

**Systematics of *Okenia* from the Pacific Coast of North America (Nudibranchia: Goniodorididae) with Descriptions of Three New Species**

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The systematics of the eastern Pacific species of *Okenia* are reviewed. The anatomy of *Okenia vancouverensis* (O'Donoghue, 1921) and *O. angelensis* Lance, 1966 is described more completely. Three new species of *Okenia* are described from the tropical eastern Pacific. *Okenia angelica* sp. nov. is characterized by its purplish body color with numerous elongate lateral papillae and short, rounded dorsal tubercles. It is known from Baja California to Jalisco, México. *Okenia cochimi* sp. nov. has a bright uniformly yellow body with numerous lateral appendages and a single medial appendage anterior to the gill. It is known from Cedros Island, the central Gulf of California and Bahía Banderas, México. *Okenia mexicorum* is white with brick red markings. It has short lateral appendages, and a mid-dorsal crest that terminates in a single elongate papilla. This species is known from the central Gulf of California to Bahía Banderas, México.

RESUMEN

La posición sistemática de las especies de *Okenia* del Pacífico Este es revisada. La anatomía de *Okenia vancouverensis* (O'Donoghue, 1921), y *O. angelensis* Lance, 1966, es descrita detalladamente. Tres especies nuevas de *Okenia* son descritas del Océano Pacífico Este Tropical. *Okenia angelica* esp. nov. es caracterizada por tener un cuerpo violeta con papilas laterales largas y numerosas y tubérculos dorsales cortos y redondeados. Esta especie es conocida de Baja California hasta Jalisco, México. *Okenia cochimi* esp. nov. tiene un cuerpo amarillo brillante y uniforme, apéndices laterales numerosos y un apéndice medio situado en frente de la branquia. Esta especie es conocida de la Isla Cedros, la región central del Golfo de California y Bahía Banderas, México. *Okenia mexicorum* esp. nov. es blanca con áreas de color rojo teja. Esta especie tiene apéndices laterales cortos y una cresta media que termina en una papila larga. Esta especie es conocida de la región central del Golfo de California hasta Bahía Banderas, México.

Recently, the systematics of *Okenia* has been reviewed based on a preliminary phylogenetic analysis (Gosliner 2004). From this analysis came the conclusion that *Hopkinsia*, *Hopkinsiella* and *Sakishimaia* should be regarded as junior synonyms of *Okenia*. Four species of *Okenia* have been recorded from the Pacific coast of North America, *Okenia vancouverensis* (O'Donoghue, 1921); *O. rosacea* (MacFarland, 1905); *Okenia angelensis* Lance, 1966 and *Okenia plana* Baba, 1960. In this work, aspects of the anatomy of two northeastern Pacific taxa were presented. The radular teeth

and reproductive anatomy of *Okenia rosacea* (MacFarland, 1905) were described. The anatomy of Indo-Pacific and non-indigenous specimens of *Okenia plana* Baba, 1960, from the Philippines and San Francisco Bay was described. The description of the anatomy of these species will not be repeated here. O'Donoghue's (1921) description of *Okenia vancouverensis* included a description of the external morphology and the radula. In Lance's (1966) original description of *O. angelensis*, he described the external anatomy, the radular teeth and the shape of dermal spicules. The description of these species is amplified here. Expeditions to Baja California over the last twenty years have produced collections of two additional species of *Okenia*. More recent collections from the Pacific coast of México by Orso Angulo Campillo and Alicia Hermosillo have yielded specimens of a third undescribed species. The descriptions of these species are presented here.

All specimens examined here are housed in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ).

## SPECIES DESCRIPTIONS

### Genus *Okenia* Menke, 1830

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

#### *Okenia vancouverensis* (O'Donoghue, 1921)

(Figs. 1–2)

*Idalia vancouverensis* O'Donoghue, 1921:177, pl., fig. 22.

**MATERIAL EXAMINED.**—CASIZ 035222, one specimen, dissected, Rose Harbor, Queen Charlotte Islands, British Columbia, Canada, 4 July, 1913, Will F. Tompson.

**DISTRIBUTION.**—Known only from the Queen Charlotte Islands (present study), Vancouver Island, British Columbia, Canada to Puget Sound, Washington (Behrens 1991).

**NATURAL HISTORY.**—Found in about 15 meters of water on hard mud substrate.

**EXTERNAL MORPHOLOGY.**—The body is broad and ovoid (30 mm in length, in the preserved specimen) with nine to ten pairs of elongate, acutely pointed papillae situated along the notal margin and with an additional 24 similarly-shaped papillae on the remainder of the notum. The living animal is depicted by Behrens (1991) and Rudman (2003). The body is brownish with opaque white spots and an opaque white medial line along posterior portion of the foot. The rhinophores also contain patches of brown pigment. The rhinophores are elongate with 24 densely arranged lamellae. The gill consists of 12 bipinnate to tripinnate branches. Ventrally the foot is broad. The head (Fig. 1A) surrounding the mouth is broad and contains a pair of rounded oral lobes extending laterally. The reproductive opening is situated on the lateral side of the body, approximately one third of the length of the body posterior to the anterior margin.

**DIGESTIVE SYSTEM.**—The buccal mass (Fig. 1B) is thick and muscular with an elongate buccal pump directed posteriorly. Numerous minute oral glands are present at the opening of the buccal mass into the mouth. The radular sac is elongate and extends ventrally and anteriorly from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A large, flat, 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 32 X 1.1.0.1.1. in the single specimen examined (Fig. 2A). The inner lateral teeth (Fig. 2B) are wide basally with an elongate acutely pointed cusp. The masticatory margin of the inner lateral bears 7–9 triangular denticles that increase in size in

the direction of the outer margin. The outer laterals are large and hook-shaped (Fig. 2B) with a curved, acutely-pointed cusp.

**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 entirely 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. 1C) The preampullary duct is thin and elongate and expands into the relatively short, 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 enters a large spherical

prostate that consists of numerous nodular bodies. From the prostate gland the ejaculatory duct emerges as a thin convoluted duct, which widens and forms several coils on top of the female gland mass. It then straightens and continues as an elongate duct that eventually widens slightly into the muscular penial bulb. The vagina is very wide at its exit adjacent to the penis, and consists of several folds. More distally it narrows and continues as a curved duct that again narrows and consists of a section that is folded and twisted together as convolutions. It then straightens again as it enters the base of the large, rounded bursa copulatrix. From the base of the bursa is a second duct that joins with the equally-sized, more pyriform 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 vancouverensis* is immediately identifiable by its broad body and brown color with opaque white markings. The present material agrees closely with that originally described by O'Donoghue (1921). O'Donoghue did not describe the anatomy of the reproductive system. *Okenia vancouverensis* appears to be unique among described *Okenia* species in having a discrete prostate gland rather than a prostate that merely represents an expansion of the deferent duct. The external anatomy of *O. vancouverensis* is similar to that described for *O. aspersa* (Alder & Hancock, 1845) and *O. leachi* (Alder & Hancock, 1854), both known from the northern Atlantic.

