

Review of the Flabellinidae (Nudibranchia: Aeolidacea) from the Tropical Indo-Pacific, with the Descriptions of Five New Species

by

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Abstract. The morphology and systematics of seven members of the Flabellinidae are described and discussed. *Coryphella* Gray, 1850, and *Coryphellina* O'Donoghue, 1929, are maintained as synonyms of *Flabellina* Voigt, 1834. The morphological variability of *F. bicolor* (Kelaart, 1858) is fully described and *F. annuligera* (Bergh, 1900), *F. ornata* (Risbec, 1928), and *F. alisonae* Gosliner, 1980, are considered as synonyms. *Flabellina rubrolineata* (O'Donoghue, 1929) is recorded from several localities from Aldabra Atoll to Enewetak Atoll.

Five new species of *Flabellina* are described. *Flabellina riwo* sp. nov., *F. bilas* sp. nov., and *F. rubropurpurata* sp. nov. have perfoliate rhinophores and are closely allied to *F. bicolor*. Two other species, *F. delicata* sp. nov. and *F. exoptata* sp. nov., have papillate rhinophores and are most closely allied to *F. rubrolineata*, *F. poenicia*, and *F. marcusorum*.

The phylogeny of two clades of flabellinids is further elucidated, based upon the examination of several new taxa. The biogeography of the Flabellinidae is discussed relative to the proposed phylogenetic hypothesis.

INTRODUCTION

The Flabellinidae have received considerable attention in recent years (MILLER, 1971; KUZIRIAN, 1979; GOSLINER & GRIFFITHS, 1981; GOSLINER & KUZIRIAN, 1990), but the emphasis of most systematic treatments has been upon temperate species, rather than upon tropical members of the family.

Recent collections of opisthobranchs from several localities within the Indo-Pacific tropics, including Fiji, Australia, Papua New Guinea, the Seychelles, Madagascar and Aldabra, have brought to light specimens of seven species of Flabellinidae. The members of this family are poorly known in the Indo-Pacific and provide the focus of this systematic and morphological study.

SPECIES DESCRIPTIONS

Flabellina bicolor (Kelaart, 1858)

(Figures 1A, 2-5)

Eolis bicolor KELAART, 1858:115; KELAART 1859:490.

Aeolis bicolor (Kelaart, 1858): KELAART, 1883:104.

Samla annuligera BERGH, 1900:237, pl. 20, figs. 47-55.

Samla bicolor (Kelaart, 1858): ELIOT, 1906:685, pl. 45, fig. 4.

Coryphella ornata RISBEC, 1928:266, pl. 11, fig. 1, text fig. 89, nos. 1, 2; RISBEC, 1953:143, fig. 98a; BABA, 1936:44, fig. 26, pl. 2, fig. b., **syn. nov.**

Flabellina ornata (Risbec, 1928): BABA, 1955:29, fig. 48, pl. 15, figs. 42, 43; WILLAN & COLEMAN, 1984:42, fig. 134. **syn. nov.**

Flabellina alisonae GOSLINER, 1980:40, figs. 1, 2; BERTSCH & JOHNSON, 1981:88; JOHNSON & BOUCHER, 1984:283. *syn. nov.*

Flabellina ornata Angas: ORR, 1981:72. (*non Flabellina ornata* Angas, 1864). *syn. nov.*

Distribution: This species is widespread throughout the Indo-Pacific and is known from the Hawaiian Islands (BERGH, 1900; GOSLINER, 1980; BERTSCH & JOHNSON, 1981; present study), the Marshall Islands (JOHNSON & BOUCHER, 1984); Fiji (present study), New Caledonia (RISBEC, 1928); Guam (present study); Australia (WILLAN & COLEMAN, 1984); Okinawa (BABA, 1936; present study), Japan (BABA, 1955), Hong Kong (ORR, 1981), Papua New Guinea (present study), Sri Lanka (KELAART, 1858, 1859, 1883; ELIOT, 1906), the Seychelles (present study), Reunion (present study), Madagascar (present study) and South Africa (present study).

Material: Twelve specimens, California Academy of Sciences, San Francisco, CASIZ 070558, 1 dissected, N end Mahe Island, Republic of Seychelles, 21 April 1984, T. M. Gosliner. One specimen, CASIZ 070563, 1 km N of Mahe Beach Hotel, Mahe Island, Republic of Seychelles, 3 May 1984, T. M. Gosliner. Three specimens, CASIZ 070564, Anse Takamaka, Mahe Island, Republic of Seychelles, 2 May 1984, T. M. Gosliner. Ten specimens, CASIZ 070565, N of Beau Vallon, Mahe Island, Republic of Seychelles, 21 April 1984, T. M. Gosliner. One specimen, CASIZ 070559, lagoon between Passe Femme and Passe DuBois, Aldabra Atoll, Seychelles, 19 March 1986, T. M. Gosliner. Three specimens, CASIZ 070560, Middle Camp, Aldabra Atoll, Seychelles, 18 March 1986, T. M. Gosliner. Seven specimens, CASIZ 070561, 070562, 070610, Passe Femme, Aldabra Atoll, Seychelles, 19–23 March 1986, T. M. Gosliner. One specimen, CASIZ 070600, reef flat, NE of pass through reef 5 km WSW of Mora Mora Village, Madagascar, 8 April 1988, T. M. Gosliner. Six specimens, CASIZ 070601, near Sea Stack, NW side of Nosy Tanikely, Madagascar, 14 April 1989, T. M. Gosliner. Two specimens, CASIZ 070602, point on N side of Andilana Beach, Nosy Be, Madagascar, 15 April 1989, T. M. Gosliner. Two specimens, CASIZ 070603, point NW of Village Beach, Nosy Komba, Madagascar, 16 April 1989, T. M. Gosliner. One specimen, CASIZ 070566, Barracuda Point, Pig Island, Madang, Papua New Guinea, 13.7 m depth, 29 January 1988, T. M. Gosliner. Two specimens, CASIZ 070568, dissected, N side of patch reefs, N side of Kranket Island, Madang, Papua New Guinea, 22.7 m depth, 24 January 1988, T. M. Gosliner. One specimen, CASIZ 070569, dissected, Rempi Lagoon, N of Madang, Papua New Guinea, 13.7 m depth, 3 February 1988, T. M. Gosliner. One specimen,

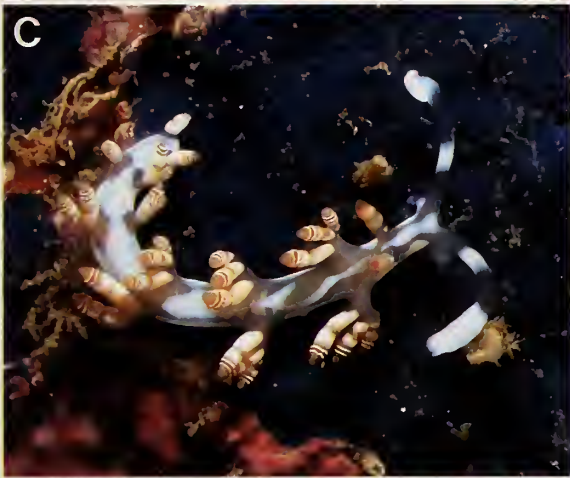
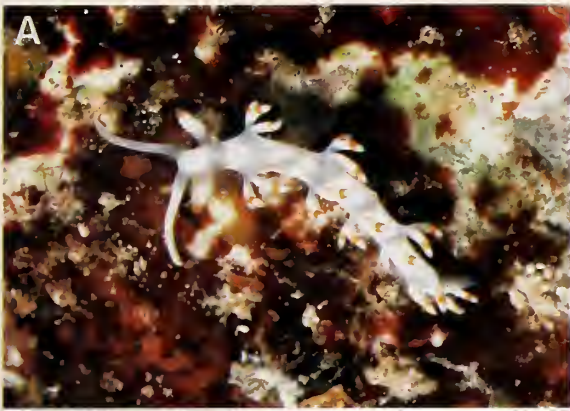
CASIZ 070604, Cement Mixer Reef, Madang, Papua New Guinea, 17 October 1986, T. Frohm. One specimen, CASIZ 070605, Cement Mixer Reef, Madang, Papua New Guinea, 6.1–7.6 m depth, 20 October 1986, M. Ghiselin. Three specimens, CASIZ 070606, Cement Mixer Reef, Madang, Papua New Guinea, 6 m depth, 19 October 1986, T. M. Gosliner. One specimen, CASIZ 070607, patch reef, N end Kranket Island, Madang, Papua New Guinea, 10.7 m depth, 1 October 1986, T. M. Gosliner. One specimen, CASIZ 070608, opposite lab, between Pig Island and Massis Island, Madang, Papua New Guinea, 15.2 m depth, 30 September 1986, T. M. Gosliner. One specimen, CASIZ 070609, near lighthouse, Madang, Papua New Guinea, 33.5 m depth, 15 January 1988, T. M. Gosliner. Nine specimens, CASIZ 070567, intertidal, Kewalo Basin, Mamala Bay, Honolulu, Oahu, Hawaii, 7 February 1986, T. M. Gosliner. One specimen, South African Museum, NB 63, Natal, South Africa, 29 December, 1958. One specimen, Kings Headland, Caloudra, Sunshine Coast, N of Brisbane, Queensland, 6 m depth, 31 May 1981, P. Gofton. One specimen, channel between main islets, Shag Rock, NW of Point Lookout, North Stradbroke Island, Queensland, 10 m depth, 17 June 1981, R. C. Willan. One specimen, under coral slab, outer reef flat, W end of Heron Island, Capricornia Section, Great Barrier Reef, Queensland, low intertidal, 16 July 1981, R. C. Willan. One specimen, "The Nursery," NW side of Julian Rocks, off Cape Byron, New South Wales, 5 September 1987, C. Buchanan.

External morphology: The living animals (Figure 1A) reach a maximum length of 22 mm. The general body color is translucent white or bluish white. Opaque white pigment may be present sparsely or densely on the oral tentacles, head, notum, and cerata. This pigment may entirely overlie the translucent white notum or may be present as discrete patches, separated by areas of translucence, usually at the bases of the ceratal peduncles. Generally, the bases of the oral tentacles, rhinophoral stalks, and cerata are devoid of opaque white, even in the most heavily pigmented individuals. The rhinophoral stalks may be either opaque or translucent white. More distally, a brownish band is present in some individuals and the apical portion is cream or orange. A vivid orange spot or incomplete or complete ring is present subapically on each ceras. The upper and lower boundaries of the orange pigment are sharply demarcated.

The body is narrow and elongate. The notum is high and rounded in profile, continuing as a ridge to the tip of the tail. The tail is elongate and pointed. The oral tentacles are elongate, approximately three times the length of the rhinophores. The tentacles are usually laterally com-

Figure 1

Living animals. A. *Flabellina bicolor* (Kelaart, 1858). B. *F. riwo* sp. nov. C. *F. bilas* sp. nov. D. *F. rubropurpurata* sp. nov. E. *F. rubrolineata* (O'Donoghue, 1929). F. *F. exoptata* sp. nov. G. *F. delicata* sp. nov.



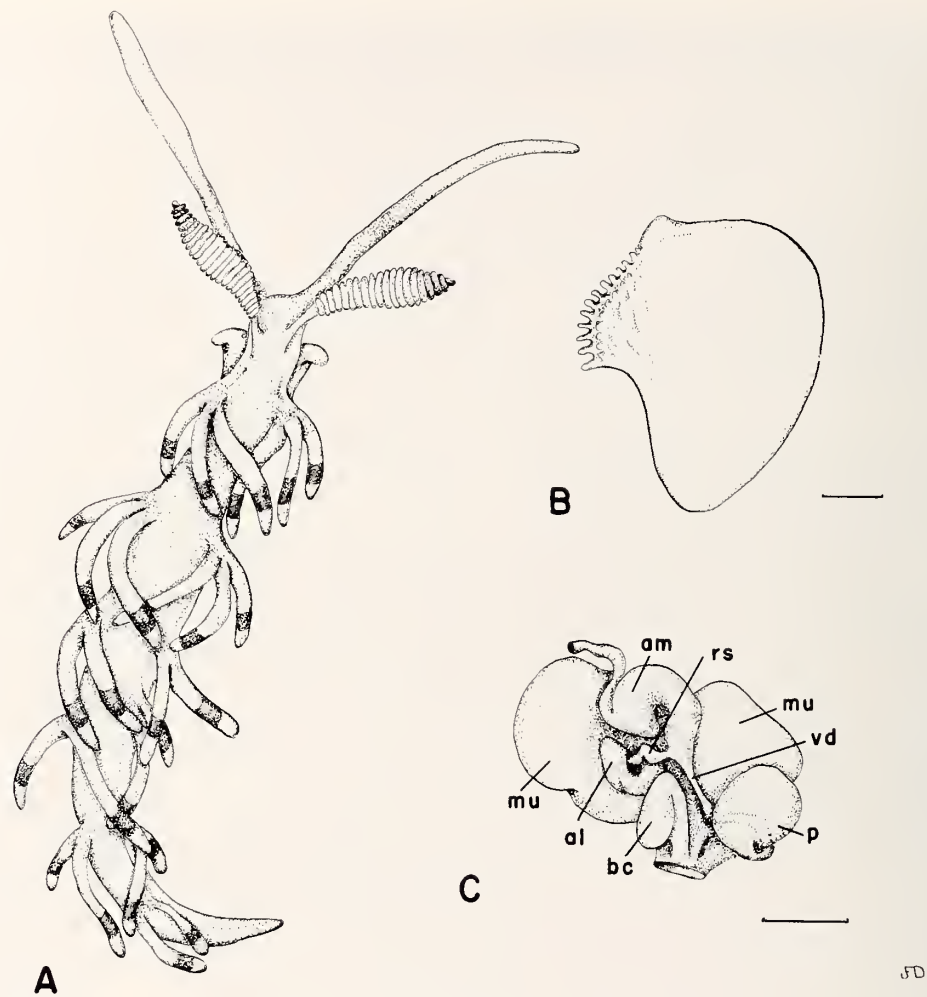


Figure 2

Flabellina bicolor (Kelaart, 1858). A. Dorsal view of 13 mm living animal. B. Jaw, scale = 0.1 mm. C. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; mu, mucous gland; p, penis; rs, receptaculum seminis; vd, vas deferens; scale = 0.3 mm.

pressed, but may become shorter and more cylindrical in animals held in aquaria for more than 24 hr. The rhinophores are perfoliate with 11–19 lamellae. The anterior foot corners are short, recurved and tentacular, but not acutely pointed. The cerata are generally held erectly in life. They are arranged in 4–8 discrete clusters per side of the body, each elevated on a short but distinct peduncle (Figure 2A). The precardiac and first 1–3 postcardiac rows each contain 3 or 4 cerata. The succeeding 2–4 posterior rows each contain 1 or 2 cerata. The gonopore is situated on the right side of the body, ventral to the anteriormost ceratal cluster. The pleuroproct anus is located immediately below the notal brim, between the precardiac and first postcardiac ceratal rows, nearer the postcardiac cluster (Figure 2A). The nephroproct is immediately dorsal to the anus.

Buccal mass: The buccal mass is short and muscular. From the anterior portion of the buccal mass, a pair of highly ramified oral glands extends posteriorly, and fills much of the first ceratal peduncle.

The jaws (Figure 2B) are thin and ovoid, with a well-developed masticatory border. The border (Figure 3A) bears approximately 3 rows of denticles. The outer row contains approximately 20 denticles, which are stronger and more prominent than the inner ones.

