glands. These taxa are restricted to the margins of the western Pacific. The other subclade contains *O. kendi*, and the sister species, *O. lambat* and *O. virginiae*. This clade is supported by the presence of a short vaginal duct and a uterine duct that emerges from the vagina. *Okenia barnardi* Baba, 1937, also appears to be a member of this clade. This is suggested by its body shape, arrangement of lateral papillae and the presence of a single medial papillae anterior to the gill. The anatomy of this species remains largely undescribed.

Several systematic conclusions are evident from this phylogenetic analysis. On the basis of this preliminary phylogeny, *Sakishimaia* must be considered to be a junior synonym of *Hopkinsia*, since it is nested within *Hopkinsia* and maintaining it would render *Hopkinsia* paraphyletic.

The monophyly of the ingroup is supported when only single outgroup taxa are included (either *Diaphorodoris luteocincta* or *Goniodoris nodosa*) and the other taxon is included in the ingroup. The monophyly of *Hopkinsia* (including *Sakishimaia kondoi*) is well supported. However, *Okenia* is paraphyletic when *Hopkinsia* is maintained, as the latter taxon is nested well within *Okenia*. One possible systematic solution is to create a series of subgeneric names in order to maintain *Hopkinsia*. This does not seem to add any information not already contained in the phylogeny and adds unnecessary names to the nomenclature. A second solution is to include all of the ingroup taxa within a single monophyletic taxon, *Okenia*. In this case, *Hopkinsia*, *Hopkinsiella* and *Sakishimaia* would be junior synonyms of *Okenia*.

It is with regret that I feel compelled to adopt this latter solution. *Hopkinsia* is a much beloved name that honors the founding of the Hopkins Marine Station of Stanford University and was erected by Frank Mace MacFarland, former Stanford Professor of Biology and President of the California Academy of Sciences. Nevertheless, it is the most simple solution that preserves monophyly and does not create a nomenclature that is unnecessarily complicated. Therefore, *Hopkinsia*, *Hopkinsiella* and *Sakishimaia* are here considered as junior synonyms of *Okenia*.