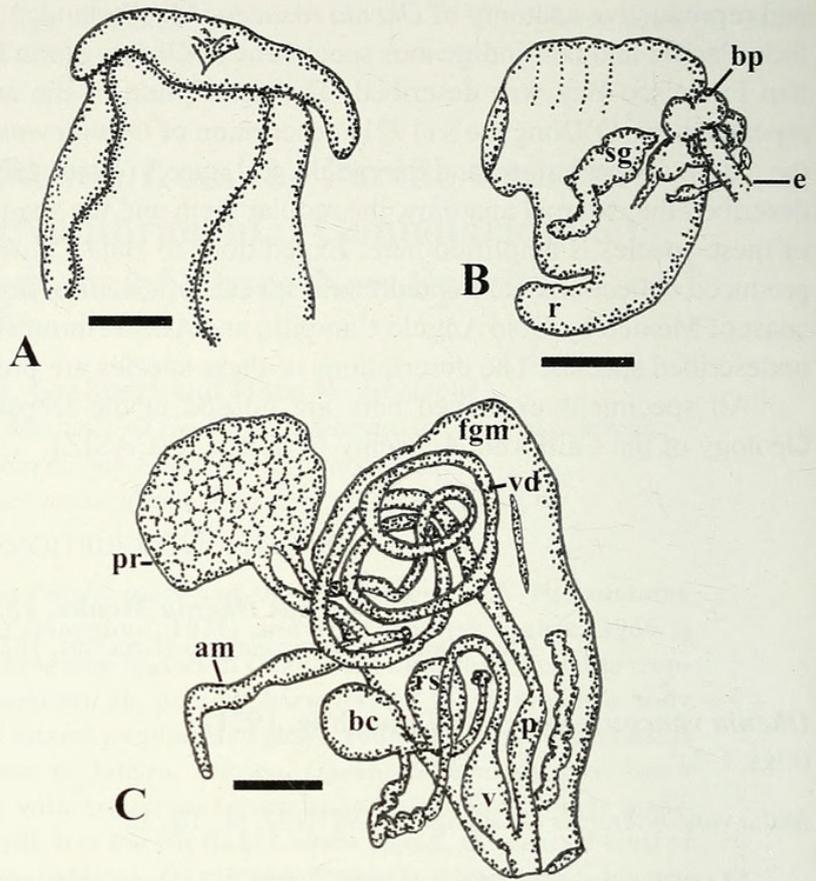


FIGURE 1. *Okenia vancouverensis* (O'Donoghue, 1921). A. Ventral view of head region, scale = 8.0 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radular sac, sg = salivary gland, scale = 0.75 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 1.0 mm.

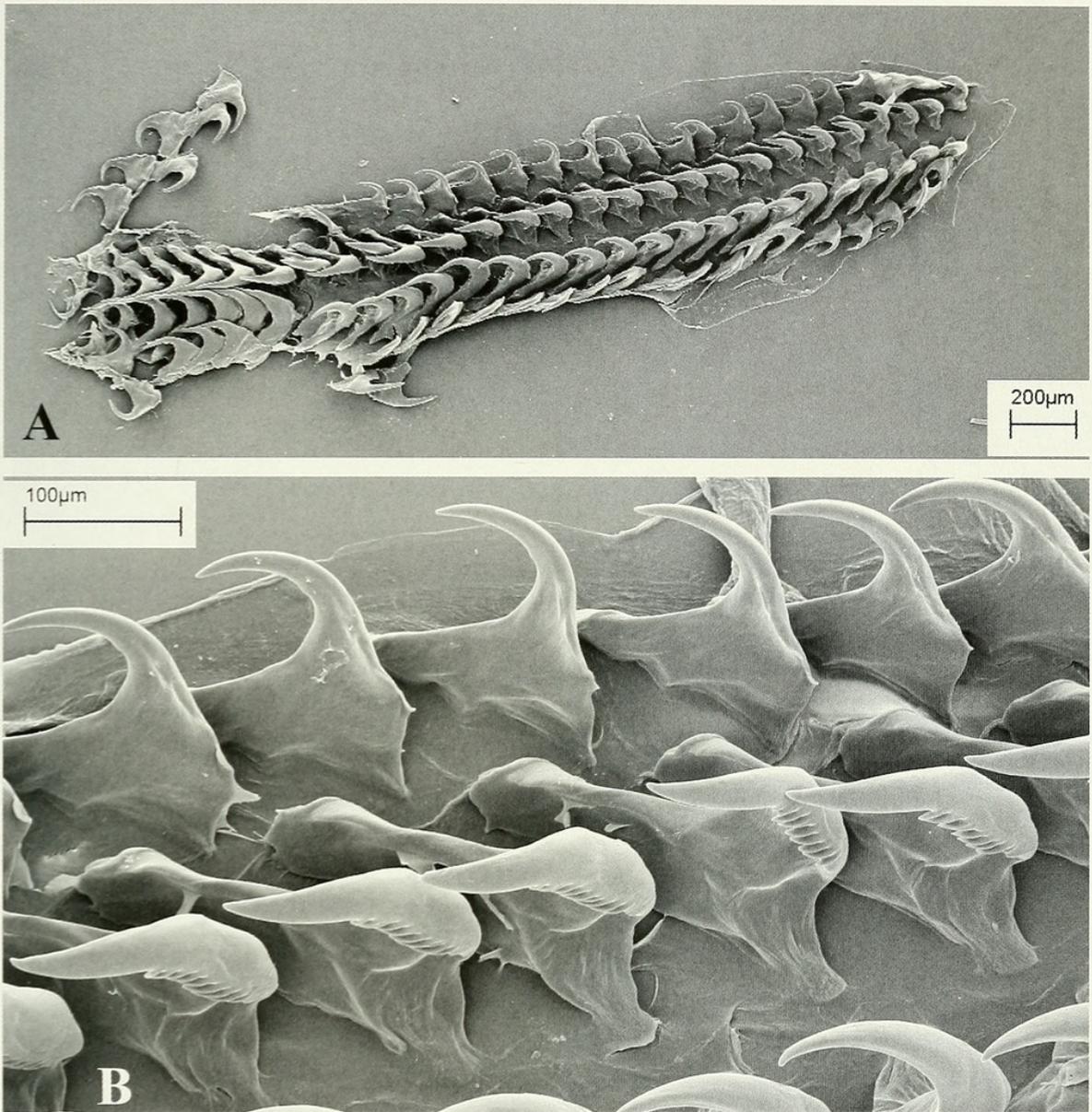


FIGURE 2. *Okenia vancouverensis* (O'Donoghue, 1921). Scanning electron micrographs of radular teeth. A. Entire radula. B. Inner and outer lateral teeth.

These two species, like *O. vancouverensis*, are also found on muddy substrate. *Okenia aspersa* differs from *O. vancouverensis* in having unevenly sized lateral appendages, with the anteriormost pair being the most elongate. *Okenia leachi* is similar to *O. vancouverensis* in having uniformly-sized lateral and notal papillae except the papillae are much longer in *O. leachi*. The radular teeth of *O. leachi* differ from those of *O. vancouverensis* in having far more denticles on the inner lateral teeth and in having a proportionately smaller outer lateral tooth with a shorter cusp (Thompson and Brown 1984, fig. 7h). The radular teeth of *O. aspersa* are very similar in shape and size to those of *O. vancouverensis* (Thompson and Brown 1984, fig. 7g). The inner lateral teeth of *O. aspersa* bear up to 17 denticles while those of *O. vancouverensis* have only 7–9 denticles.

*Okenia angelensis* Lance, 1966

(Figs. 3–4)

*Okenia angelensis* Lance, 1966:76, figs. 9–12.