The radula (Figure 3B–D) has a formula of 14–20 × 1·1·1 in the 10 specimens examined. The rachidian teeth (Figure 4) are evenly curved with a pair of elongate posterior limbs. There are 7–12 elongate denticles on either side of the longer, wider central cusp. When the rachidian tooth is viewed laterally (Figure 4D), the central cusp is higher than the adjacent denticles. The lateral teeth (Fig-

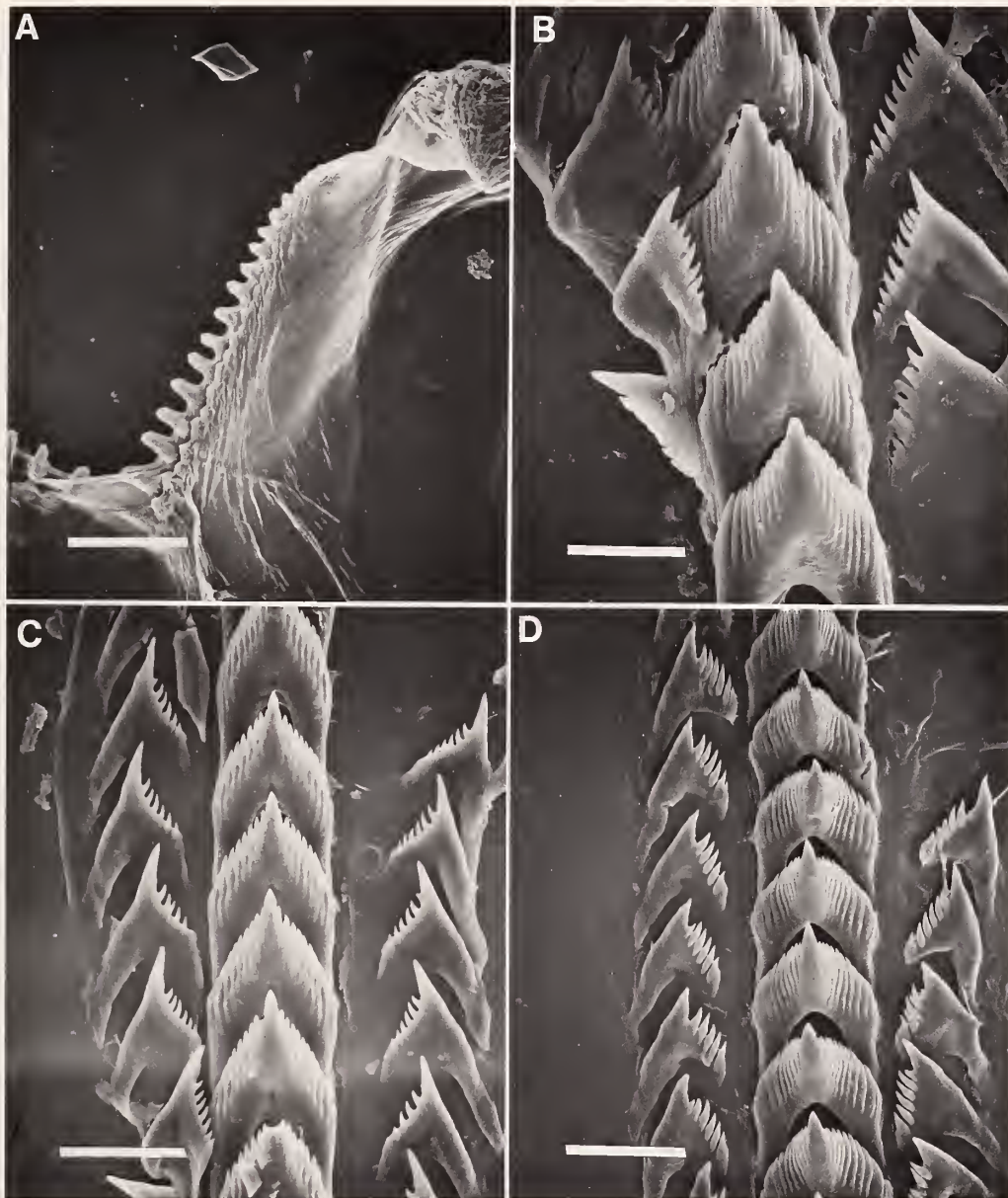


Figure 3

Flabellina bicolor (Kelaart, 1858), scanning electron micrographs. A. Masticatory border of jaw, scale = 40 μm . B. Entire radular width, Oahu, Hawaii, scale = 20 μm . C. Entire radular width, Madang, Papua New Guinea, scale = 30 μm . D. Entire radular width, Mahe, Seychelles, scale = 40 μm .

ure 5) are broadly triangular with a basal portion of variable length. The primary cusp is triangular and acutely pointed. There are 4-10 denticles along the masticatory margin of the laterals. The size and number of denticles may vary considerably between specimens from a single locality.

Reproductive system (Figure 2C): The preampullary duct is elongate and narrow. It widens into a saccate am-

pulla. The ampulla divides into a short oviduct and a more elongate vas deferens. The oviduct widens into the serial receptaculum seminis (*sensu* EDMUNDS, 1970) and narrows again as it enters the albumen gland of the female gland mass. A small membrane gland is also present. The bulk of the female gland mass is composed of the mucous gland. Near the exit of the mucous gland into the genital aperture is a thick, recurved bursa copulatrix. The vas deferens widens into a curved prostatic portion. The pro-

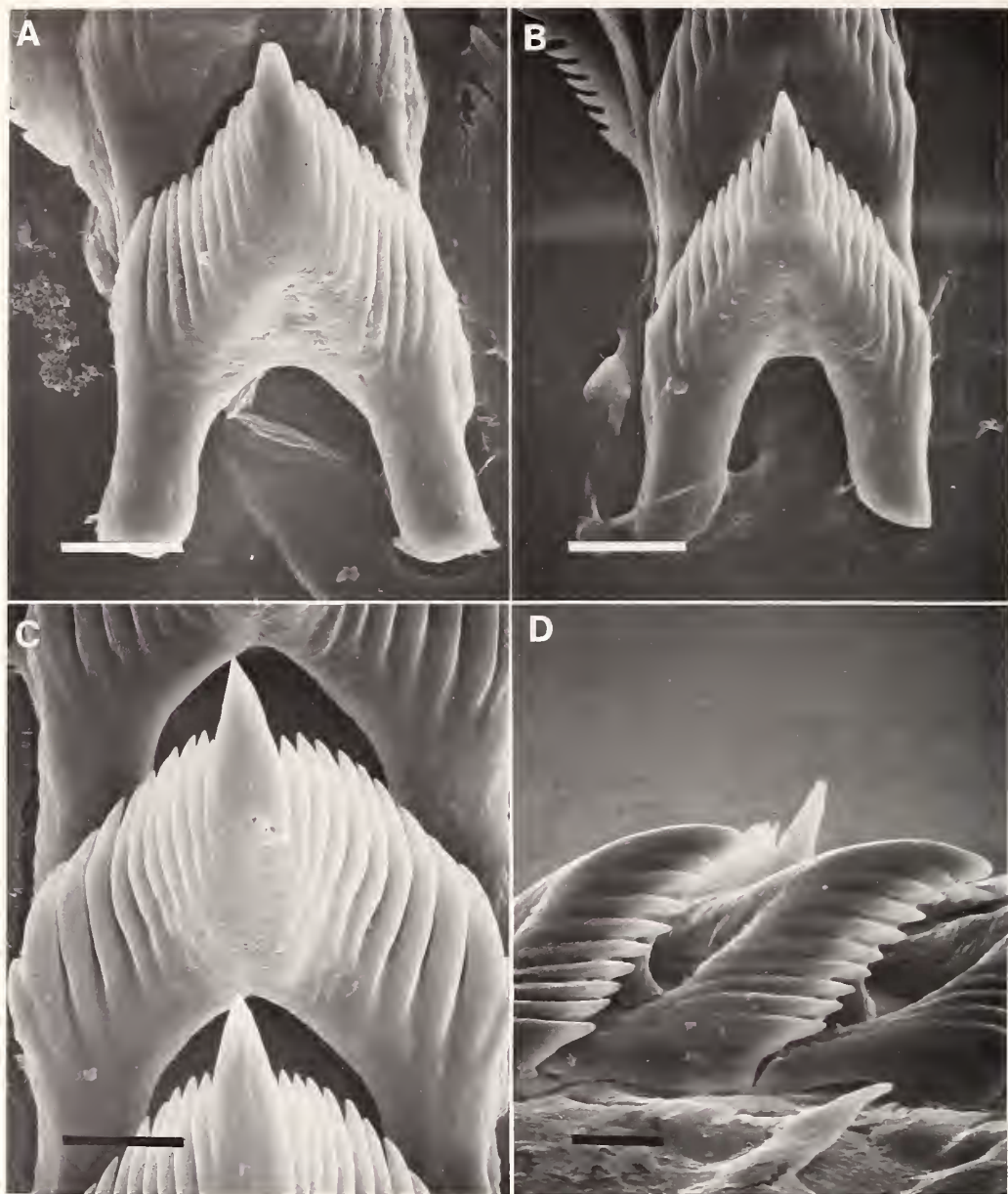


Figure 4

Flabellina bicolor (Kelaart, 1858), scanning electron micrographs of rachidian teeth, scales = 10 μm . A. Dorsal view, Oahu, Hawaii. B. Dorsal view, Madang, Papua New Guinea. C. Dorsal view, Mahe, Seychelles. D. Lateral view, Madang, Papua New Guinea.

static portion exits directly into the short, indistinct penial papilla adjacent to the female gonopore.

Discussion: The systematic status of this widespread species has been poorly understood. Much of this confusion stems from the incomplete and often inaccurate original descriptions of *Eolis bicolor* Kelaart, 1858, *Samla annuligera* Bergh, 1900, and *Coryphella ornata* Risbec, 1928. BABA (1936, 1955) provided an accurate depiction of the mor-

phology of specimens from Okinawa and Japan. GOSLINER (1980) considered specimens from Hawaii as conspecific with Baba's animals, but distinct from both Bergh's and Risbec's species. On this basis *Flabellina alisonae* was described. The examination of specimens from much of the Indo-Pacific tropics provides an estimate of the range of variability of this species within and between populations. The color and ceratal arrangement of *E. bicolor*, *S. annuligera*, and *F. alisonae* are virtually identical. The only

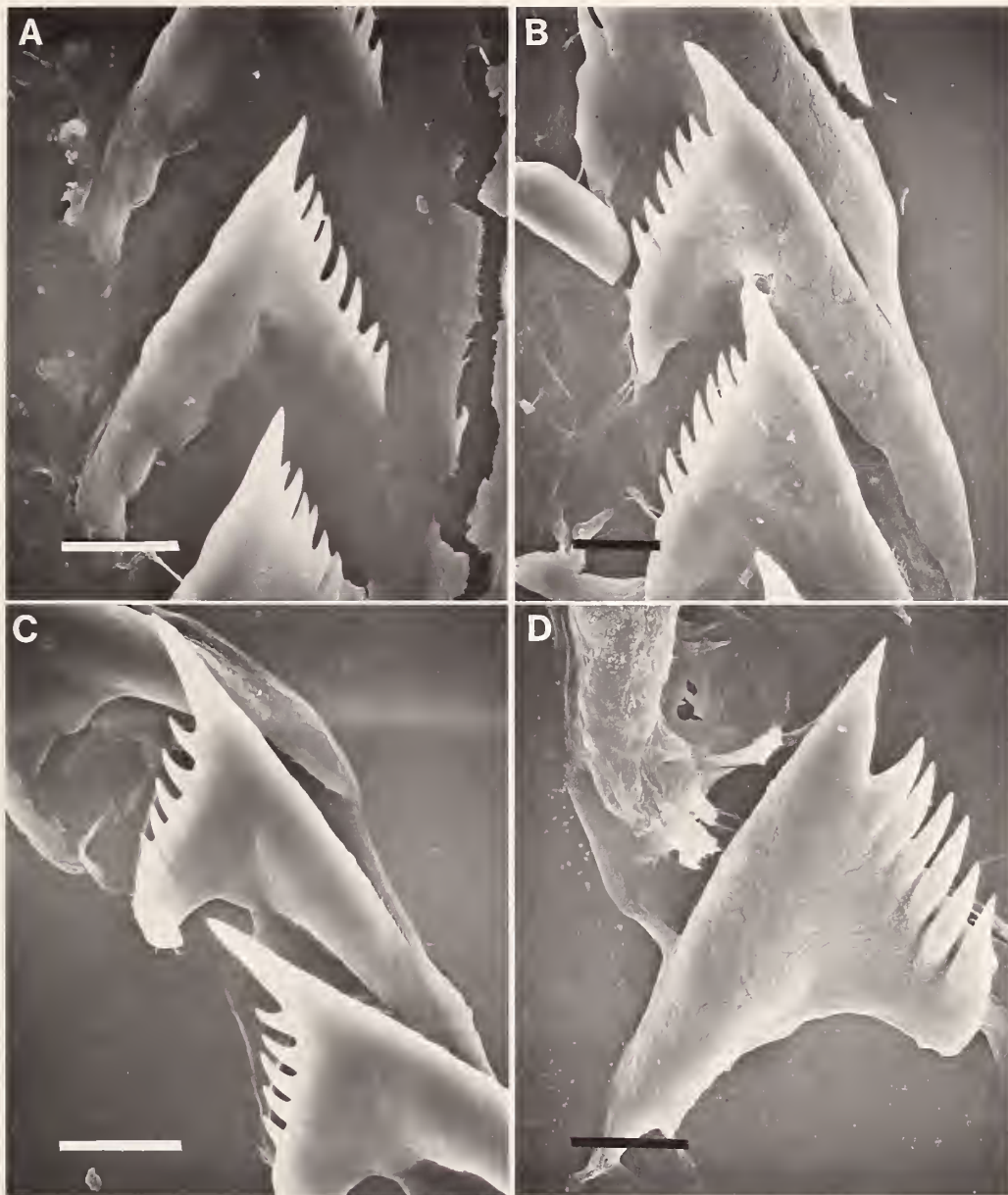


Figure 5

Flabellina bicolor (Kelaart, 1858), scanning electron micrographs of lateral teeth, scales = 10 μ m. A. Oahu, Hawaii. B, C. Madang, Papua New Guinea. D. Mahe, Seychelles.

significant differences between the three species are in the anterior end of the foot (stated to be rounded in *E. bicolor* and *S. annuligera* and tentacular in *F. alisonae*) and the number of rows of denticles on the masticatory border of the jaw (one in *F. annuligera* and two or three in *F. alisonae*). The corners of the foot may be difficult to differentiate when the animal has contracted during preservation. The difference in masticatory border of the jaw may be a result of a poorly prepared specimen where the secondary denticles were not visible. When separating the

jaws, part of the masticatory border often pulls away from the rest of the jaw. It may be that only the primary denticles of the border were present on the portion that Bergh illustrated. More importantly, no other member of the Flabellinidae has only a single row of denticles on the masticatory margin.

There are several apparent differences between *Eolis bicolor* and *Coryphella ornata* on one hand and *Flabellina alisonae* on the other. It is not apparent from either Kelaart's or Risbec's figure, or from the descriptions, that the

Table 1
Morphology of *Flabellina* species with perfoliate rhinophores.