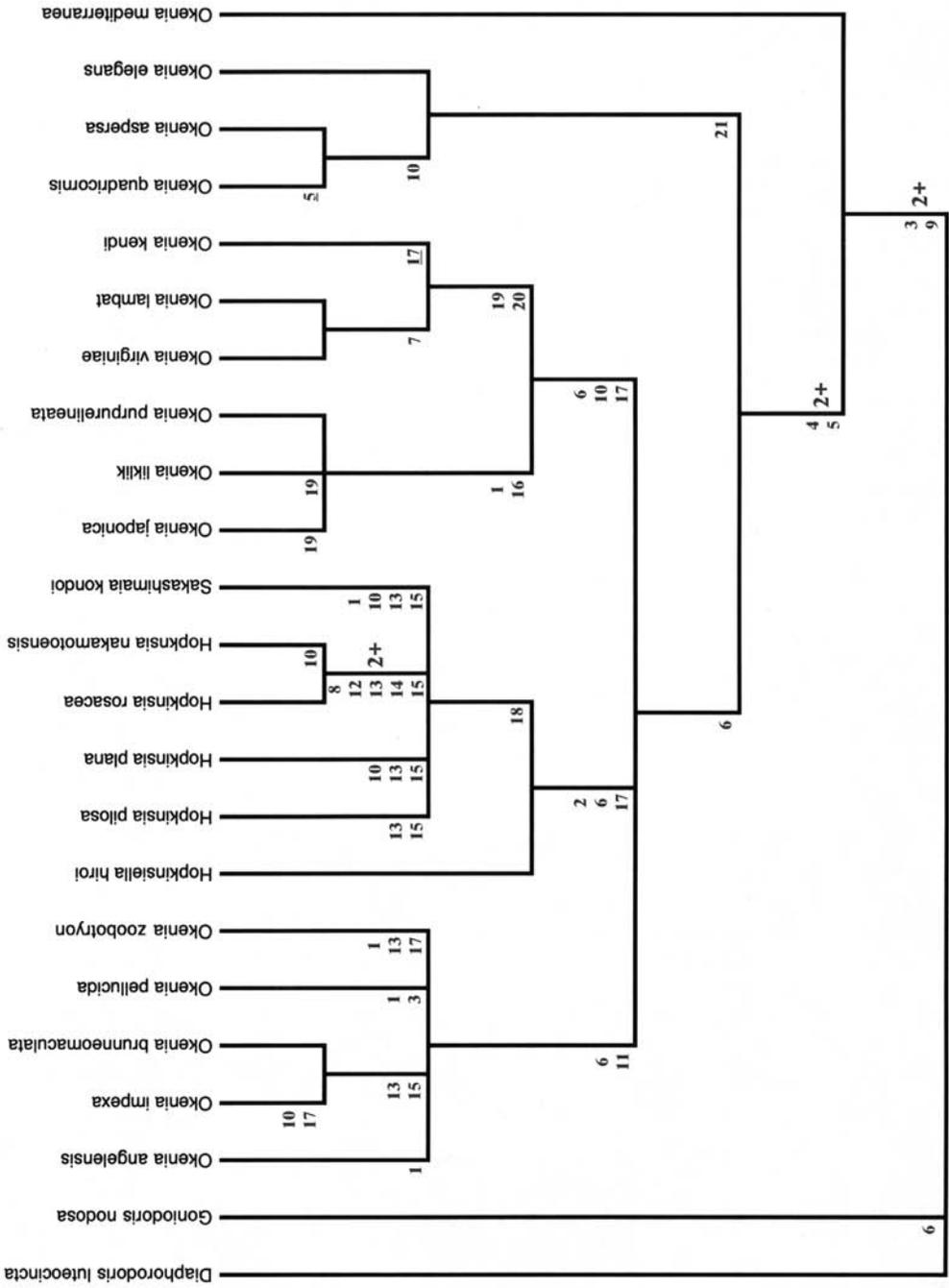


FIGURE 29. Strict consensus tree of preliminary phylogeny. Apomorphies are indicated by character numbers included in the analysis. Characters which exhibit reversal are underlined. Bremer support values for each node are indicated as large numerals on the right side of each node. Bremer values not indicated on figure are 1.

At least 12 additional described species of *Okenia* have not been fully studied for the anatomical characters included in this study. At least four undescribed species of *Okenia* are known to occur in the eastern Pacific tropics and two undescribed species are known from Australian waters. These taxa should be examined and incorporated into subsequent phylogenetic studies. Additional phylogenetic studies of the remaining goniodoridid and onchidoridid genera are also necessary to produce a broader understanding of the phylogeny and systematics of these poorly understood dorid nudibranchs.

ACKNOWLEDGMENTS

This research has been supported by a grant from the National Science Foundation, PEET Program (DEB-9978155). Fieldwork was supported by the California Academy of Sciences, the Christensen Fund and the Christensen Research Institute and the South African Museum. Kit Stewart also provided financial support for some fieldwork. Specimens were also collected by several colleagues including Jerry Allen, Dave Behrens, Bob Bolland, Yolanda Camacho, Shireen Fahey, Pauline Fiene Severns, Mike Ghiselin, Rebecca Johnson, Scott Johnson, Gary McDonald, Mike Miller, Ángel Valdés, Yvonne Vallès and Gary Williams. Their assistance and support is greatly appreciated.