**MATERIAL EXAMINED.**— CASIZ 072351, 4 specimens, one dissected, Morro Bay, California, May–June 1981, David Behrens. CASIZ 170047, 5 specimens, 2 dissected, Mission Bay, San Diego, California, on floating docks, 25 June 1987, Terrence M. Gosliner. CASIZ 070471, 10 specimens, 2 dissected, Texaco Marina, Morro Bay, California, 26 October, 1975, Gary McDonald.

**DISTRIBUTION.**— Known from San Francisco Bay to México and then disjunctly to southern Chile (Behrens, 1991, Muñoz et al., 1996).

**NATURAL HISTORY.**— Found from shallow embayments on floating docks or in the shallow subtidal zone.

**EXTERNAL MORPHOLOGY.**— The body is elongate (3–10 mm in length) with seven to eight pairs of elongate, rounded papillae situated along the notal margin and with an additional 8 papillae situated on the notum. The body is translucent yellowish white with numerous fine brownish spots scattered uniformly over the surface of the notum. The rhinophores are elongate with two to three well-spaced lamellae. The gill consists of five to seven unipinnate branches. The anterior margin of the head includes two elongate oral tentacles that extend anterolaterally.

**DIGESTIVE SYSTEM.**— The buccal mass (Fig. 3A) is thin 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 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. No discrete polygonal plates were evident. The cuticle expands as it enters the buccal pump. The radular formula is 19 X 1.1.0.1.1 and 24 X 1.1.01.1 in two specimens examined. The inner lateral teeth (Fig. 4) are wide basally with an elongate acute bifid cusp. The masticatory margin of the inner lateral bears 15–19 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced with two short, acutely pointed cusps along the outer edge.

**REPRODUCTIVE SYSTEM.**— (Fig. 3B) 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

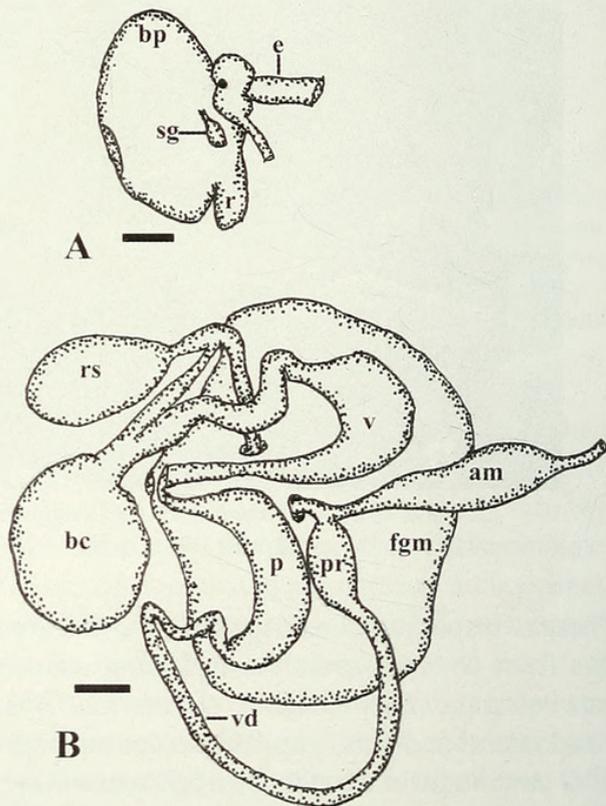


FIGURE 3. *Okenia angelensis* Lance, 1966. A. Buccal mass, bp = buccal pump, e = esophagus, r = radular sac, sg = salivary gland, scale = 0.15 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 0.17 mm.

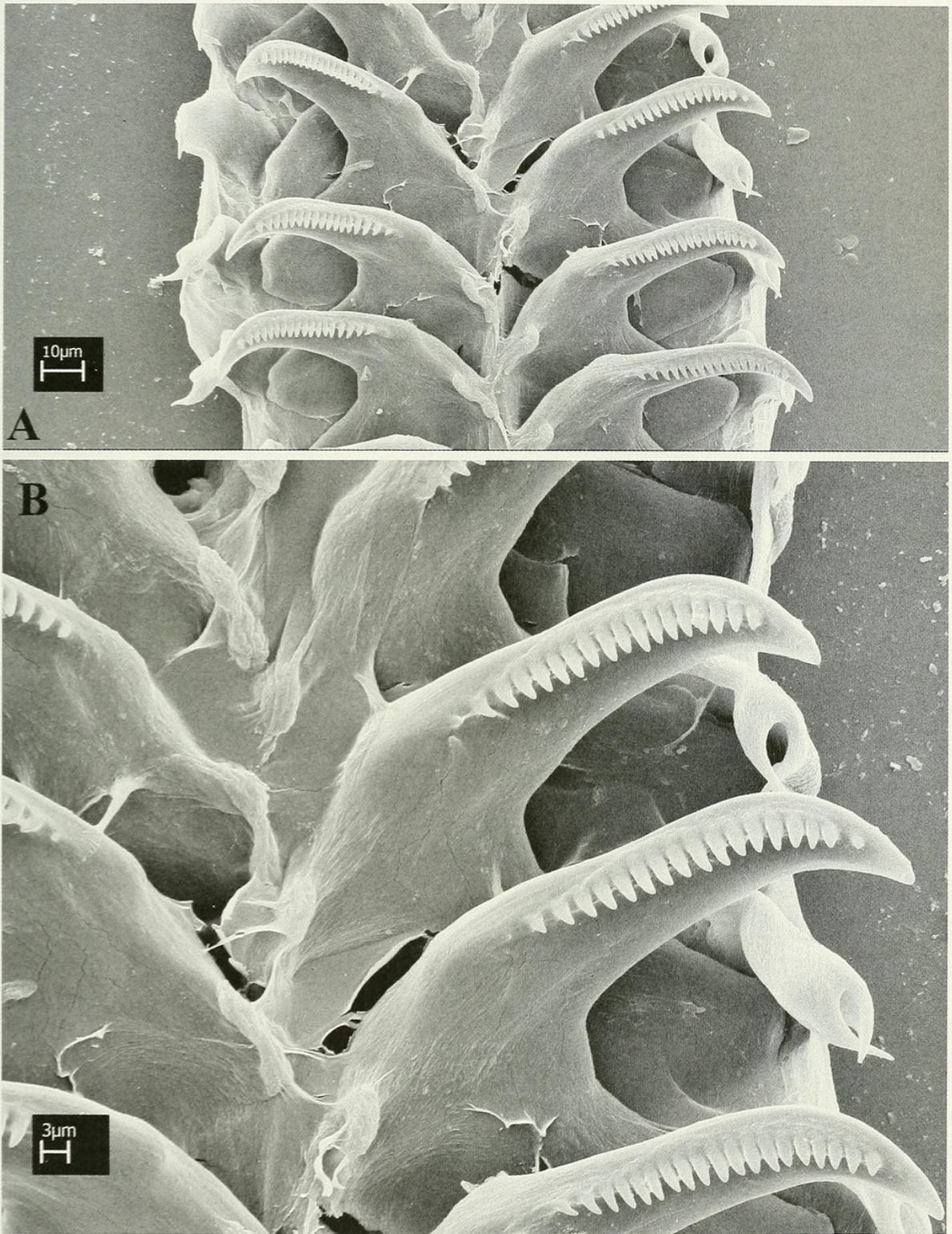


FIGURE 4. *Okenia angelensis* Lance, 1966. Scanning electron micrographs of radular teeth. A. Entire radular width. B. Inner and outer lateral teeth.

deferens is prostatic but very short. It narrows and continues as an elongate loop that eventually narrows slightly into the highly convoluted muscular, proximal ejaculatory portion. The penial bulb is wide and curved. The vagina is 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, spherical bursa copulatrix. From the base of the bursa is a second duct that joins with the smaller, more pyriform 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 angelensis* is immediately identifiable by its translucent yellowish white body color with minute brown spots. The present material agrees closely with that originally described by Lance (1966). Additional details of the anatomy including the morphology of the digestive and reproductive systems are added here.