Species	Color	Anterior right digestive branch	Radular rows	Denticles on inner laterals	Denticles on rachidian	Central cusp	Receptaculum seminis	Bursa copulatrix
<i>bicolor</i>	white to blue with orange rings on cerata	1 row	14-20	4-10	7-12	elevated	serial	recurved
<i>babai</i>	blue white with orange rings on cerata	2 rows	18-24	5-8	5-10	depressed	serial	absent
<i>bilas</i>	white with opaque white diamonds, red rings on cerata	1 row	21	2-4	9-10	depressed	serial	short stalk
<i>engeli</i>	orange with blue tinge and cream markings, cerata with orange bands	2 rows	19-20	5-10	7-11	depressed	semiserial	absent
<i>macassarana</i>	pink-yellow	2 rows	17	4-5	5	—	—	—
<i>riwo</i>	translucent white with opaque white network, blue rings on cerata	1 row	15-23	4-7	7-11	elevated	absent	reduced
<i>rubropurpurata</i>	body purple with red on cerata, rhinophores red	3	23-30	3-6	7-9	depressed	semiserial	stalked
<i>telja</i>	reddish with white spots	3-4 rows	14-28	6-9	6-11	depressed	semiserial	stalked

cerata are elevated from the notum on distinct peduncles. Also, the shapes of the jaws and radular teeth depicted by Risbec differ from those described by BABA (1936, 1955) and GOSLINER (1980). It should be noted, however, that Risbec's drawings are not known for their accuracy. The primary distinction between the two species cited by Gosliner, was the difference in ceratal arrangement. Gosliner interpreted the formula provided by Risbec as indicating that two precardiac rows of cerata are present on either side of the body. An alternative interpretation is possible. It appears that there may be two rows per side, with each row containing 3 cerata. The first of these rows could be precardiac, the second postcardiac. This would be consistent with the distribution of cerata observed in the present material.

Since the description of *Flabellina alisonae* from Hawaii (GOSLINER, 1980), several additional Indo-Pacific records of *Flabellina* specimens with orange ceratal rings have been published (BERTSCH & JOHNSON, 1981; JOHNSON & BOUCHER, 1984; ORR, 1981; WILLAN & COLEMAN, 1984). The only external differences in these specimens are the amount of opaque white pigment covering the surface of the animal and the completeness of the orange ceratal rings. The range of pigment variability of specimens may vary as much within a locality as between disparate localities. Generally, Hawaiian specimens lack any trace of opaque white pigment, while specimens from Australia and Papua New Guinea may be densely covered with this opaque pigment. Specimens collected from Nosy Be, Madagascar, varied from no opaque white pigment to being densely covered. The amount of orange pigment on the cerata

varies considerably within populations of specimens from Australia, Papua New Guinea, and Madagascar.

The remainder of the external and internal anatomy of specimens examined in this study varied only slightly and was not correlated to the coloration differences noted above. The radular and reproductive morphology are highly consistent within and between populations.

It would appear that the described differences between *Flabellina bicolor*, *F. annuligera*, *F. ornata*, and *F. alisonae* can be attributed to errors in the original descriptions of the former three species. It is more parsimonious to consider that a single species of *Flabellina*, which bears orange pigment on its cerata, is widespread in the Indo-Pacific tropics, in light of the widespread distribution and variability of the species described here. Therefore, *F. annuligera* (Bergh, 1900), *F. ornata* (Risbec, 1928), and *F. alisonae* Gosliner, 1980, are considered to be junior subjective synonyms of *F. bicolor* (Kelaart, 1858).

Two other species of *Flabellina* have orange ceratal rings, *F. engeli* Ev. Marcus & Er. Marcus, 1968, and *F. babai* Schmekel, 1970. Contrary to *F. bicolor*, both of these species have two precardiac rows of cerata per side (SCHMEKEL, 1970; EDMUNDS & JUST, 1983) and a depressed central cusp of the rachidian radular teeth. One of us (R.C.W.) has examined live specimens of *F. babai* from European waters. Jeff Hamann (personal communication) has provided us with photos of *F. engeli* from the Caribbean. The coloration of living specimens of these two species is strikingly different from that of *F. bicolor*.

The species of *Flabellina* with perfoliate rhinophores are compared in Table 1.

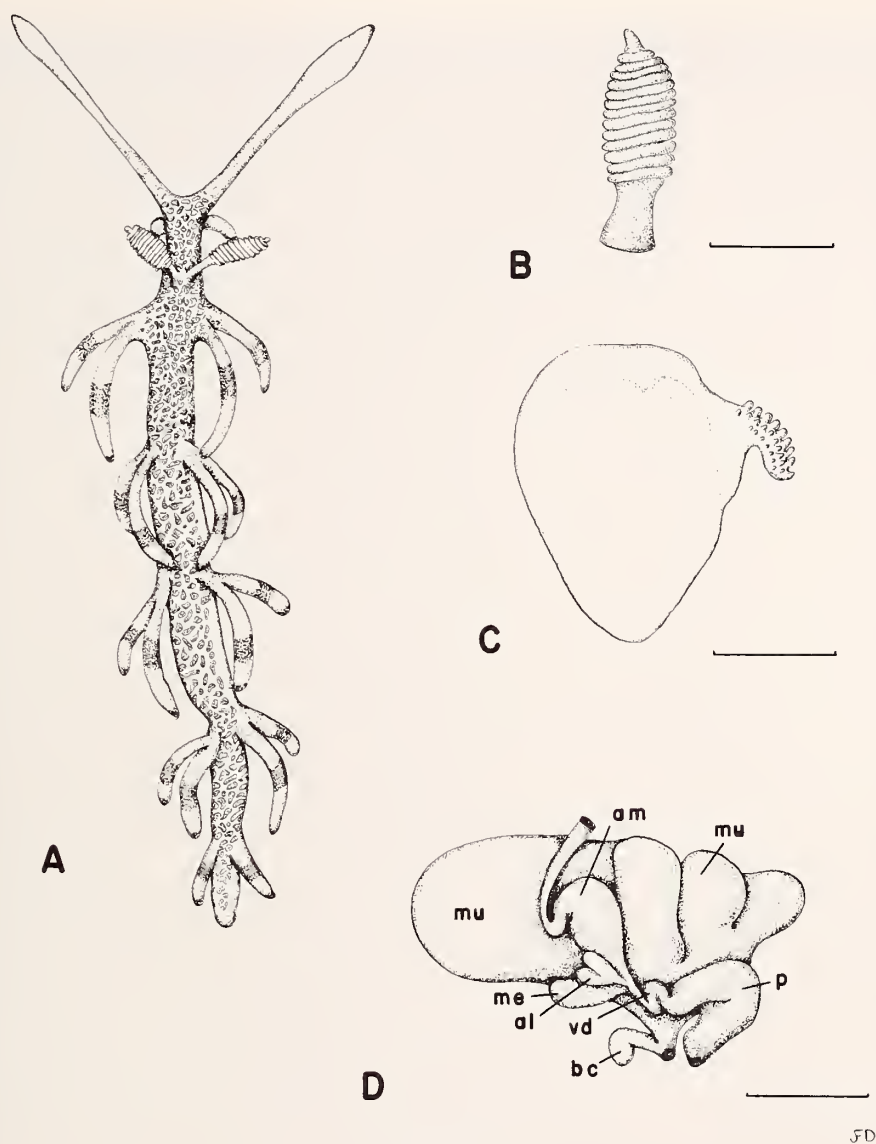


Figure 6

Flabellina riwo Gosliner & Willan, sp. nov. A. Dorsal view of 14 mm living animal. B. Rhinophore, scale = 1.0 mm. C. Jaw, scale = 0.2 mm. D. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; vd, vas deferens; scale = 0.5 mm.

Flabellina riwo Gosliner & Willan,
sp. nov.

(Figures 1B, 6-8)

Distribution: This species is known from the northern coast of Papua New Guinea (present study), Manado, Sulawesi, Indonesia (Paulene Fiene-Severns, personal communication), Okinawa (Robert Bolland, personal communication), and the northeastern coast of Madagascar (present study).

Etymology: The epithet *riwo* refers to Riwo Village, approximately 15 km north of Madang, Papua New Guinea, where this species was first found.

Type material: Holotype, CASIZ 070952, Cement Mixer Reef, Madang, Papua New Guinea, 3 m depth, 18 October 1986, T. M. Gosliner.

One paratype, CASIZ 070953, between Pig Island and Massis Island, near Madang, Papua New Guinea, 15.2 m depth, 30 September 1986, T. Frohm. One paratype, CASIZ 070954, patch reef, Kranket Island, Madang, Papua New Guinea, 10.7 m depth, 1 October 1986, T. M. Gosliner. Three paratypes, CASIZ 070955, patch reef, Kranket Island, Madang, Papua New Guinea, 10.4 m depth, 4 October 1986, T. M. Gosliner. One paratype, CASIZ 070956, Rasch Pass, Madang, Papua New Guinea.

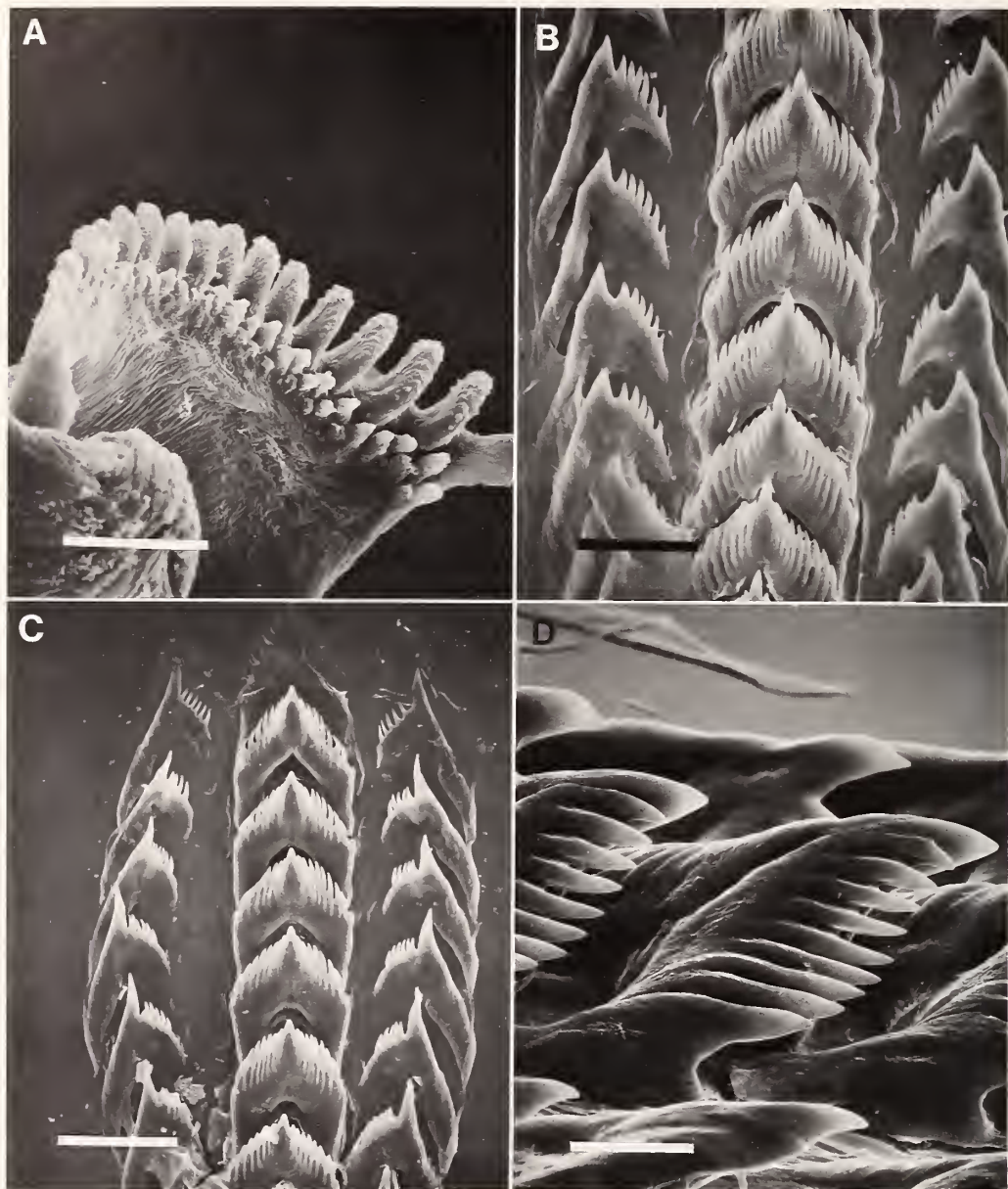


Figure 7

Flabellina riwo Gosliner & Willan, sp. nov., scanning electron micrographs. A. Masticatory border of jaw, Nosy Be, Madagascar, scale = 20 μm . B. Entire width of radula, Madang, Papua New Guinea, scale = 30 μm . C. Entire width of radula, Nosy Be, Madagascar, scale = 40 μm . D. Lateral view of rachidian teeth, Madang, Papua New Guinea, scale = 10 μm .

ea, 12.2 m depth, 5 October 1986, T. M. Gosliner. One paratype, CASIZ 070957, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 6 October 1986, T. M. Gosliner. One paratype, CASIZ 070958, dissected, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 12.2 m depth, 8 October 1986, T. M. Gosliner. Two paratypes, CASIZ 070959, lighthouse, Madang, Papua New Guinea, 12.2 m depth, 17 October 1986, T. M. Gosliner. Two paratypes, CASIZ 070960, Cement

Mixer Reef, Madang, Papua New Guinea, 3 m depth, 18 October 1986, T. M. Gosliner. Two paratypes, CASIZ 070961, Cement Mixer Reef, Madang, Papua New Guinea, 6.1 m depth, 19 October 1986, T. M. Gosliner. Three paratypes, CASIZ 070962, Cement Mixer Reef, Madang, Papua New Guinea, 21 October 1986, T. M. Gosliner. One paratype, CASIZ 070968, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 15.2 m depth, 13 January 1988, T. M. Gosliner. Four paratypes, USNM

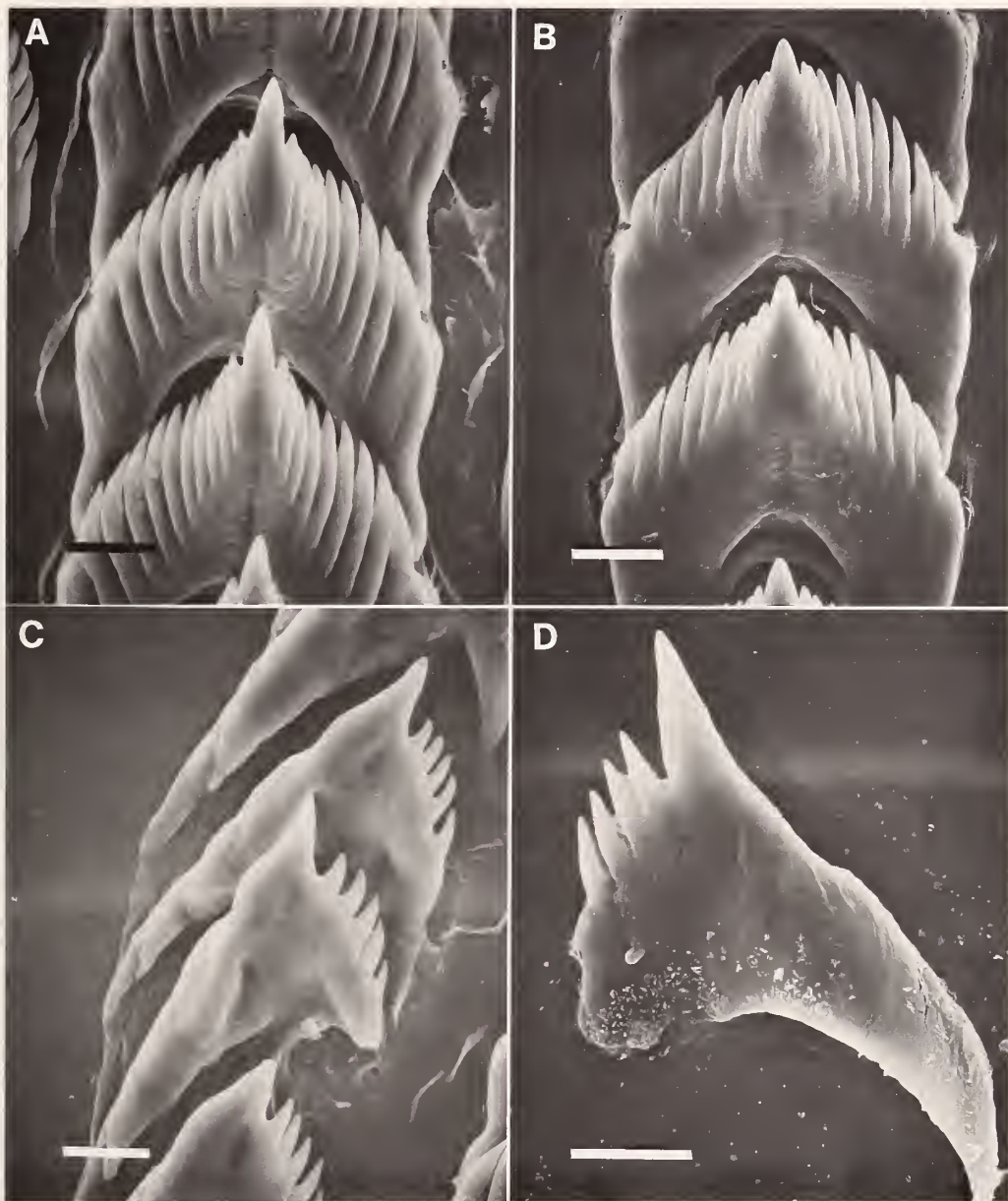


Figure 8

Flabellina riwo Gosliner & Willan, sp. nov., scanning electron micrographs, scales = 10 μm . A. Dorsal view of rachidian teeth, Madang, Papua New Guinea. B. Dorsal view of rachidian teeth, Nosy Be, Madagascar. C. Lateral teeth, Madang, Papua New Guinea. D. Lateral tooth, Nosy Be, Madagascar.