LITERATURE CITED

- BABA, K. 1937. Opisthobranchia of Japan (II). *Journal of the Department of Agriculture, Kyushu Imperial University* 5:289-344.
- BABA, K. 1938. Opisthobranchia of Kii, Middle Japan. *Journal of the Department of Agriculture, Kyushu Imperial University* 6(1):1-19.
- BABA, K. 1949. *Opisthobranchia of Sagami Bay*. Iwanami Shoten, Tokyo, Japan. 211 pp.
- BABA, K. 1960. The genera *Okenia*, *Goniodoridiella* and *Goniodoris* from Japan (Nudibranchia-Goniodorididae). *Publications of the Seto Marine Biological Laboratory* 8(1):79-83.
- BEHRENS, D. 1991 Pacific Coast Nudibranchs. *Sea Challengers: Monterey*. 107 pp., 217 plates.
- BEHRENS, D. 2001. <http://slugsite.us/bow/nudwk275.htm>
- BERGH, R. 1902. The Danish Expedition to Siam 1899-1900. I. Gasteropoda Opisthobranchiata. Det Kongelige Danske Videnskaberne Selskabs Skrifter. 6 Raekke. *Naturvidenskabelig og Matematisk Afdeling* 12(2):153-218.
- BOUCHET, P., AND J. ORTEA. 1983. A new *Hopkinsia* feeding on Bryozoa in the South Pacific (Mollusca: Opisthobranchia). *Venus* 42(3):227-233.
- BURN, R.F. 1967. Descriptions of two new species of *Okenia* (Nudibranchia, Doridacea) from south-eastern Australia. *Proceedings of the Royal Zoological Society of New South Wales* 1965/1966:52-57.
- DEBELIUS, H. 1996. *Nudibranchs and Sea snails. Indo-Pacific Field Guide*. IKAN Unterwasserarchiv, Frankfurt, Germany. 321 pp., 1000 unnumbered figs.
- GOSLINER, T.M. 1987. *Nudibranchs of Southern Africa*. *Sea Challengers*, Monterey, California. 136 pp., 268 pls.
- GOSLINER, T.M., D. BEHRENS, AND G. WILLIAMS. 1996. *Coral Reef Animals of the Indo-Pacific*. *Sea Challengers*, Monterey, California. 314 pp., 1103 pls.
- GOSLINER, T.M., S. JOHNSON, AND H. BERTSCH. 1986. Additions to the opisthobranch gastropod fauna of the Hawaiian Islands. *Western Society of Malacologists, Annual Report* 18:14-17.
- HAMATANI, I. 2001. Two new species of Goniodorididae (Opisthobranchia; Nudibranchia) with a new genus from Kuroshima Island, Okinawa, Japan. *Venus* 60(3):151-156.
- KURIHARA, T. 1999. *Sea Slug Forum*: <http://www.seaslugforum.net/display.cfm?base=okenpell&id=1399> (first record of *Okenia pellucida* from Japan).

- LANCE, J. 1966. New distributional records of some northeastern Pacific Opisthobranchiata (Mollusca: Gastropoda) with descriptions of two species. *The Veliger* 9(1):69–81.
- MACFARLAND, F.M. 1905. A preliminary account of the Dorididae of Monterey Bay, California. *Proceedings of the Biological Society of Washington* 18:35–54.
- MACFARLAND, F.M. 1906. Opisthobranchiate Mollusca from Monterey Bay, California and vicinity. *Bulletin of the Bureau of Fisheries* 25:109–151.
- MARCUS, E. 1957. On Opisthobranchia from Brazil (2). *Zoological Journal of the Linnean Society* 43(292): 390–486.
- RUDMAN, W.B. 1987. The genus *Trapania* (Nudibranchia, Goniodorididae) in the Indo-West Pacific. *Journal of Molluscan Studies* 53(2):189–212.
- RUDMAN, W.B. 1998. <http://www.seaslugforum.net/hopkplan.htm>.
- RUDMAN, W.B., AND DARVELL, B.W. 1990. Opisthobranch molluscs of Hong Kong. Part 1. Goniodorididae, Onchidorididae, Triophidae, Gymnodorididae, Chromodorididae, (Nudibranchia). *Asian Marine Biology* 7:31–79.
- SCHMEKEL, L., AND A. PORTMANN. 1982. *Opisthobranchia des Mittelmeeres, Nudibranchia und Saccoglossa. Faune flora del Golfo di Napoli*. Monografia della Stazione Zoologica di Napoli, no. 40, 410 pp., 36 pls. Springer-Verlag, Heidelberg, Germany.
- Steinberg, J. 1963. Notes on the opisthobranchs of the West Coast of North America III. Further nomenclatural changes in the Order Nudibranchia. *The Veliger* 6(2):63–67.
- THOMPSON, T., AND G. BROWN. 1984. *Biology of Opisthobranch Mollusks*, vol. 2. Ray Society, London, UK. 229 pp., 41 pls.
- VALDÉS, Á., AND J. ORTEA. 1995. Revised taxonomy of some species of the genus *Okenia*, Menke, 1830 (Mollusca: Nudibranchia) from the Atlantic Ocean, with the description of a new species. *The Veliger* 38(3): 223–234.