***Okenia angelica* Gosliner and Bertsch, sp. nov.**

(Figs. 5A, 6–7)

**TYPE MATERIAL.**— HOLOTYPE: CASIZ 170088, 1 specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, Oct. 2, 1984, Terrence M. Gosliner. PARATYPES: CASIZ 166889, 1 specimen, dissected, Baja California, México, Feb. 18, 1999, Sandra Millen. CASIZ 170089, 1 specimen, San Carlos, Sonora, México, Dec. 1970. CASIZ 170090, 2 specimens, 1 dissected, Punta Gringa, Bahía de los Ángeles, Baja California, México, June 30, 1987, Terrence M. Gosliner. CASIZ 116929, 1 specimen, Isla Cedros, Pista, Baja California, México, April, 23, 1998, Hans Bertsch. CASIZ 170085, 1 specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, Sept. 20, 1985, Terrence M. Gosliner. CASIZ 170087, one specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, 6 October, 1984, Terrence M. Gosliner. CASIZ 170086, one specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, 24 October, 1986, Hans Bertsch. CASIZ 167395, 1 specimen, Mismaloya, Bahía de Banderas, Jalisco, México, 28 February 2003, Alicia Hermosillo.

**ETYMOLOGY.**— The specific name, *angelica*, comes from the fact that this species has an angelic appearance.

**DISTRIBUTION.**— This species is known only from Bahía de los Ángeles, Baja California to the Bahía de Banderas region near Puerta Vallarta, Jalisco, México (present study).

**NATURAL HISTORY.**— This species is found on small stones in 1–2 meters of water. It appears to be associated with bryozoans. The white egg mass is a thick cylindrical coil of approximately 1.25–1.5 whorls. This species has been documented over a decade from Bahía de los Ángeles where its presence is highly seasonal and variable (Tables 1–2).

**EXTERNAL MORPHOLOGY.**— The living animals (Fig. 5A) are small, 10–20 mm in length. The preserved specimens are 3–4 mm long. The body is moderately wide and ovoid and relatively high in lateral profile. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is deep purplish with an extensive opaque white patch on the center part of the notum. The white patch may also have areas of orange pigment. The margins of the notum, foot, bases of the rhinophores, lateral papillae, tubercles and gill are all covered with dark purple pigment. The apices of the lateral papillae and rhinophores are covered with light orange pigment. The tips of the gill branches are covered with dark brown. There is a lateral band of chocolate brown and irregular tubercles of the same color scattered over the notum over the opaque white. Seven to nine elongate and slightly curved papillae are scattered along either side of the notum. The posterior pair of papillae on either side share a common base. No mid-dorsal papillae are present on the notum, but rounded irregular tubercles are present. The gill consists of 5–10 unipinnate branches. The rhinophores are elongate with 16–18 congested lamellae. The anterior end of the broad foot (Fig. 6A) contains two elongate triangular velar 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.

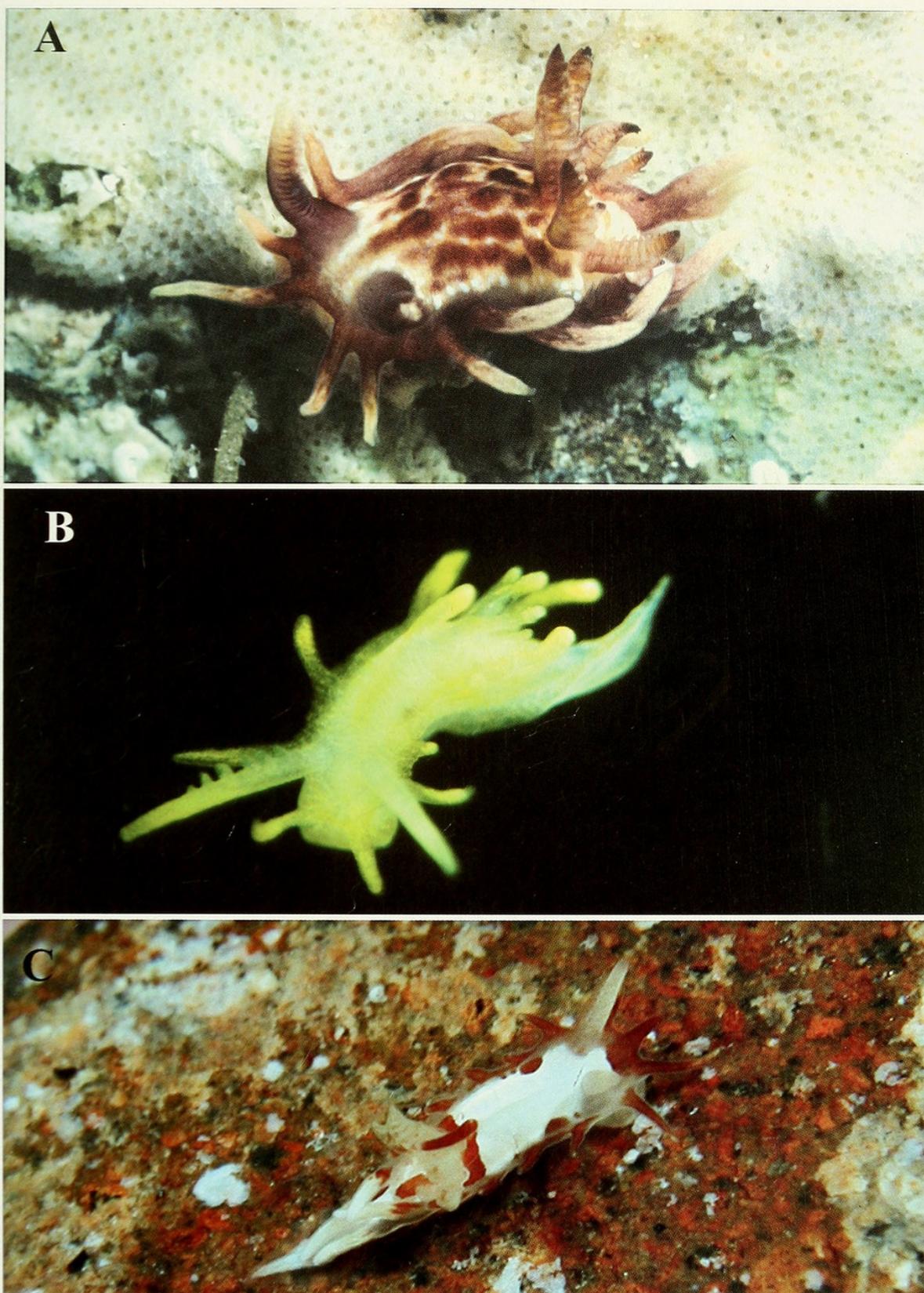


FIGURE 5. Living animals. A. *Okenia angelica* sp. nov., Punta Gringa, Bahía de los Ángeles, Baja California, México, photo by Terrence M. Gosliner. B. *Okenia cochimi* sp. nov., Las Ballenas, Espiritu Santo Island, Baja California Sur, México, photo by Terrence M. Gosliner. C. *Okenia mexicorum* sp. nov., Bahía de Banderas, Jalisco, México, photo by Alicia Hermosillo.