859085, LACM 2465, ANSP A 13614, Australian Museum, AMS C164081, from same lot as previous specimen. Three paratypes, CASIZ 070969, lighthouse, Madang, Papua New Guinea, 33.5 m depth, 15 January 1988, T. M. Gosliner. One paratype, CASIZ 070970, harbor wharf, Madang, Papua New Guinea, 10.4 m depth, 15 January 1988, T. M. Gosliner. Four paratypes, AMS C164082, coral rubble, the Quarry, near Bunu Village, 30 km N of Madang, Papua New Guinea, 3–5 m depth, 21 January

1988, R. C. Willan. Two paratypes, CASIZ 070971, dissected, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 24.4 m depth, 23 January 1988, T. M. Gosliner. Two paratypes, CASIZ 070972, patch reef off Kranket Island, near Madang, Papua New Guinea, 22.7 m depth, 24 January 1988, T. M. Gosliner. One paratype, CASIZ 070973, near the Pinnacle, between Pig Island and Rasch Pass, near Madang, Papua New Guinea, 30.5 m depth, 25 January 1988, T. M. Gosliner. One para-

type, CASIZ 070974, Hole in the Wall, near Hussein Village, N of Madang, Papua New Guinea, 15.2 m depth, 27 January 1988, R. C. Willan. One paratype, CASIZ 070975, Hole in the Wall, near Hussein Village, N of Madang, Papua New Guinea, 18.3 m depth, 3 February 1988, R. C. Willan. Two paratypes, CASIZ 070976, N point Christmas Bay, Bagabag Island, Papua New Guinea, 21.3 m depth, 5 February 1988, T. M. Gosliner and R. C. Willan. One paratype, CASIZ 070977, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 10.4 m depth, 8 February 1988, R. C. Willan. One paratype, CASIZ 070963, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 25 m depth, 16 July 1989, T. M. Gosliner. Two paratypes, CASIZ 070965, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 6.1 m depth, 31 August 1989, T. M. Gosliner. Three paratypes, CASIZ 070966, one dissected, Sea Stack, NW side Nosy Tanikely, Madagascar, 14 April 1989, T. M. Gosliner. Two paratypes, CASIZ 070967, one dissected, Cement Mixer Reef, Madang, Papua New Guinea, 3–7.6 m depth, 11 February 1989, T. M. Gosliner.

External morphology: The living animals (Figure 1B) reach a maximum of 20 mm in length. Most of the body is translucent white, adorned with a dense, lacy reticulum of opaque white lines. The oral tentacles are opaque white for most of their length, but possess a translucent basal portion near their junction with the head. The basal portion of the rhinophores is translucent white; the bulbous, lamellate portion is dull peach to light orange and the apex is translucent white. The base of the cerata may be either translucent white or obscured by opaque white pigment. When translucent, the cream, lobate digestive gland is visible. The apical portions of the cerata are covered with opaque white. Near the middle or in the distal third of each cerata is a broad purple ring.

The body is narrow and elongate (Figure 6A). The oral tentacles are three to four times the length of the rhinophores. The bases of the tentacles are terete whereas the distal third is markedly laterally compressed and paddle-shaped. The rhinophores (Figure 6B) are cylindrical basally and expand into a perfoliate club containing 16–22 densely crowded lamellae. The anterior foot corners are short, tentacular, and recurved. The cerata are arranged in 3–6 pedunculate clusters per side of the body. Each peduncle contains a single row of cerata inserted into an expanded portion of the notal brim. The notal brim is only evident in areas where the cerata are inserted. The peduncles contain 1–4 cerata. The ceratal formula varies considerably from small to large individuals. The first postcardiac row generally contains the largest number of cerata. The gonopore is located ventrally to the precardiac ceratal peduncle, on the right side of the body. The anus is situated between the precardiac and first postcardiac rows, generally closer to the more posterior peduncle. The

nephroproct is immediately dorsal or slightly anterior to the anal papilla.

Buccal mass: The anterior portion of the buccal mass forms a ring immediately inside the mouth. The paired ducts of the highly ramified oral glands originate from this area of the mass. These glands extend into the precardiac ceratal peduncle. The remainder of the buccal mass is highly muscular and contains the ovoid, chitinous jaws (Figure 6C). The masticatory border (Figure 7A) bears 3 or 4 distinct rows of denticles. The outermost row contains 18 elongate denticles with irregular papillae along their surface. The inner denticles decrease in size and papillation.

The radula (Figure 7B, C) has a formula of 15–23 × 1·1·1· in three specimens examined. The rachidian teeth (Figures 7D, 8A, B) are broad with an evenly curved posterior end. A deep cleft is present from the postero-medial end of the tooth to the base of the central denticle. The rachidian teeth bear 7–11 narrow denticles on either side of the more elongate central cusp. In lateral view, the central cusp of the rachidian is higher than the adjacent denticles (Figure 7D). The lateral teeth are roughly triangular with an elongate base. The primary denticle is elongate and acutely pointed. The masticatory border of the laterals bears 4–7 acutely pointed denticles.

Reproductive system (Figure 6D): The preampullary duct is narrow and expands into the saccate ampulla. The ampulla again narrows and divides into the short oviduct and the vas deferens. The oviduct does not expand into a discernible receptaculum seminis. It enters directly into the small albumen gland. The membrane gland is about the same size as the albumen gland and is situated immediately ventral to it. The mucous gland comprises the bulk of the female gland and forms the largest portion of the reproductive system. The mucous gland empties into the female gonopore adjacent to the small, thin-walled bursa copulatrix. The vas deferens expands abruptly into a short, thick prostatic portion that is contiguous with the penis. The penial papilla is simple and unarmed.

Discussion: *Flabellina riwo* differs markedly from *F. bicolor*. It is characterized by an opaque white network of pigment on the body as compared to a powdering of pigment in *F. bicolor*. The cerata bear a bluish purple ring rather than an orange one. Specimens of *F. riwo* generally have fewer cerata per cluster than does *F. bicolor*. Internally, *F. riwo* has broader rachidian teeth, with a distinct medial cleft, which is absent in *F. bicolor*. The reproductive system differs markedly between the two species; in *F. riwo*, there is no distinct receptaculum seminis and the bursa copulatrix is reduced, whereas in *F. bicolor*, both of these receptacles are well developed. The vas deferens is shorter in *F. riwo* than in *F. bicolor*. These differences are consistent throughout the extensive geographical ranges of the two species.

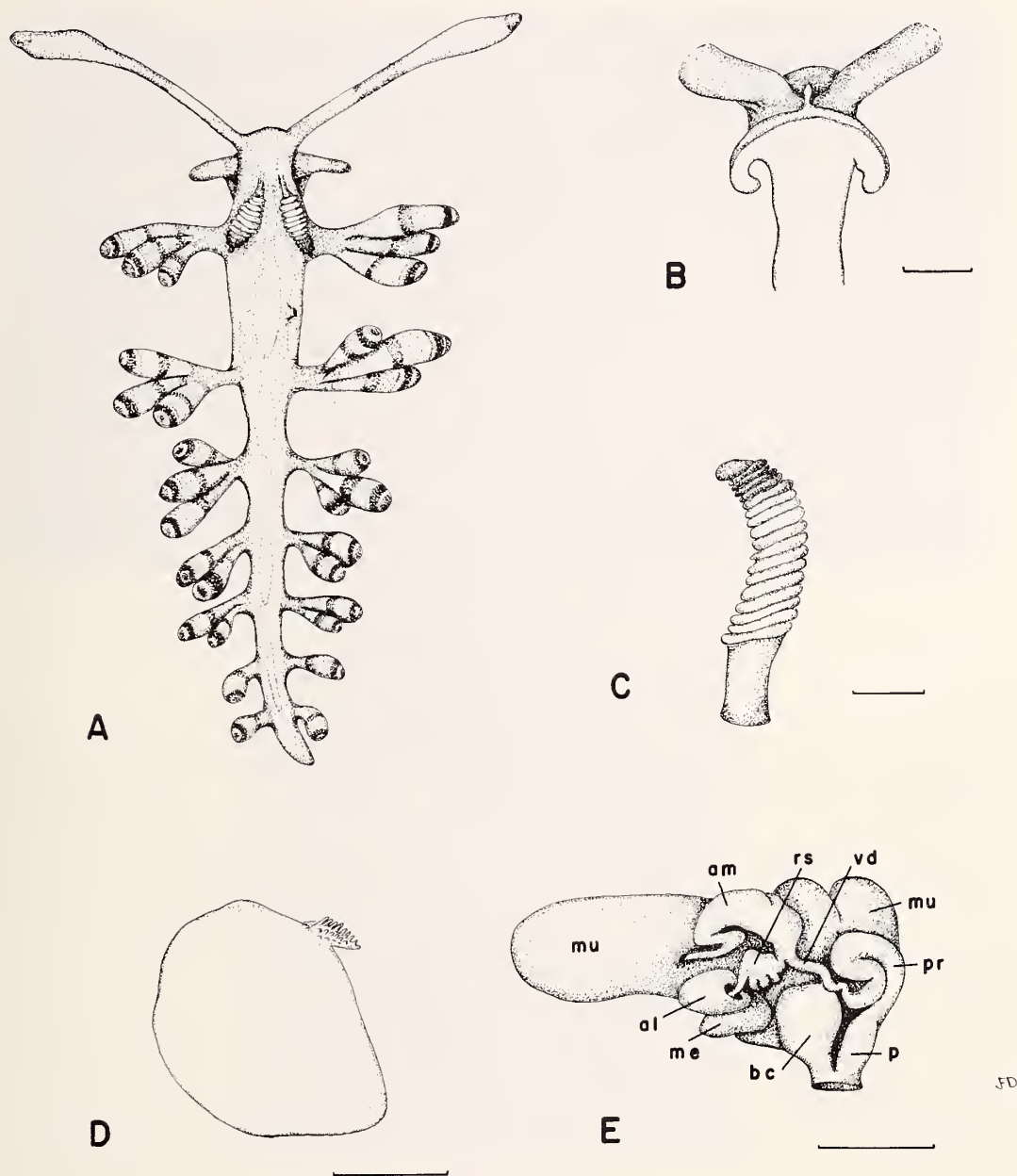


Figure 9

Flabellina bilas Gosliner & Willan, sp. nov. A. Dorsal view of 18 mm living animal. B. Ventral view of head and foot, scale = 1.0 mm. C. Rhinophore, scale = 0.5 mm. D. Jaw, scale = 0.2 mm. E. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; vd, vas deferens; scale = 0.5 mm.

Flabellina bilas Gosliner & Willan,
sp. nov.

(Figures 1C, 9-11)

Distribution: *Flabellina bilas* has been found from Kwajalein Island, Marshall Islands (Scott Johnson, personal

communication) and from Madang, Papua New Guinea (present study).

Material: Holotype, California Academy of Sciences, San Francisco, CASIZ 070993, living animal 17 mm in length, 20 m depth, Barracuda Point, Pig Island, near Madang,

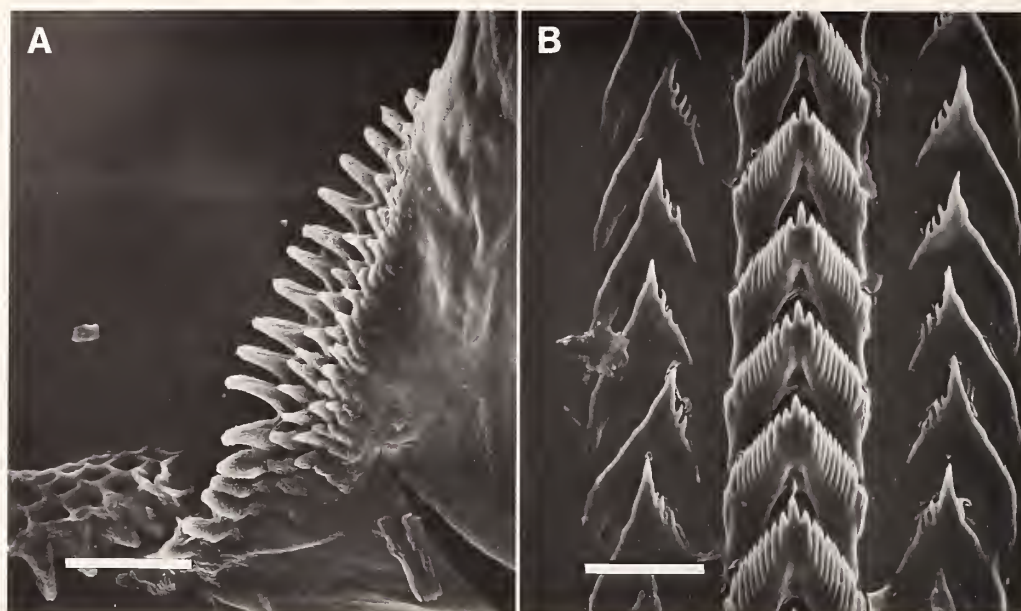


Figure 10

Flabellina bilas Gosliner & Willan, sp. nov., scanning electron micrographs. A. Masticatory border, scale = 30 μm . B. Entire width of radula, scale = 50 μm .

Papua New Guinea, 8 February 1988, G. Williamson. Paratype, CASIZ 070994, living animal 23 mm in length, dissected, collected with the holotype.

Etymology: The specific epithet *bilas* is a New Guinea Pidgin word meaning "decoration," referring to the brilliant crimson and blue markings of this species.

External morphology: The living animals were 17 and 23 mm in length. The larger individual (the paratype) had lost the posterior portion of its body, perhaps as much as 3–4 mm. The living animals (Figure 1C) are vividly colored in a distinctive manner. The general body color is translucent white. There is an orange tinge on either lateral side of the head. The oral tentacles bear two opaque white areas, separating the translucent base, medial region, and apex. Opaque white pigment is also present on the foot corners and as a series of ovoid patches along either side of the body extending from the head to the tail. A series of sky-blue diamond or lozenge-shaped patches is present medially on the notum. These patches may be continuous or well separated. The rhinophores are translucent basally, medially, and apically. They possess two bands of opaque cream pigment and a sharply defined subapical blood-red ring. At the translucent base of some cerata a thin, blood-red digestive diverticulum is visible. More distally, are two broad areas of opaque cream separated by a small area of translucence. Subapically, a broad crimson ring is bordered on either side by a thinner irregular band of opaque white.

The animals are elongated and slender (Figure 9A). The oral tentacles are thin and elongate, approximately

three times the length of the rhinophores. The distal third of these tentacles is broadly expanded and paddlelike. The foot corners are short and tentacular, and are held nearly perpendicularly to the longitudinal axis of the body, or they may be recurved posteriorly. The anterior margin of the foot is bilabiate (Figure 9B). The perfoliate rhinophores (Figure 9C) bear 25–28 densely packed lamellae. The notal brim gives rise to a series of pedunculate cerata. There are 7 pairs of ceratal rows in the smaller, intact specimen. The larger one has 6 pairs of ceratal rows, but is missing the posterior portion of its body and tail. The ceratal formulae are: R 4,P,4,3,3,2,1, L 4,P,4,4,2,2,2 in the larger specimen and R & L 4,P,4,3,2,2,1,1 in the smaller individual. The gonopore is located immediately ventral to the preanal ceratal arch while the anus is situated slightly anterior to the median of the interhepatic space, below the notal brim. The nephroproct is immediately dorsal to the anus, but still below the notal brim.

Buccal mass: The buccal mass is highly muscular. From its anterior end emanates a pair of oral glands. These begin as simple ducts and branch many times into highly ramified glands, which are present in the precardiac ceratal peduncles. The jaws (Figure 9D) are thin and ovoid. Their masticatory border (Figure 10A) contains 4 or 5 rows of denticles. The outermost row bears approximately 20 elongate denticles. The denticles of the inner rows are increasingly short.

The radula (Figure 10B) has a formula of $21 \times 1 \cdot 1 \cdot 1 \cdot$ in the paratype. The rachidian teeth (Figure 11A, B) are broad with 9 or 10 elongate denticles on either side of



Figure 11

Flabellina bilas Gosliner & Willan, sp. nov., scanning electron micrographs. A. Dorsal view of rachidian teeth, scale = 20 μ m. B. Lateral view of rachidian teeth, scale = 30 μ m. C. Lateral teeth, scale = 20 μ m.

the equally narrow central cusp. They are deeply indented posteriorly without a distinct medial cleft. When viewed laterally, the central cusp (Figure 11B) is depressed below the level of the adjacent laterals. The lateral teeth are triangular with an elongate base. The primary cusp is irregularly triangular and acutely pointed. The inner cutting edge bears 2-4 curved denticles.

Reproductive system (Figure 9E): The preampullary duct expands into the saccate ampulla. The ampulla nar-

rows and divides into the oviduct and vas deferens. The oviduct expands into a lobate serial receptaculum seminis and again narrows immediately prior to its entrance into the albumen and membrane glands. The albumen and membrane glands are small and are adjacent to each other. The mucous gland forms the bulk of the reproductive system and has a large lateral lobe. The mucous gland exits at the female gonopore. Adjacent to the gonopore is a large, bulbous bursa copulatrix with a short, thick stalk. The vas deferens is narrow for approximately half of its length and expands

into a coiled prostatic portion. The prostatic section is contiguous with the simple unarmed penis.

Discussion: *Flabellina bilas* can be readily distinguished from the other species with perfoliate rhinophores by its unique pattern of coloration. It is the only species with red bands on the cerata and rhinophores. Together with *F. engeli* Ev. Marcus & Er. Marcus, 1968, *F. bilas* has whitish or bluish markings on the notum, between the cerata. However, *F. engeli* has two precardiac ceratal rows (EDMUNDS & JUST, 1983) rather than one. The reproductive morphology also differs considerably. In *F. bilas* the receptaculum seminis is serial and the bursa copulatrix is present on a short stalk, whereas in *F. engeli* the receptaculum seminis is semiserial and the bursa copulatrix is apparently absent (Ev. MARCUS & ER. MARCUS, 1968).

Flabellina bilas is unique among described species of Indo-Pacific flabellinids with perfoliate rhinophores and a single precardiac ceratal row, in having a depressed cusp on the rachidian teeth.

Flabellina rubropurpurata Gosliner & Willan,
sp. nov.

(Figures 1D, 12–14)

Flabellina sp. 3: GOSLINER, 1987:114, fig. 223.

Distribution: This species is known from Natal, South Africa, Enewetak, Marshall Islands (GOSLINER, 1987), and from Papua New Guinea (present study).

Etymology: The epithet *rubropurpurata* refers to the red cerata and purple body of this species.

Type material: Holotype, California Academy of Sciences, CASIZ 070995, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 30.5 m (maximum) depth, 11 February 1988, T. M. Gosliner.

Two paratypes, CASIZ 070996, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 12.2 m depth, 8 October 1986, T. M. Gosliner. One paratype, CASIZ 070997, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 10.4 m (maximum) depth, 12 February 1988, T. M. Gosliner. One paratype, CASIZ 070998, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 24.4 m depth, 20 February 1988, T. M. Gosliner. One paratype, South African Museum, Cape Town, SAM A35718, radula only, 9 mile Reef, Sodwana Bay National Park, Natal, South Africa, 10 May 1981, T. M. Gosliner.

External morphology: The living animals (Figure 1D) are 4–9 mm in length. The general body color is a deep purple. The distal one-third to one-half of the oral tentacles is opaque white, while the basal portion is purple. The base of each rhinophore is purple; the central portion is opaque white and the distal third is red orange. Opaque white pigment is present along either edge of the notum from the level of the precardiac ceratal cluster to the pos-

terior end of the animal. The opaque white pigment may extend onto the lateral and dorsal surfaces of the animal. The cerata are purple basally and orange-red in the middle third; the apical cnidosac is orange.

The body (Figure 12A) is elongate and narrow. The notum is high and rounded in profile. The tail is elongate and pointed posteriorly. The oral tentacles are elongate, approximately twice the length of the rhinophores. They are rounded in cross section throughout their length, exhibiting no obvious lateral compression. The rhinophores (Figure 12B) are perfoliate with 12 or 13 densely packed lamellae. The anterior foot corners are short, tentacular, and may be extended perpendicularly to the body axis or may be curved. The cerata are short, fusiform, and thickest near the middle of their length. The cerata are arranged on distinct peduncles. The precardiac peduncle contains 3 distinct rows, with 2 or 3 cerata per row. The precardiac ceratal rows are crowded and difficult to differentiate in living specimens. There are 5–7 postcardiac ceratal peduncles per side, each consisting of a single row of 1–4 cerata. A distinct notal brim is absent between the peduncles. The gonopore is situated on the right side of the body, ventral to the third ceratal row of the precardiac peduncle. The pleuroproct anus is located immediately below the notum, between the precardiac and postcardiac ceratal peduncles. The nephroproct is immediately anterodorsal to the anus.

Buccal mass: The muscular buccal mass is small and occupies the anteriormost portion of the body cavity. Extending from the anterior end of the buccal mass are the paired ducts of the oral glands. The glands are highly ramified and occupy much of the precardiac ceratal peduncles. The jaws (Figure 12C) are thin and ovoid. They bear 2 or 3 rows of denticles on the surface of the masticatory border.

The radula (Figure 13) has a formula of 23–30 × 1·1·1 in the two specimens examined. The rachidian teeth (Figure 14A, B) are broadest posteriorly. The posterior limbs are elongate appendages used in articulation of the teeth with each other. The cutting edge of each tooth bears 7–9 elongate denticles on either side of the longer central cusp. In lateral view (Figure 13C) the central cusp of each rachidian tooth is depressed below the level of the adjacent denticles. The lateral teeth (Figure 14C, D) are elongate and triangular with a narrow base and extended primary cusp. There are 3–6 acutely pointed denticles on the masticatory border of the teeth.

Reproductive system (Figure 12E): The preampullary duct is short and narrow. It widens into the saccate ampulla, narrows again, and divides into the oviduct and vas deferens. After a short distance, the narrow oviduct gives rise to the pyriform, semiserial receptaculum seminis. From this point, the oviduct again narrows and enters the female gland mass near the albumen gland. The three portions of the female gland mass were not well differentiated from

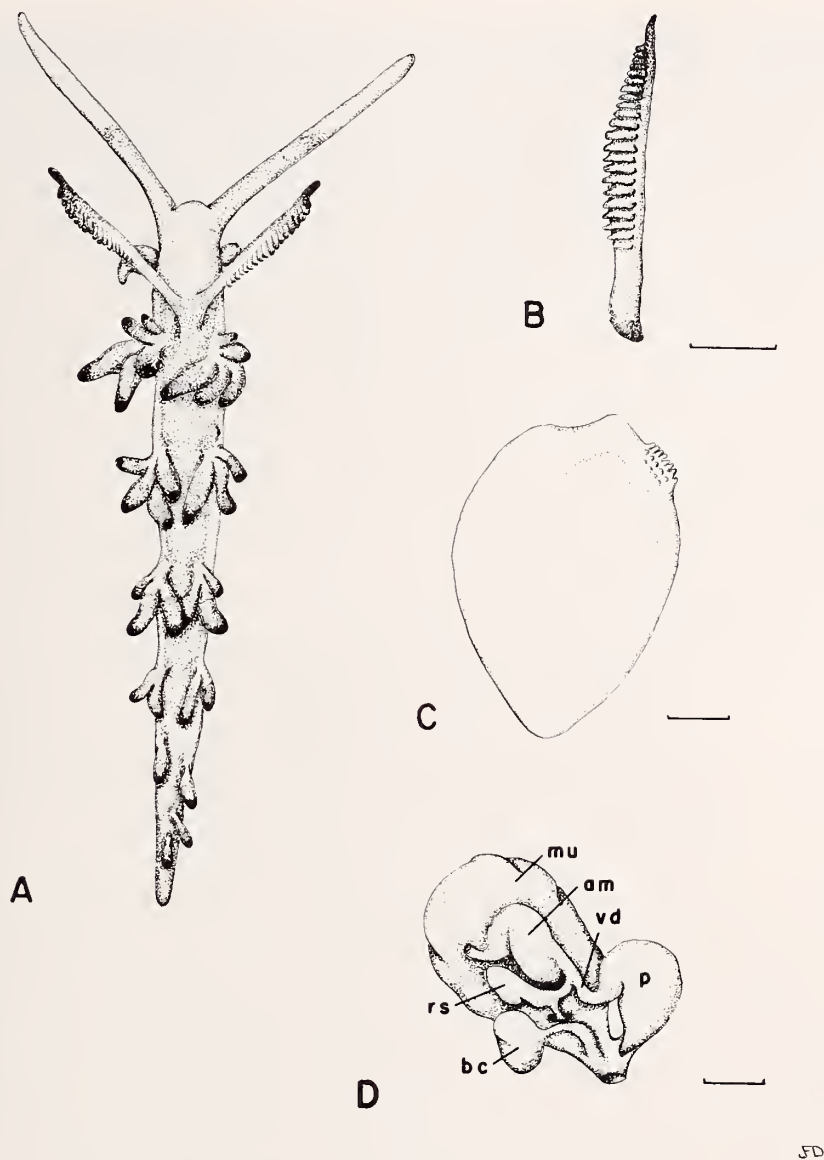


Figure 12

Flabellina rubropurpurata Gosliner & Willan, sp. nov. A. Dorsal view of 8 mm living animal. B. Rhinophore, scale = 0.5 mm. C. Jaw, scale = 0.1 mm. D. Reproductive system: am, ampulla; bc, bursa copulatrix; mu, mucous gland; p, penis; rs, receptaculum seminis; vd, vas deferens; scale = 0.1 mm.

each other. The female gland mass exits at the female genital aperture, adjacent to the bursa copulatrix. The bursa is spherical and exits via a long, narrow duct. The vas deferens is narrow and enlarges into the thick penis. No distinct prostatic portion of the vas deferens was observed. The simple unarmed penis terminates at the male gonopore.

Discussion: Based on a single specimen collected from southern Africa, GOSLINER (1987) indicated that the coloration of this species was distinct from all described spe-

cies of *Flabellina*. The arrangement of cerata, with three rows of cerata in the precardiac peduncle, is similar to that described for *F. telja* Er. Marcus & Ev. Marcus, 1967, and *F. stohleri* Bertsch & Ferreira, 1974.

Flabellina telja and *F. stohleri* are similar to each other in external morphology and coloration, and are sympatric within the Gulf of California. These two species are likely synonymous with each other. They differ in their coloration from *F. rubropurpurata*. These species are orange with opaque white spots and reddish cerata, whereas *F. rubropurpurata* has a purple body with reddish cerata.

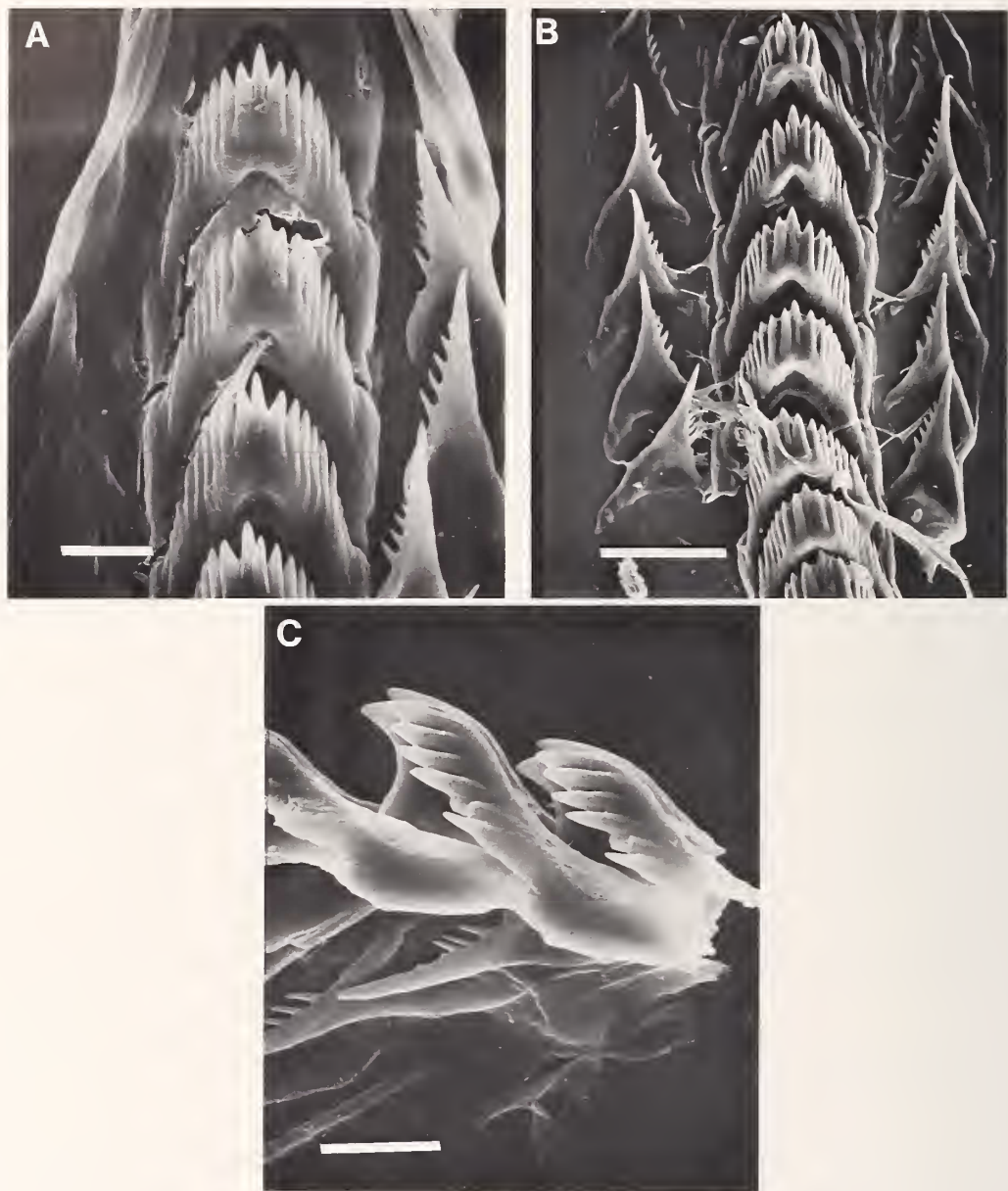


Figure 13

Flabellina rubropurpurata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Entire width of radula, Madang, Papua New Guinea, scale = 10 μm . B. Entire width of radula, Sodwana Bay, South Africa, scale = 25 μm . C. Lateral view of radula, Madang, Papua New Guinea, scale = 10 μm .