TABLE 1. Summary of annual observations of *Okenia angelica* at Bahía de los Ángeles during the 10 year period of 1992–2001. Columns indicate year, total hours of search time, number of animals seen, and density per hour.

Year	Hours	# Specimens	Density/hour
1992	27.52	2	.072
1993	23.57	8	.339
1994	42	25	.6
1995	30.3	5	.165
1996	24.8	1	.04
1997	36.55	1	.027
1998	13.7	4	.29
1999	18.15	7	.39
2000	15.7	1	.064
2001	18.05	13	.72

TABLE 2. Summary of monthly observations of *Okenia angelica* at Bahía de los Ángeles during the 10 year period of 1992–2001. Columns indicate totals for each month of hours searched, number of specimens, and density per hour.

Month	Hours	# Specimens	Density/hour
Jan	18.34	0	— (1 egg mass)
Feb	16.47	0	—
Mar	16.7	2	.12
Apr	11.27	0	—
May	17.1	1	.058
June	33	0	— (1 egg mass)
July	39.92	30	.75 (egg masses)
Aug	9.65	1	.1 (egg masses)
Sept	26.47	6	.23 (egg masses)
Oct	4.55	1	.22
Nov	34.35	22	.64 (egg masses)
Dec	17.08	3	.18

**DIGESTIVE SYSTEM.**— The buccal mass (Fig. 6B) is thick and muscular with a rounded buccal pump directed dorsally. There are 3–4 minute, simple pyriform oral glands on either side of the mouth. The radular sac is short and extends ventrally from the buccal mass. The cuticle expands as it enters the buccal pump. A labial cuticle surrounds the lips at the opening of the mouth. Discrete jaw elements are visible at the apex of the cuticle. The labial elements (Fig. 7A) have a broad quadrangular shape with 2–4 rounded apical lobes. The radular formula is 25 X 1.1.0.1.1. in one specimen examined. The inner lateral teeth (Fig. 7B) are broad basally with an elongate, acutely pointed cusp and 29–31 elongate fine, acutely pointed denticles along the elongate masticatory margin. The outer laterals are slightly smaller (Fig. 7B) with a quadrangular shape and rounded margin without a distinct cusp.

**REPRODUCTIVE SYSTEM.**— (Fig. 6C) 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

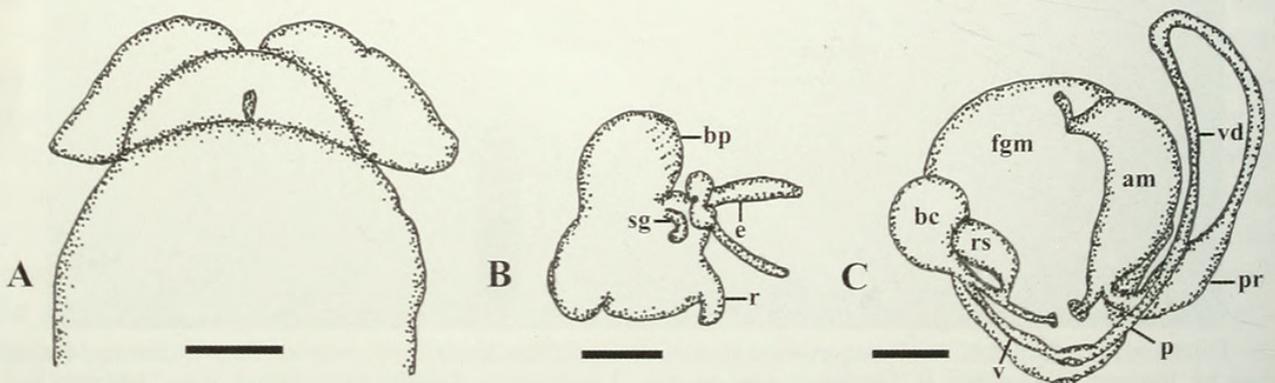


FIGURE 6. *Okenia angelica* sp. nov., A. ventral view of head, scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac, sg = salivary gland, scale = 0.38 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 0.5 mm.

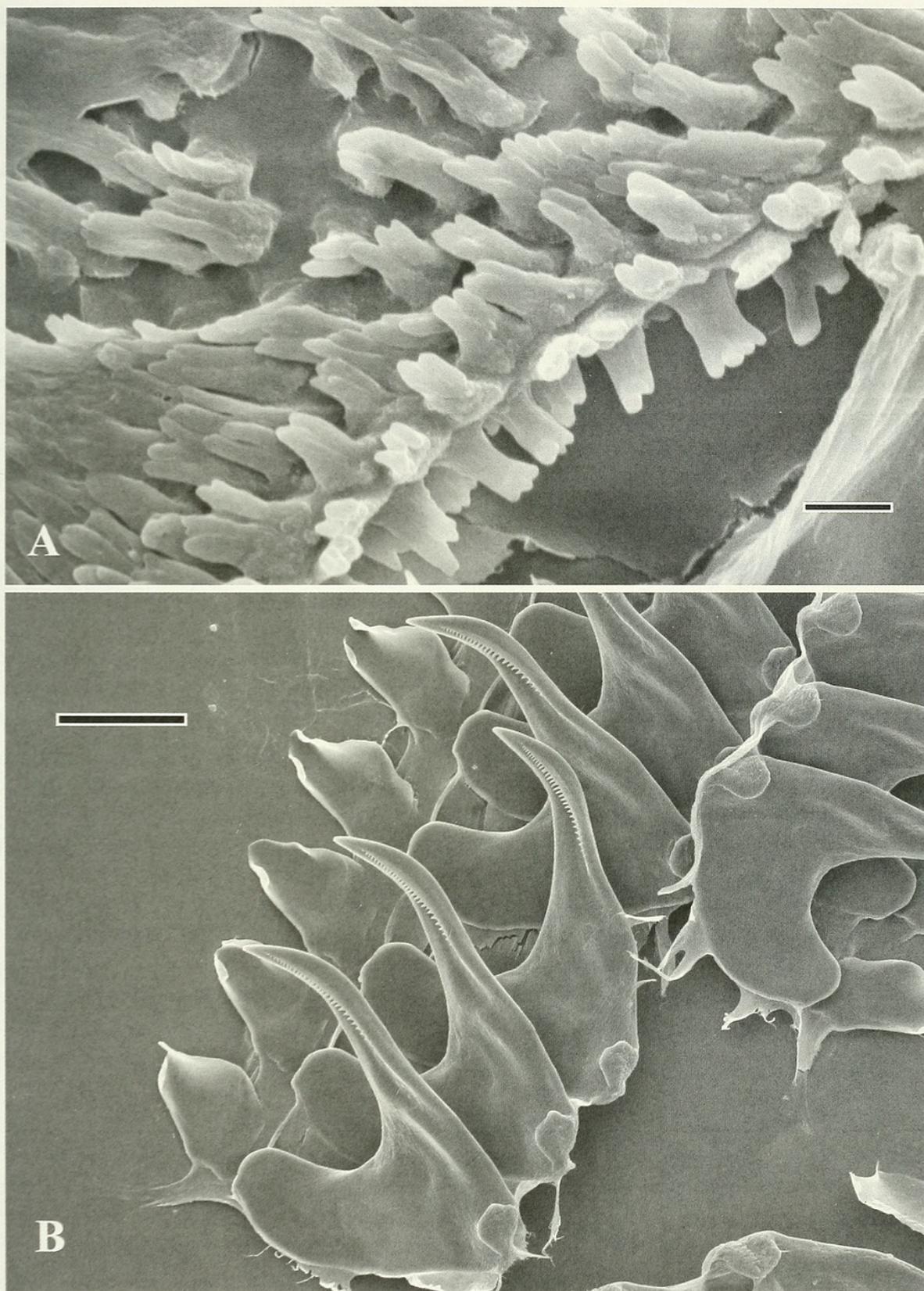


FIGURE 7. *Okenia angelica* sp. nov.. Scanning electron micrographs. A. Jaw rodlets, scale = 10  $\mu$ m. B. Radular teeth, scale = 40  $\mu$ m.