Flabellina telja and *F. stohleri* have more cerata per row (up to 6) than *F. rubropurpurata* (maximum of 4). Internally, the lateral radular teeth of *F. telja* and *F. stohleri* possess more denticles than those of *F. rubropurpurata*. The male atrium of *F. telja* bears numerous papillae, whereas that of *F. rubropurpurata* is devoid of any ornamentation.

Flabellina rubrolineata (O'Donoghue, 1929)

(Figures 1E, 15–17)

Coryphella ornata RISBEC, 1928, in part:267, variété violacée, fig. 89, 3; pl. 9, fig. 6. (This taxon has no systematic status because it was described as a vernacular name, see discussion).

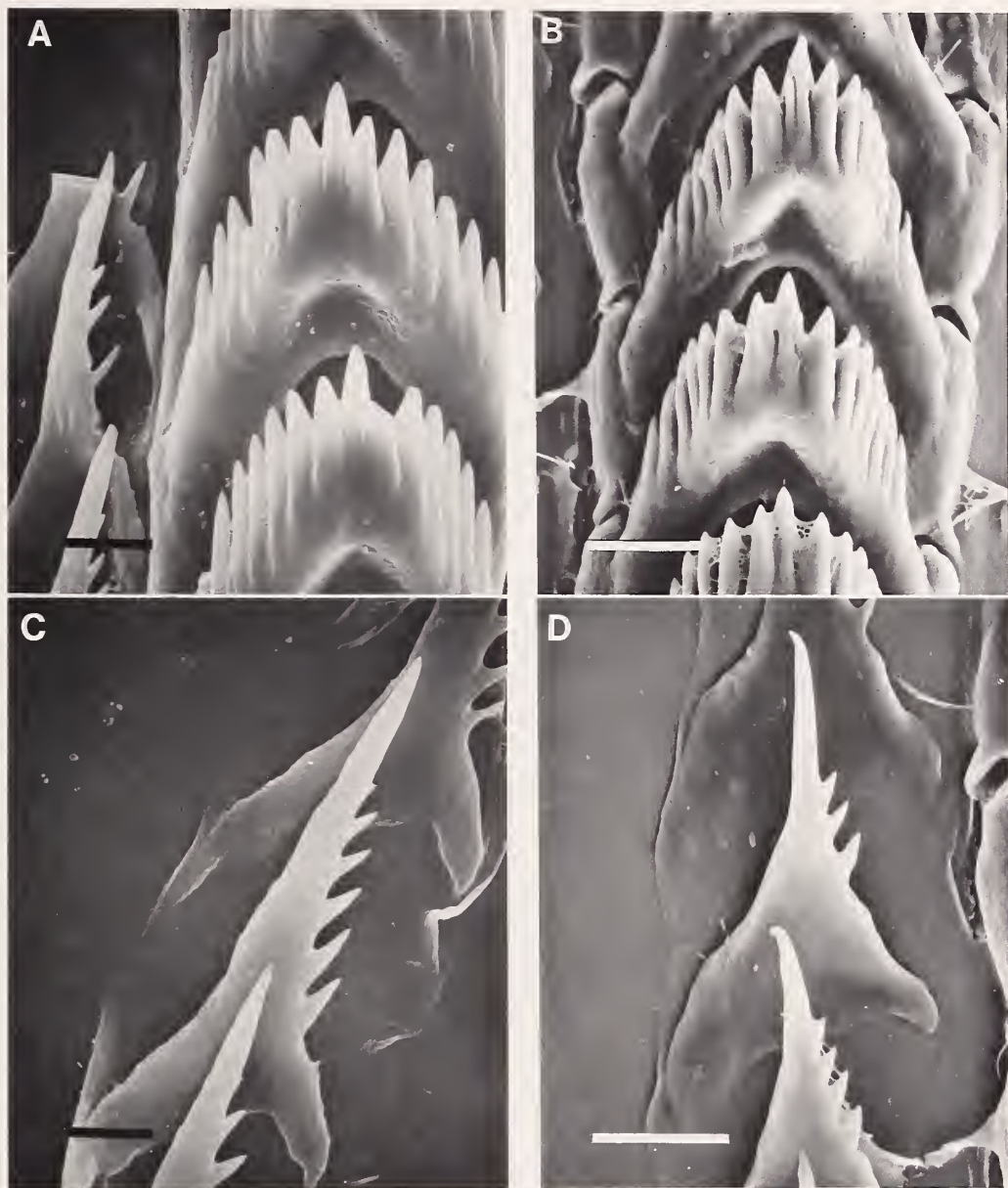


Figure 14

Flabellina rubropurpurata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Dorsal view of rachidian teeth, Madang, Papua New Guinea, scale = 5 μ m. B. Dorsal view of rachidian teeth, Sodwana Bay, South Africa, scale = 5 μ m. C. Lateral teeth, Madang, Papua New Guinea, scale = 10 μ m. D. Lateral teeth, Sodwana Bay, South Africa, scale = 10 μ m.

Coryphellina rubrolineata O'DONOGHUE, 1929:798, fig. 219; BABA, 1955:26, figs. 40, 41, pl. 13, fig. 37; BABA, 1990:51, pl. 13, fig. 37.

Coryphella ornata var. *violacea* RISBEC, 1953:fig. 98a. **syn. nov.**

Coryphella violacea Risbec: GOSLINER, 1980:41. **syn. nov.**

Coryphella sp.: COLEMAN, 1981a:67, color fig.

Coryphella rubrolineata (O'Donoghue): COLEMAN, 1981b:31, color fig., 100.

Flabellina rubrolineata (O'Donoghue): GOSLINER & GRIF-FITHS, 1981:114; WILLAN & COLEMAN, 1984:42, fig. 133; MIENIS & GAT, 1986:683; GOSLINER & KUZIRIAN, 1990:9, fig. 6.

Distribution: This species is widely distributed in the Indo-Pacific tropics where it is known from New Caledonia (RISBEC, 1928), Australia (WILLAN & COLEMAN,

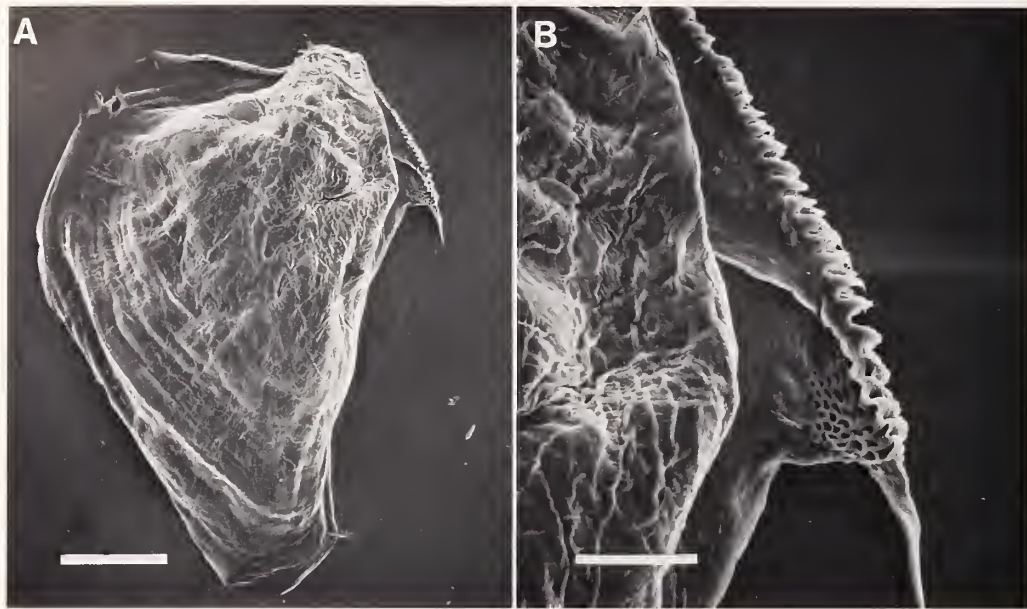


Figure 15

Flabellina rubrolineata (O'Donoghue, 1929), scanning electron micrographs. A. Jaw, Madang, Papua New Guinea, scale = 150 μm . B. Masticatory border, Madang, Papua New Guinea, scale = 40 μm .

1984), Japan (BABA, 1955), Papua New Guinea (GOSLINER & KUZIRIAN, 1990; present study), Malaysia (Ho Soon Lin, personal communication), Aldabra Atoll (present study), and the Red Sea (O'DONOGHUE, 1929; MIENIS & GAT, 1986; Christopher Todd, personal communication).

Material: One specimen, California Academy of Sciences, San Francisco, CASIZ 070557, Passe Femme, Aldabra Atoll, Republic of Seychelles, 19 March 1986, T. M. Gosliner. Four specimens, CASIZ 070547, 070549, 070550, Barracuda Point, Pig Island, Madang, Papua New Guinea, 10–27 m depth, 29 January–14 February 1988, T. M. Gosliner. One specimen, CASIZ 070553, Barracuda Point, Pig Island, Madang, Papua New Guinea, 6 October 1986, T. M. Gosliner. Two specimens, CASIZ 070556, SE side of Barracuda Point, Pig Island, Madang, Papua New Guinea, 24.4 m depth, 23 January 1988, J. Mizeu. One specimen, CASIZ 070548, Sek Passage, Madang, Papua New Guinea, 10.7 m depth, 15 October 1986, T. M. Gosliner. One specimen, CASIZ 070551, N side Rasch Pass, Madang, Papua New Guinea, 18.3 m depth, 16 February 1988, T. M. Gosliner. Three specimens, CASIZ 070552, the Quarry, 30 km N of Madang, Papua New Guinea, 30.5 m (maximum) depth, 11 February 1988, T. M. Gosliner. Three specimens, CASIZ 070554, Kranket Wall, E side of Kranket Island, Madang, Papua New Guinea, 30.5 m depth, 4 February 1988, R. C. Willan. One specimen, CASIZ 070555, near lighthouse, Madang, Papua New Guinea, 12.2 m depth, 17 October 1986, T. M. Gosliner.

One specimen, "The Nursery," N side of Julian Rocks,

off Cape Byron, New South Wales, Australia, 6 m depth, 12 July 1980, R. C. Willan. Two specimens, in channel between main islands, Shag Rocks, off Point Lookout, North Stradbroke Island, Queensland, Australia, 13 m depth, 5 August 1980, R. C. Willan. Two specimens, base of Heron Bommie, W side Heron Island, Capricornia Group, Great Barrier Reef, Queensland, Australia, 10 m depth, 13 November 1980, R. C. Willan.

External morphology: The living animals (Figure 1E) reach 42 mm in length. The coloration is variable, even within a population from a single locality. The general body color is translucent pinkish white. Varying amounts of opaque white may be present on the sides of the body and notum. Three purple or reddish longitudinal lines extend from the head to the posterior limit of the tail. One of these is middorsal and extends from the anterior border of the head to the tail. A lateral line runs below the notum along either side of the body. Purple pigment may also be present on the distal third of the oral tentacles, on the apices of the foot corners, on the apices of the rhinophores, and on the cerata. The anterior face of the rhinophores is the same color as the body. Their posterior surface, where the papillae are situated, is opaque white or yellow. The cerata are translucent white or opaque white basally with red, purple, or yellow pigment on the distal portion. In one specimen from Papua New Guinea, the entire surface of the cerata was red.

The body is narrow and elongate. The notum is high and well developed and its brim undulate, widening at the level of each ceratal group. The oral tentacles are thin and

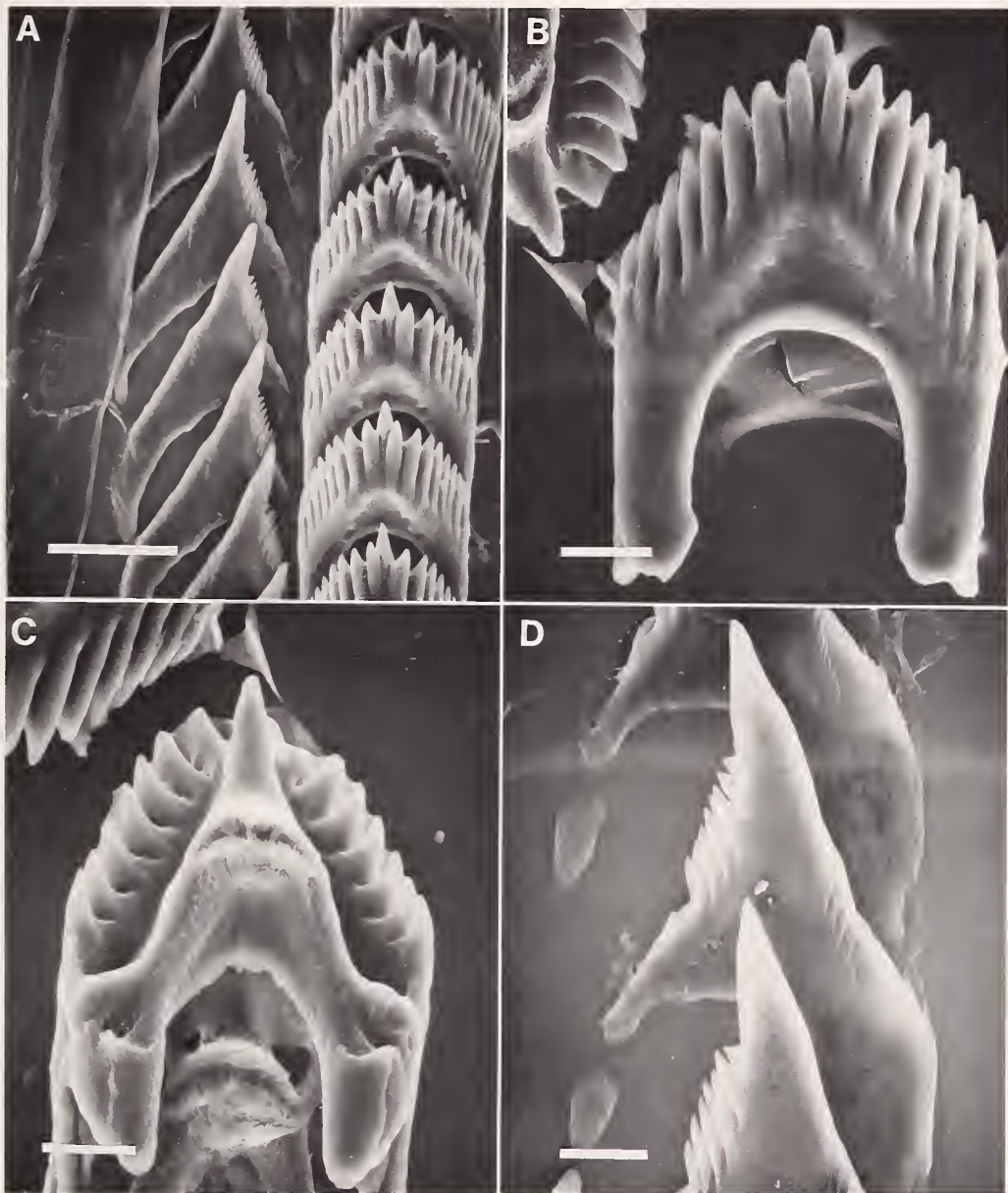


Figure 16

Flabellina rubrolineata (O'Donoghue, 1929), scanning electron micrographs. A. Rachidian and lateral teeth, Madang, Papua New Guinea, scale = 30 μm . B. Dorsal view of rachidian teeth, Madang, Papua New Guinea, scale = 10 μm . C. Ventral view of rachidian tooth, Madang, Papua New Guinea, scale = 10 μm . D. Lateral teeth, Madang, Papua New Guinea, scale = 10 μm .

cylindrical in cross section, longer than the rhinophores. The rhinophores are elongate with an acute apex. The posterior surface is ornamented with approximately 100 elongate papillae. The anterior foot corners are elongate and tentacular. The cerata are variable in length and may be short and bulbous or elongate and cylindrical. The cerata are arranged in 5 or 6 distinct groups, each elevated from the notum. The precardiac cluster consists of 3 or 4

distinct rows of cerata, with 1–3 cerata per row. The first 3 or 4 postcardiac groups are arranged in arches consisting of 3–6 cerata per arch. The posterior 1 or 2 clusters consist of only 1 or 2 cerata. The gonopore is situated ventral to the 2 posterior ceratal rows of the precardiac ceratal group. The pleuroproctical anus is located in the interhepatic space, below the notum. The nephroproct is immediately anterodorsal to the anus, but still below the notal brim.

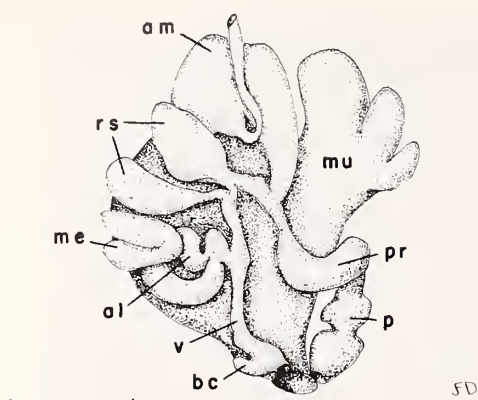


Figure 17

Flabellina rubrolineata (O'Donoghue, 1929). Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; scale = 0.5 mm.

Buccal mass: The muscular buccal mass is ovoid and occupies the portion of the body cavity anterior to the rhinophores. The large ramified oral glands emanate from the anterior portion of the buccal mass and extend posteriorly along the mass and into the notal expansions of the precardiac ceratal cluster. The jaws (Figure 15A) are well developed and thick. The masticatory border (Figure 15B) is broad and elongate, bearing 5–7 rows of denticles.

The radula (Figure 16A) has a formula of 29–30 × 1·1·1· in three specimens examined. The rachidian teeth (Figure 16B, C) are broad, with a wide arch between the posterior limbs. The posterior end of either limb has an articulatory appendage on its outer side. The cutting edge of the rachidian teeth has 7 or 8 denticles on either side of the more elongate central cusp. The central cusp is depressed below the level of the adjacent denticles. The lateral teeth (Figure 16D) are broadly triangular with an elongate, curved basal limb. There are 7 or 8 acutely pointed denticles along the inner margin of the laterals. The outer side of the teeth bears 4 or 5 irregular striations.

Reproductive system (Figure 17): The arrangement of the organs is triaulic. The preampullary duct is narrow and elongate. It expands into a wide, saccate ampulla, which again narrows and divides into the oviduct and vas deferens. After a short distance, the oviduct gives rise to two distinct pyriform receptacula seminis. From this point the oviduct continues towards the gonopore and enters the albumen gland portion of the female gland mass. The membrane gland is situated adjacent to the albumen gland. Most of the female gland mass is formed by the various lobes of the mucous gland. From the point where the oviduct enters the female gland mass, a vaginal duct extends to its own aperture, adjacent to the penis. A minute bursa copulatrix is present adjacent to the vaginal pore. The opening of the mucous gland is immediately ventral

to the vaginal pore. The vas deferens expands into a short prostatic portion, which widens again at the conical, un-armed penial papilla.

Discussion: When it was described, *Coryphellina* O'Donoghue was monotypic, its type species being *Coryphellina rubrolineata* O'Donoghue, 1929. *Coryphellina* has been considered as a junior synonym of *Coryphella* Gray, 1850, by MILLER (1971). GOSLINER & GRIFFITHS (1980) considered both of these genera as junior synonyms of *Flabellina* Voigt, 1834. This view has been widely accepted, and is further supported by GOSLINER & KUZIRIAN's recent (1990) cladistic analysis of the family.

The systematic status of *Flabellina rubrolineata* (O'Donoghue, 1929) has recently been revised by GOSLINER & KUZIRIAN (1990). Specimens identified by EV. MARCUS & ER. MARCUS (1961, 1970) from Brazil and the Gulf of California have been shown to represent a distinct species, *Flabellina marcusorum* Gosliner & Kuzirian, 1990, and *F. rubrolineata* is restricted to the Indo-Pacific tropics.

Flabellina rubrolineata is morphologically similar to specimens described by RISBEC (1928, 1953) from New Caledonia. In the discussion of *F. bicolor*, in the present work, difficulties with the systematic status of Risbec's *Coryphella ornata* were resolved. GOSLINER (1980) discussed the status of Risbec's "variété violacée" of *F. ornata*, noting that it appeared to be distinct from *F. ornata*. Its triseriate radula, with denticulate lateral teeth, clearly establish its placement within the genus *Flabellina*. RISBEC's (1928:pl. 9, fig. 6) description of the color of the violet variety of *F. ornata* indicates that the animal is rose violet with three longitudinal red lines. This pattern is identical to that described for *F. rubrolineata*. The rhinophores are described as perfoliate only on the posterior side with very long lamellae. We interpret this as meaning papillate rather than perfoliate rhinophores. The radular morphology of this variety of *F. ornata* (RISBEC, 1928:fig. 89, 3) is virtually identical to that depicted by BABA (1955:fig. 41c) for *F. rubrolineata*.

It is apparent that these two species are synonymous. However, the *International Code of Zoological Nomenclature* states that vernacular names have no systematic status. Thus, Risbec's 1928 taxon cannot have priority over *Coryphellina rubrolineata* O'Donoghue, 1929. It appears that *Coryphella ornata* var. *violacea* Risbec, 1953, constitutes a validly described subspecies. Nevertheless, it is here considered a junior subjective synonym of *Flabellina rubrolineata* (O'Donoghue, 1929) due to priority of publication.

Species of *Flabellina* with papillate rhinophores and a triaulic reproductive system are compared in Table 2.

Flabellina exoptata Gosliner & Willan,
sp. nov.

(Figures 1F, 18–20)

Distribution: This species has been found from Enewetak, Marshall Islands (Scott Johnson, personal communica-

Table 2
Morphological variation in *Flabellina* species with elongate papillae on rhinophores.

Species	Color	Ceratal arrangement	Radular formula	Denticles on either side of rachidian	Denticles on lateral	Receptaculum seminis	Bursa copulatrix	Vas deferens
<i>delicata</i>	body reddish purple, rhinophores red, cerata with opaque white & yellow & opaque white band	all arches	31 × 1.1.1	6-9	15-18	bilobed	reduced	short
<i>exoptata</i>	body pinkish-purple, rhinophores red with yellow spots, cerata with purple & white bands	preanal arch, postanal rows	23-37 × 1.1.1	7-10	13-20	bilobed	absent	short
<i>marcusorum</i> Gosliner & Kuzirian, 1990	body pink, cerata, rhinophores & oral tentacles purple & white	all arches	27-34 × 1.1.1	5-8	4-12	bilobed	well developed, stalked	elongate
<i>poenicia</i> (Burn, 1957)	body translucent white with red cerata, purple spots on head	all arches	34 × 1.1.1	6-7	4	—	—	—
<i>rubrolineata</i> (O'Donoghue, 1929)	body whitish or purple; 3 longitudinal red or purple lines	all arches	30-32 × 1.1.1	6-9	7-10	bilobed	reduced	short

tion), Guam (Clay Carlson and Patty Jo Hoff, personal communication), Fiji (present study), Queensland, Australia (present study), Western Australia (Neville Coleman, personal communication), Papua New Guinea (present study), Malaysia (Ho Soon Lin, personal communication), and Aldabra Atoll (present study).

Etymology: The epithet *exoptata* means "much desired" and refers to the strikingly beautiful color of this species.

Type material: Holotype, CASIZ 070988, Planet Rock, 10 km S of Madang, Papua New Guinea, 24.4 m (maximum) depth, 19 January 1988, T. M. Gosliner.

One paratype, CASIZ 070979, Passe Femme, Aldabra Atoll, Seychelles, 0.5 m depth, 12 March 1986, T. M. Gosliner. Eight paratypes, CASIZ 070980, 2 dissected, Passe Femme, Aldabra Atoll, Seychelles, 17 March 1986, T. M. Gosliner. One paratype, CASIZ 070978, Passe Femme, Aldabra Atoll, Seychelles, 17 March 1986, T. M. Gosliner. Two paratypes, USNM 859084, Passe Femme, Aldabra Atoll, Seychelles, 17 March 1986, T. M. Gosliner. One paratype, CASIZ 070981, dissected, Madang, Papua

New Guinea, 4 October 1986, J. Darr. Two paratypes, CASIZ 070982, N end Rasch Pass, Madang, Papua New Guinea, 18.3 m depth, 6 October 1986, T. M. Gosliner. One paratype, CASIZ 070983, lighthouse, Madang, Papua New Guinea, 18.3 m depth, 17 October 1986, M. T. Ghiselin. Two paratypes, CASIZ 070984, lighthouse, Madang, Papua New Guinea, 15.2 m depth, 21 October 1986, T. M. Gosliner. One paratype, CASIZ 070985, Anemone Reef, E of Riwo Island, Madang, Papua New Guinea, 13.7 m depth, 10 January 1988, T. M. Gosliner. One paratype, CASIZ 070986, lighthouse, Madang, Papua New Guinea, 33.5 m depth, 15 January 1988, T. M. Gosliner. Two paratypes, CASIZ 070987, the Blowhole, approximately 1 km S of Cape Croiselles, N of Madang, Papua New Guinea, 24.4 m depth, 18 January 1988, T. M. Gosliner. One paratype, AMS C164085, coral rubble, the Quarry, near Bunu Village, 30 km N of Madang, Papua New Guinea, 3-5 m depth, 21 January 1988, R. C. Willan. Two paratypes, CASIZ 070989, lighthouse, Madang, Papua New Guinea, 7.6 m average depth (27.4 m maximum), 22 January 1988, T. M. Gosliner. One paratype,

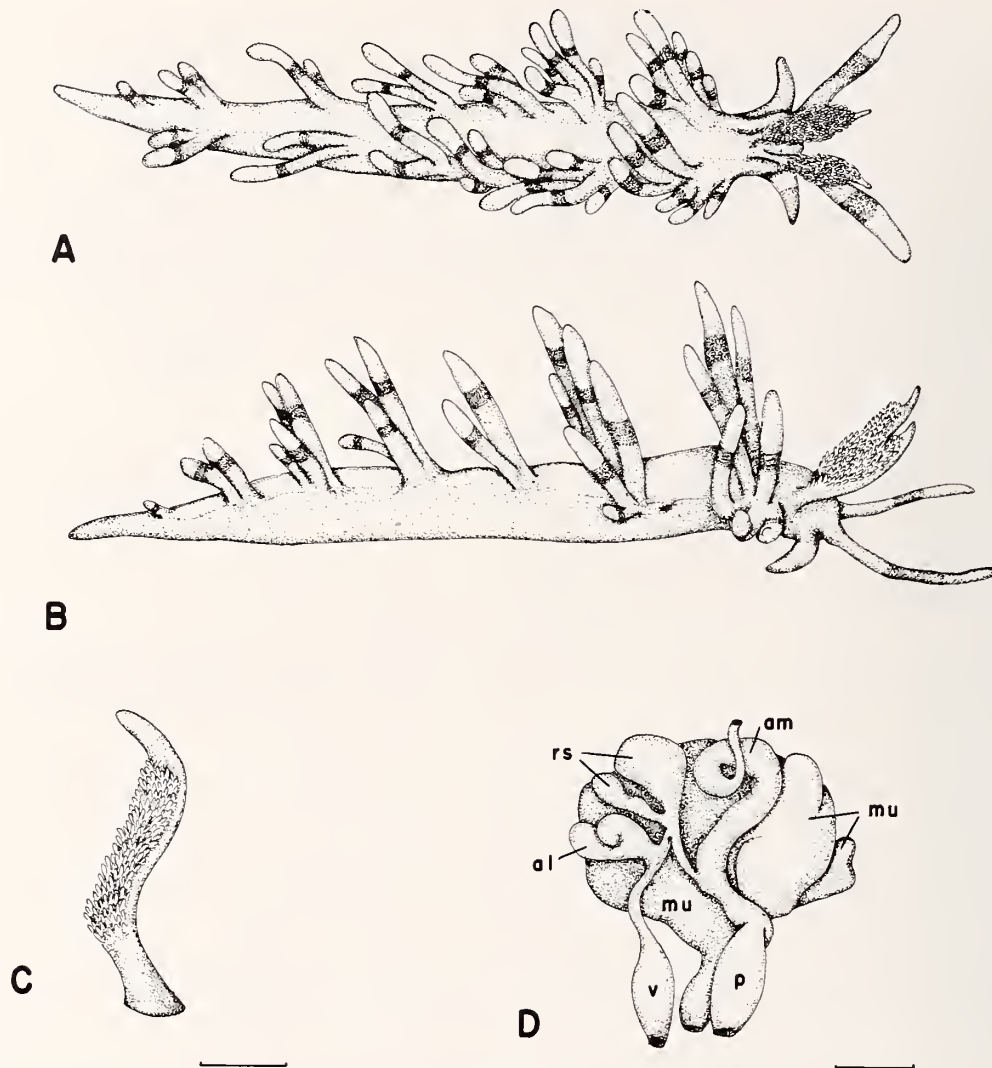


Figure 18

Flabellina exoptata Gosliner & Willan, sp. nov. A. Dorsal view of 21 mm living animal. B. Lateral view. C. Rhinophore, scale = 1.0 mm. D. Reproductive system: al, albumen gland; am, ampulla; mu, mucous gland; p, penis; rs, receptaculum seminis; v, vagina; scale = 0.5 mm.

CASIZ 060991, Barracuda Point, Pig Island, Madang, Papua New Guinea, 7.6 m depth, 7 February 1988, T. M. Gosliner. One paratype, AMS C164084, coral rubble, patch reef 1 km S Lian Island, 15 km SE of Port Moresby, Papua New Guinea, 10 m depth, D. J. Brunkhorst, 17 June 1988.