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 short and wide. The distal end of the prostate narrows into an elongate, curved ejaculatory portion that terminates in a slightly wider 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 of the bursa, the receptaculum duct emerges and joins the large, pyriform receptaculum seminis. The uterine duct emerges from near the base of the receptaculum and enters the female gland mass after paralleling the vagina for some distance.

**DISCUSSION.**— The only other described species of *Okenia*, besides *O. angelica*, that have bilobed, flat velar tentacles are *O. echinata* Baba, 1949 and *O. opuntia* Baba, 1960, both known only from Japan. All three species also have prominent jaw elements and similarly shaped radular teeth. Both of these species differ from *O. angelica* in having elongate papillae over the entire surface of the notum. *Okenia echinata* is orange or brown with minute opaque white spots. *Okenia opuntia* which also shares the character of having the posterior pair of notal appendages having a united base, is whitish with papillae that are yellow basally and white apically. *Okenia angelica* has 25 rows of radular teeth with 29–31 denticles on the inner lateral teeth. There are 40 rows of radular teeth with 30–35 denticles on the inner laterals of *O. opuntia* while in *O. echinata* there are 15 rows of radular teeth with 20–25 denticles on the inner laterals. Other details of the anatomy, including the reproductive morphology, were not described for the two Japanese species.

***Okenia cochimi* Gosliner and Bertsch, sp. nov.**

(Figs. 5B, 8–9)

**TYPE MATERIAL.**— HOLOTYPE: CASIZ 170091, one specimen, 13 m depth, Las Ballenas Espiritu Santo Island, Baja California Sur, 26 July, 1985, Terrence M. Gosliner. PARATYPES: CASIZ 170833, one specimen, 13 m depth, Las Ballenas Espiritu Santo Island, Baja California Sur, 26 July, 1985, Terrence M. Gosliner. CASIZ 170092, one specimen, dissected, Isla Cedros, Baja California, México, 29 December, 1985, Hans Bertsch.

**ETYMOLOGY.**— The specific epithet, *cochimi*, comes from the name for the Cochimí tribe of native Americans that inhabited central Baja California.

**DISTRIBUTION.**— This species is known only from the Isla Cedros on Pacific coast of Baja California, from Isla Ballena near La Paz in the Gulf of California south to Bahía Ballena near Puerto Vallarta, México (present study).

**NATURAL HISTORY.**— This species has been found in relatively shallow water of 10–15 meters depth, but has not been found in association with any prey species.

**EXTERNAL MORPHOLOGY.**— The living animals are small, 2–4 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 papillae. The body color is uniformly lemon yellow. There are 5–8 pairs of elongate lateral 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 four unipinnate branches. The rhinophores are elongate with 5–6 congested lamellae. 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 region is rounded and lacks distinct tentacles (Fig. 8A).

**DIGESTIVE SYSTEM.**— The buccal mass is thick and muscular with a rounded buccal pump directed dorsally. Numerous, large, 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 13 X 1.1.0.1.1. The inner lateral teeth (Fig. 9A–B) are wide basally with an elongate acute cusp. The masticatory margin of the inner lateral bears about 16–19 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced (Fig. 9A–B) and are triangular in shape with a short curved cusp at the apex.

**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 long 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, folded portion. The distal end of the prostatic segment narrows into a short, straight ejaculatory portion that terminates near the base of the short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow throughout its relatively short length. It connects directly to the irregularly shaped, elongated bursa copulatrix and the smaller, pyriform receptaculum seminis. Near the base of the receptaculum seminis, the uterine duct separates and enters the albumen gland.

**DISCUSSION.**— No other described species of *Okenia* has a uniformly colored yellow body. Several other species, including *O. angelensis* and *O. cupella* have a cream to yellowish color (present study; Valdés and Ortea 1995) but have scattered brownish markings, more widely separated rhinophoral lamella and a more elongate body. Several other species *Okenia* have lateral appendages with a single median dorsal papilla. In a study of the Indo-Pacific species (Gosliner 2004), these taxa were found in two primary clades, one that includes the species *O. lambat* Gosliner, 2004, *O. virginiae* Gosliner, 2004, and *O. kendi* Gosliner, 2004. These taxa are united in having a short vagina with the uterine duct emerging directly off the vagina rather than from the base of the receptaculum seminis. This differs from the elongate vagina of *O. cochimi*. These taxa also have small oral glands, unlike those found in *O. cochimi*. The second clade that includes species with a single mid-dorsal papilla is the one that includes *O. japonica* Baba, 1949; *O. pur-*

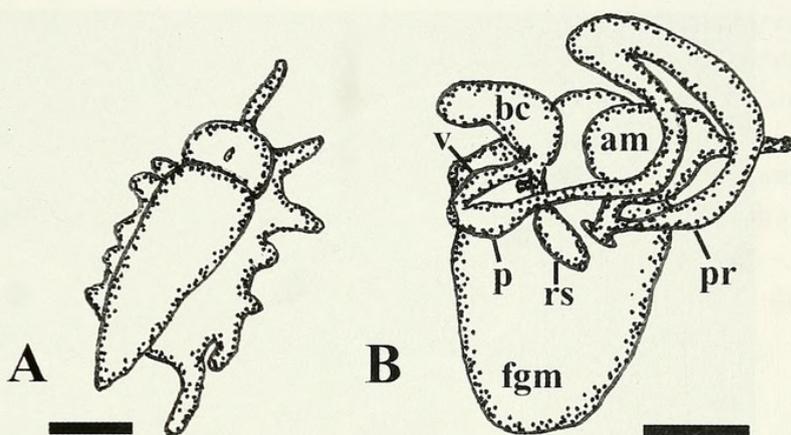


FIGURE 8. *Okenia cochimi* sp. nov., A. ventral view of head, scale = 0.2 mm. B. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, scale = 0.17 mm.

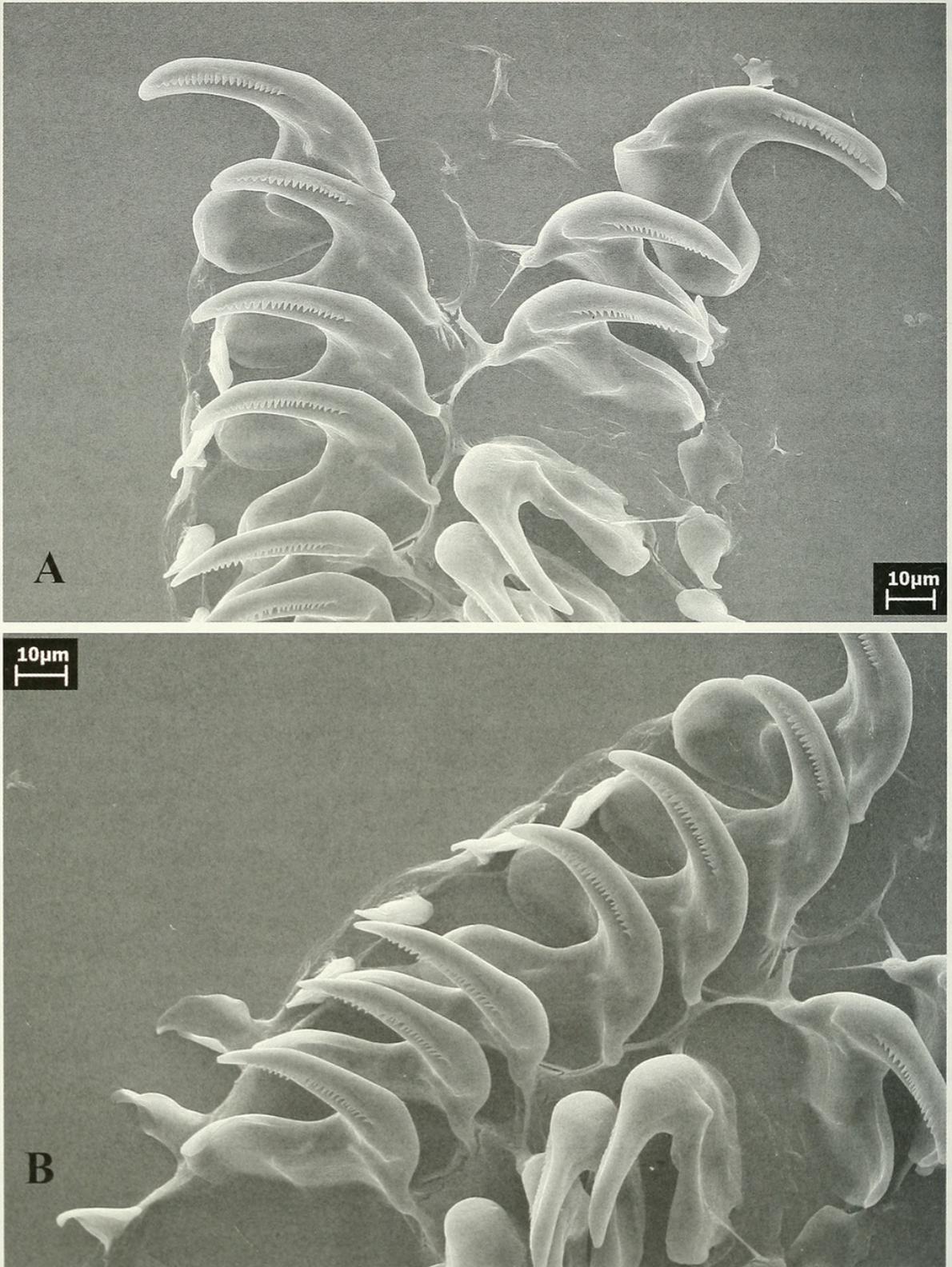


FIGURE 9. *Okenia cochimi* sp. nov. Scanning electron micrographs of radular teeth. A. Radular teeth. B. View of half row of radular teeth.

*pureolineata* Gosliner, 2004 and *O. liklik* Gosliner, 2004. Members of this group have a more elongate body shape and large oral glands, as in *O. cochimi*. All of these species are clearly distinct from *O. cochimi*. *Okenia japonica* is uniformly white with a light gray to opaque white dusting

over the entire body surface, while *O. cochimi* is yellow throughout the body. Both *O. purpureolineata* and *O. liklik* have a purple body color with darker purple lines in the case of *O. purpureolineata* or with brown and white markings in *O. liklik*. *Okenia cochimi* and *O. japonica* have a single elongate mid-dorsal papilla while *O. purpureolineata* has two elongate mid-dorsal papillae and in *O. liklik* the papilla has been modified to form a short sail-shaped ridge. The outer lateral teeth of *O. japonica* and *O. purpureolineata* are quadrangular while those of *O. cochimi* and *O. liklik* are triangular with an elongate, curved cusp.

***Okenia mexicorum* Gosliner and Bertsch, sp. nov.**

(Figs. 5C, 10–11)

**TYPE MATERIAL.**—HOLOTYPE: CASIZ 166888, one specimen, 20 m depth, Mismaloya, Bahía de Banderas, Jalisco, México, 28 February 2003, Alicia Hermsillo. PARATYPES: CASIZ 170044, 5 specimens, 2 dissected, 20 m depth, Mismaloya, Bahía de Banderas, Jalisco, México, 17 November 2003, Alicia Hermsillo. CASIZ 170043, 8 specimens, 20 m depth, Mismaloya, Bahía de Banderas, Jalisco, México, 22 November 2003, Alicia Hermsillo. CASIZ 167394, 1 specimen, 20 m depth, Majahuitas, Bahía de Banderas, Jalisco, México, 29 May 2003, Alicia Hermsillo. CASIZ 170045, 3 specimens, 1 dissected, 1 m depth, Ensenada de los Muertos, Baja California Sur, México, 25 October 2001, Orso Angulo Campillo.

**ETYMOLOGY.**—The specific name, *mexicorum*, honors our outstanding young Mexican colleagues, Alicia Hermsillo and Orso Angulo Campillo who have advanced greatly our understanding of the opisthobranch fauna of the tropical Americas.

**DISTRIBUTION.**—This species is known along the Mexican coast from Baja California Sur to Bahía de Banderas, Jalisco.

**NATURAL HISTORY.**—*Okenia mexicorum* has been found in relatively shallow water from 1–20 m depth. Specimens are found in the open on hard and soft substrate, but this species has not been found in association with prey species.

**EXTERNAL MORPHOLOGY.**—The living animals (Fig. 5C) are small, 5–8 mm in length. The preserved specimens are 2–3 mm. long. The body is moderately wide and ovoid and relatively high in lateral profile. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is translucent white with an extensive opaque white patch on the center part of the notum that extends from the level of the rhinophores to the posterior end of the foot. External to this white patch are brick red pigmented areas that extend along the notal

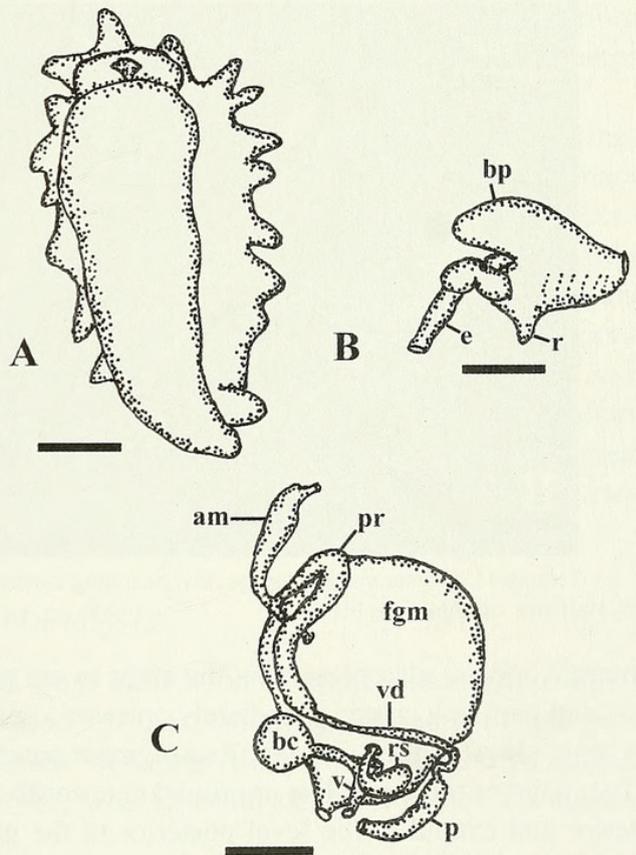


FIGURE 10. *Okenia mexicorum* sp. nov. A. ventral view of body, scale = 0.3 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac, scale = 0.2 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 0.2 mm.

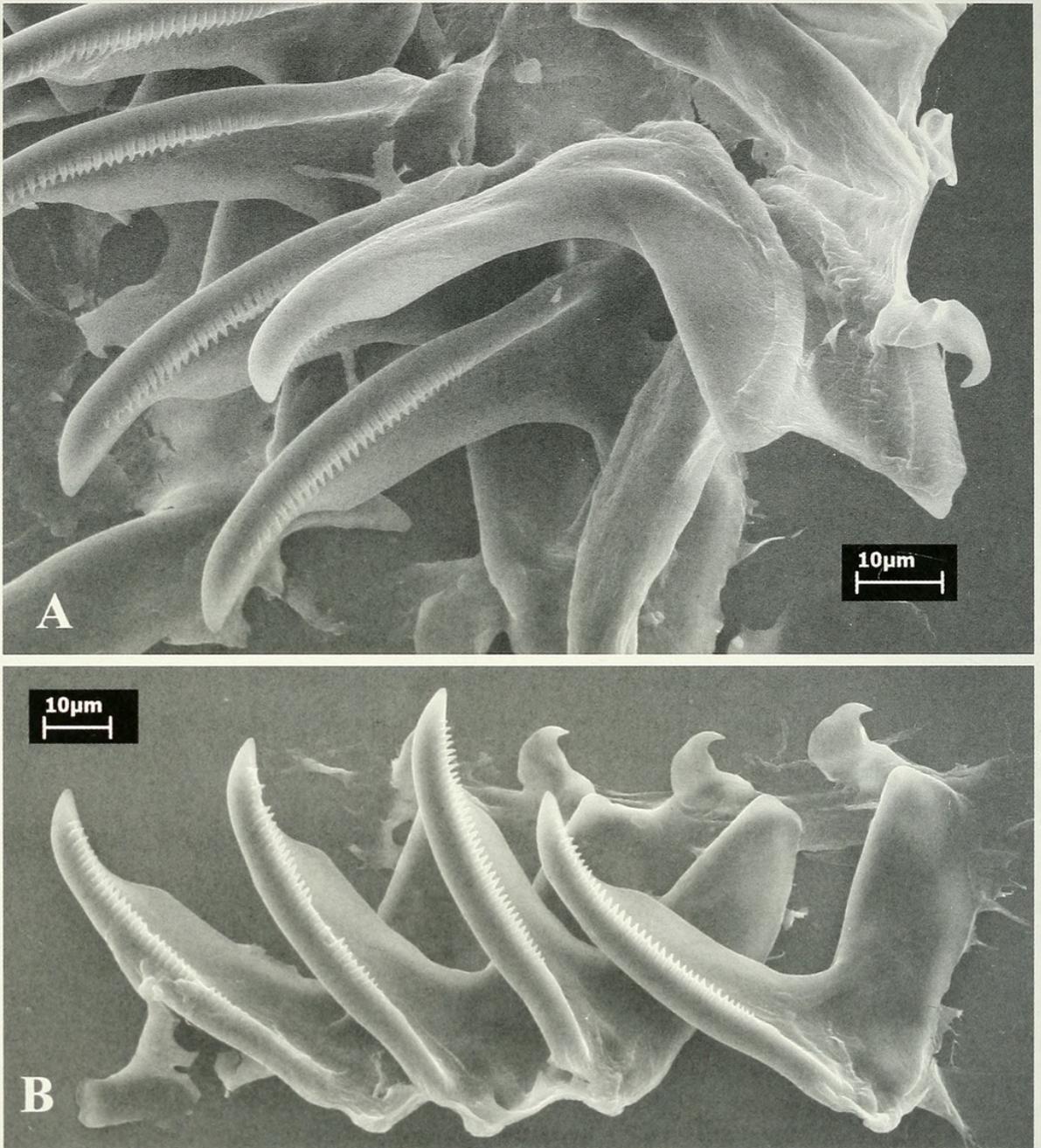


FIGURE 11. *Okenia mexicorum* sp. nov. Scanning electron micrograph of radular teeth. A. Inner and outer lateral teeth. B. Half-row of radular teeth.

margin and are also present on the eight to ten pairs of lateral papillae and on the single, elongate medial papilla located immediately anterior to the gill. This papilla is found at the posterior end of a long, elevated medial ridge. Red pigment patches are also found on the lateral sides of the body. Two pairs of these papillae are found anterior to the rhinophores while the remaining ones are posterior and extend to the level posterior to the gill. The posterior two papillae per side are much longer than the more anterior ones and do not share a common base. The rhinophores are uniformly white and have 7–9 simple lamellae. The apices of a few of the more posterior lateral papillae have opaque white or translucent white pigment. The gill consists of five to six unipinnate branches which bear mottled brick red pigment on their surfaces. The anterior end of the broad foot (Fig. 10A) is simply rounded without distinct oral tentacles. 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 (Fig. 10B) is thick and muscular with a rounded buccal pump directed dorsally. There are several small oral glands around the mouth. The radular sac is long and curved 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 15 X 1.1.0.1.1. in one specimen examined. The inner lateral teeth (Fig. 11A–B) are broad basally with a sharp curvature that places the thickened masticatory margin at a 90 degree angle relative to the basal portion. The masticatory portion has an acutely pointed cusp with 26–34 short, triangular acutely pointed denticles along its cutting edge. The outer laterals are significantly smaller and reduced (Fig. 11A–B) with a single curved, sharply pointed cusp.

**REPRODUCTIVE SYSTEM.**— (Fig. 10C) 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 an elongate, curved ejaculatory portion that terminates in a long wider, curved penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow and moderately long and connects directly to the large, spherical bursa copulatrix. Near the base of the vagina, the receptaculum duct emerges and parallels the vagina for a short 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.**— No other species of *Okenia* has a whitish body color with red markings. *Okenia mexicorum* is similar to *O. mediterranea* (Ihering, 1886), the only other *Okenia* that has a prominent medial mid-dorsal ridge (Valdés and Ortea 1995). However, *O. mediterranea* lacks a papilla at the posterior end of the ridge and differs markedly in its radular and reproductive anatomy. In *O. mediterranea*, the inner lateral radular teeth (Schmekel and Portmann 1982; Valdés and Ortea 1995) have fewer denticles (12–14) than do those of *O. mexicorum* (26–34) and the curvature of the teeth of *O. mediterranea* is more gradual rather than being sharply angled as in *O. mexicorum*. The outer lateral teeth of *O. mediterranea* have a proportionately wider base and a shorter cusp than do those of *O. mexicorum*. The vaginal duct of *O. mexicorum* is very short, whereas it is elongate in *O. mediterranea* (Valdés and Ortea 1995). *Okenia hispanica* Valdés and Ortea, 1995, is white with pink and yellow spots, but it lacks a medial ridge and a medial papilla.

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