One paratype, CASIZ 070992, Barracuda Point, Pig Island, Madang, Papua New Guinea, 25 m depth, 16 July 1989, T. M. Gosliner.

One paratype, AMS C164083, feeding on *Halocordyle disticha*, on vertical wall of a bommie, "The Canyons," SE side of Heron Island, Capricornia Section, Great Barrier Reef, Queensland, Australia, 10 m depth, 20 August 1981, M. Ready.

External morphology: The living animals reach 30 mm in length. The general body color is deep pinkish purple. Basally, the oral tentacles are the same color as the rest of the body. Their middle third is deep purple and the outer third is generally opaque cream yellow. However, in some specimens from Aldabra Atoll, there is no opaque pigment on the outer portion of the tentacles and they are the same color as the rest of the body. Purple pigment is also present on the apical portion of the foot corners. The rhinophores are vivid orange with yellow pigment on the apices of the rhinophoral papillae. The basal half to two-thirds of the cerata is pinkish purple. Above this section, a deep purple ring is present. The apical portion of the cerata is opaque cream yellow.

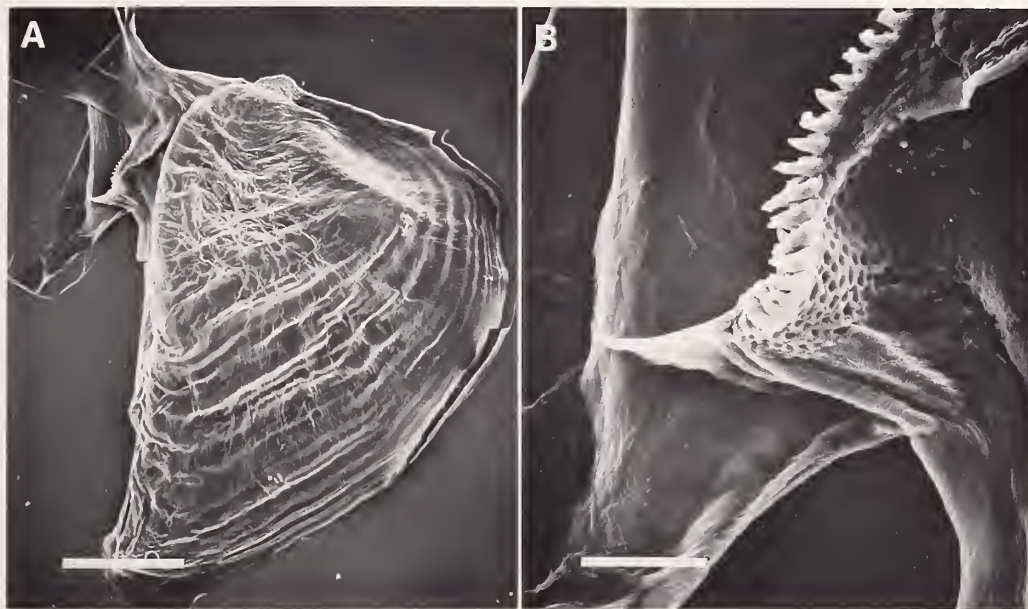


Figure 19

Flabellina exoptata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Jaw, Aldabra Atoll, scale = 200 μ m. B. Masticatory border, Aldabra Atoll, scale = 30 μ m.

The body is stockier than other members of the genus (Figure 18A). The notal brim is expanded at the level of each ceratal group, but is otherwise reduced compared to *Flabellina rubrolineata*. The oral tentacles are cylindrical throughout their length and they taper to an acute apex. The rhinophores (Figure 18B) are thick basally, and terminate in a distinctly pointed apex. The posterior side of each rhinophore bears over 120 densely packed, elongate papillae. The foot corners are elongate and tentacular, and are generally recurved posteriorly when the animal is actively crawling. The cerata are thick and cylindrical for most of their length, but taper to an acute apex. The cerata are slightly elevated from the notum on a common peduncle. The cerata are arranged in distinct rows. The precardiac ceratal cluster consists of three distinct rows, with 1–3 cerata per row. The postcardiac cerata are arranged in 4 or 5 linear rows that are well separated from each other. The anterior postcardiac row contains the most cerata (3–5). The more posterior rows contain fewer cerata, and the posteriormost row consists of only a single cerata. The gonopore is situated ventral to the second and third ceratal rows on the right side of the body. The pleuroproct anus is located below the notum within the interhepatic space. The nephroproct is immediately anterodorsal to the anus.

Buccal mass: The muscular buccal mass occupies the anterior portion of the body, from the rhinophores to the anterior end of the head. The narrow ducts of the paired oral glands emanate from the anterior end of the buccal mass. These glands are highly ramified and extend pos-

teriorly into the peduncle of the anteriormost ceratal cluster. The chitinous jaws (Figure 19A) are elongate and broad. The masticatory border (Figure 19B) bears several rows of elongate denticles. The denticles of the outermost row are longest.

The radular formula is $23-37 \times 1 \cdot 1 \cdot 1 \cdot$ in the two specimens examined. The rachidian teeth are narrow and elongate. The posterior limit of each limb bears a peduncle for attachment to the following tooth. The cutting edge of the teeth bears 7–10 elongate denticles on either side of the elongate, acutely pointed central cusp. The central cusp is depressed below the level of the adjacent denticles. The lateral teeth are triangular with a broad base and an elongate, acutely pointed primary cusp. There are 13–20 minute, acutely pointed denticles along the inner margin of the tooth.

Reproductive system (Figure 18D): The preampullary duct is narrow and elongate. It expands into an elongate, curved ampulla. The ampulla narrows again and divides into the oviduct and vas deferens. The oviduct is narrow and elongate and expands to join the two large receptacula seminis. The inner receptaculum is distinctly larger than the one closer to the female gland mass. The oviduct again narrows and enters the female gland mass near the small albumen gland. The albumen and membrane glands are much smaller than the mucous gland, which comprises the bulk of the reproductive system. The distinct vaginal duct continues from the oviduct to its own aperture, adjacent to the penis. The vagina is expanded for most of its distal portion, but a distinct bursa copulatrix is absent. The vas

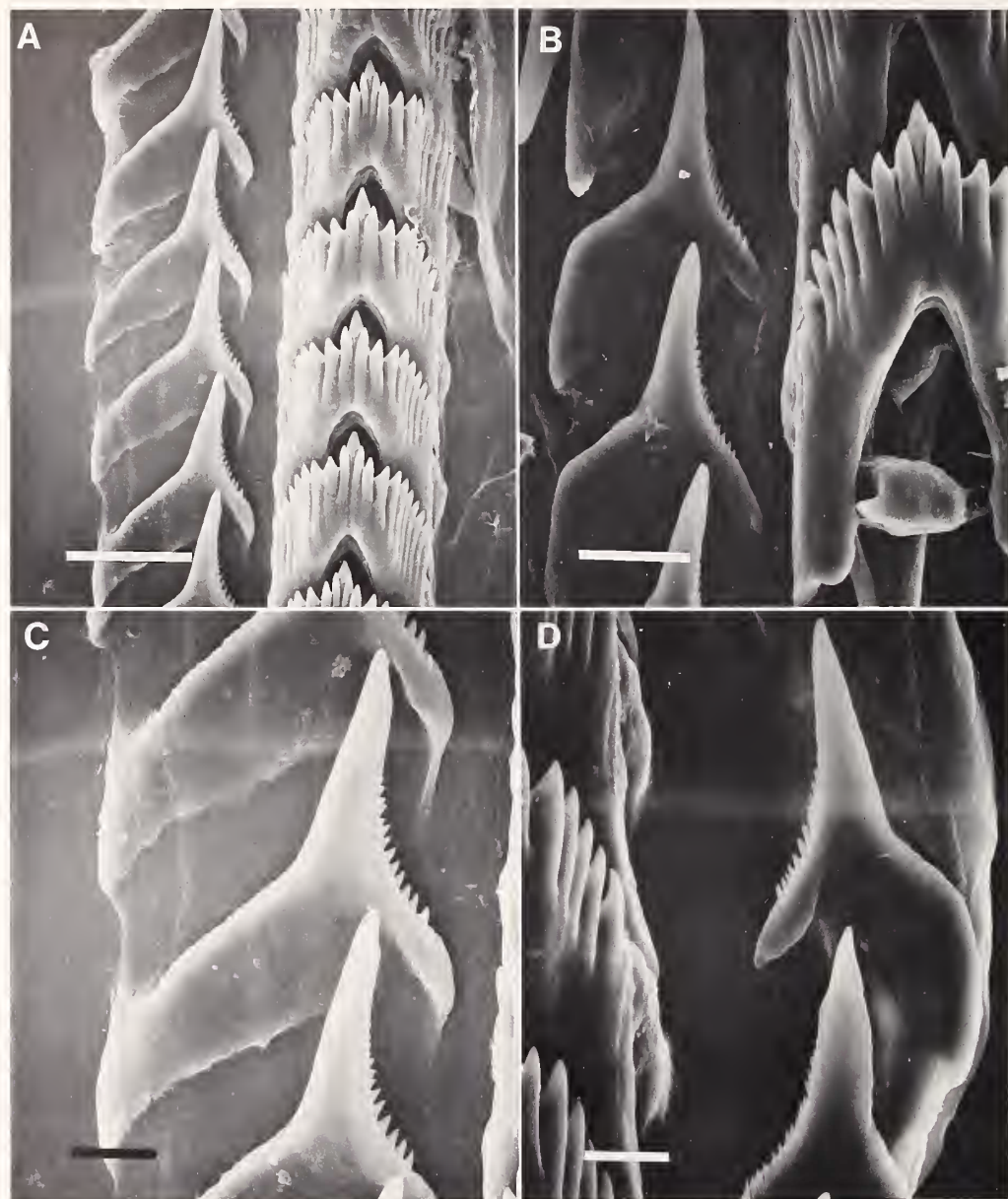


Figure 20

Flabellina exoptata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Rachidian and lateral teeth, Madang, Papua New Guinea, scale = 30 μm . B. Rachidian and lateral teeth, Aldabra Atoll, scale = 15 μm . C. Lateral teeth, Madang, Papua New Guinea, scale = 10 μm . D. Lateral teeth, Aldabra Atoll, scale = 10 μm .

deferens is short but expands into a small prostatic segment. The prostatic portion expands further into the broad penial sac containing the simple, unarmed penis.

Discussion: Its unique color pattern readily distinguishes *Flabellina exoptata* from three other described species of *Flabellina* with papillate rhinophores, *Flabellina rubrolineata*, *F. poenicia* (Burn, 1957), and *F. marcusorum* Gosliner & Kuzirian, 1990. All these species have the cerata of the

postcardiac groups arranged in horseshoe-shaped arches, whereas those of *F. exoptata* are in simple, linear rows.

In *Flabellina marcusorum*, the bursa copulatrix is large and obvious, whereas in *F. rubrolineata* and *F. delicata* it is reduced, and in *F. exoptata* it is entirely absent. The reproductive system of *F. poenicia* remains unknown. The vas deferens is shorter in *F. exoptata* than in *F. rubrolineata* and *F. marcusorum*.

In coloration, *Flabellina exoptata* is most similar to *F.*

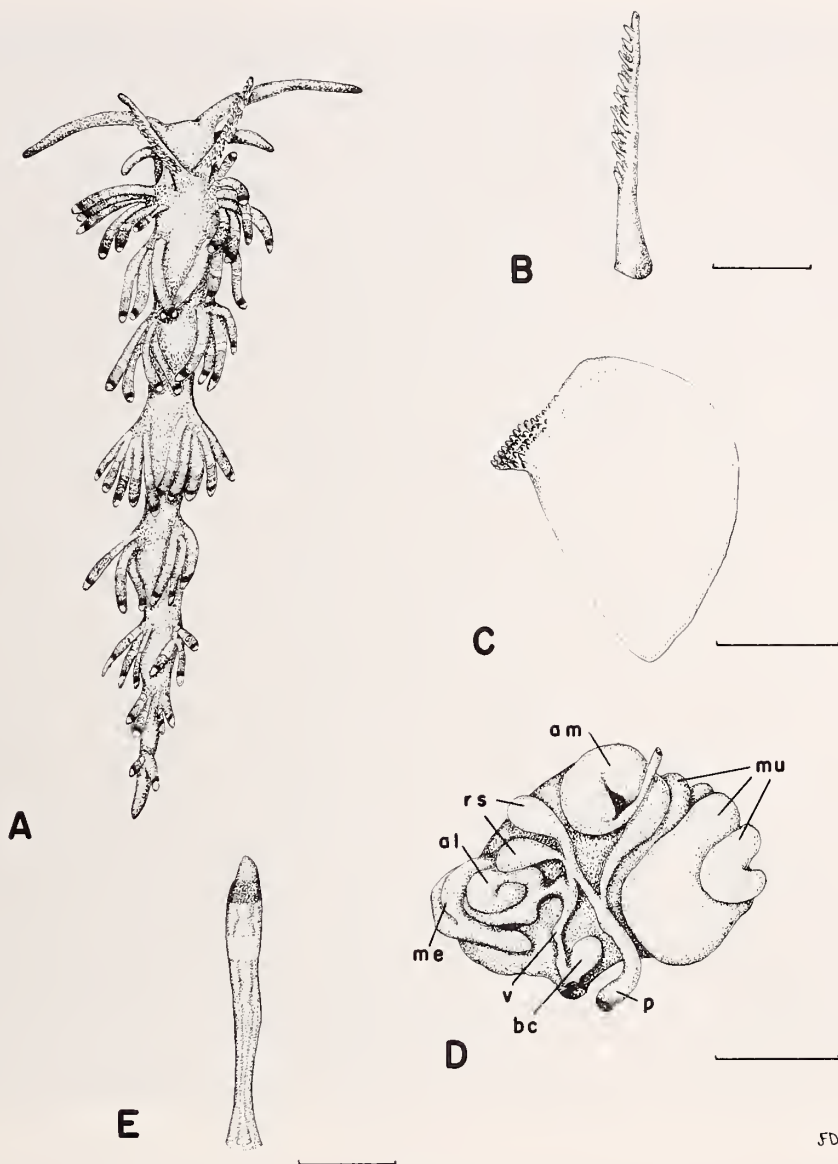


Figure 21

Flabellina delicata Gosliner & Willan, sp. nov. A. Dorsal view of 16 mm living animal. B. Rhinophore, scale = 1.0 mm. C. Jaw, scale = 0.2 mm. D. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; rs, receptaculum seminis; v, vagina, scale = 1.0 mm. E. Ceras, scale = 1.0 mm.

marcusorum, but this species lacks the yellow pigment on the posterior surface of the rhinophoral papillae, which is present in *F. exoptata*. In addition, *F. marcusorum* has opaque white pigment on the posterior end of the foot, which is not present in *F. exoptata*.

This species has been erroneously identified as *Flabellina macassarana* Bergh, 1905, on a Malaysian postage stamp. However, *F. macassarana* differs from *F. exoptata* in several important aspects. The color of *F. macassarana* is pinkish yellow without the striking purple and yellowish bands that distinguish *F. exoptata*. Also, *F. macassarana*

has perfoliate rather than papillate rhinophores. The shape and denticulation of the radular teeth differ markedly between the two species. *Flabellina macassarana* has only 20 rows of teeth in the radula, whereas *F. exoptata* has 23–37 rows. Both the rachidian and lateral teeth of *F. macassarana* have far fewer denticles than do the teeth of *F. exoptata*. Therefore, *F. exoptata* can be clearly distinguished from *F. macassarana*. *Flabellina macassarana* is known only from Bergh's original description and the unique holotype could not be located in the in the Zoologisch Museum, Amsterdam (R. Moolenbeek, personal

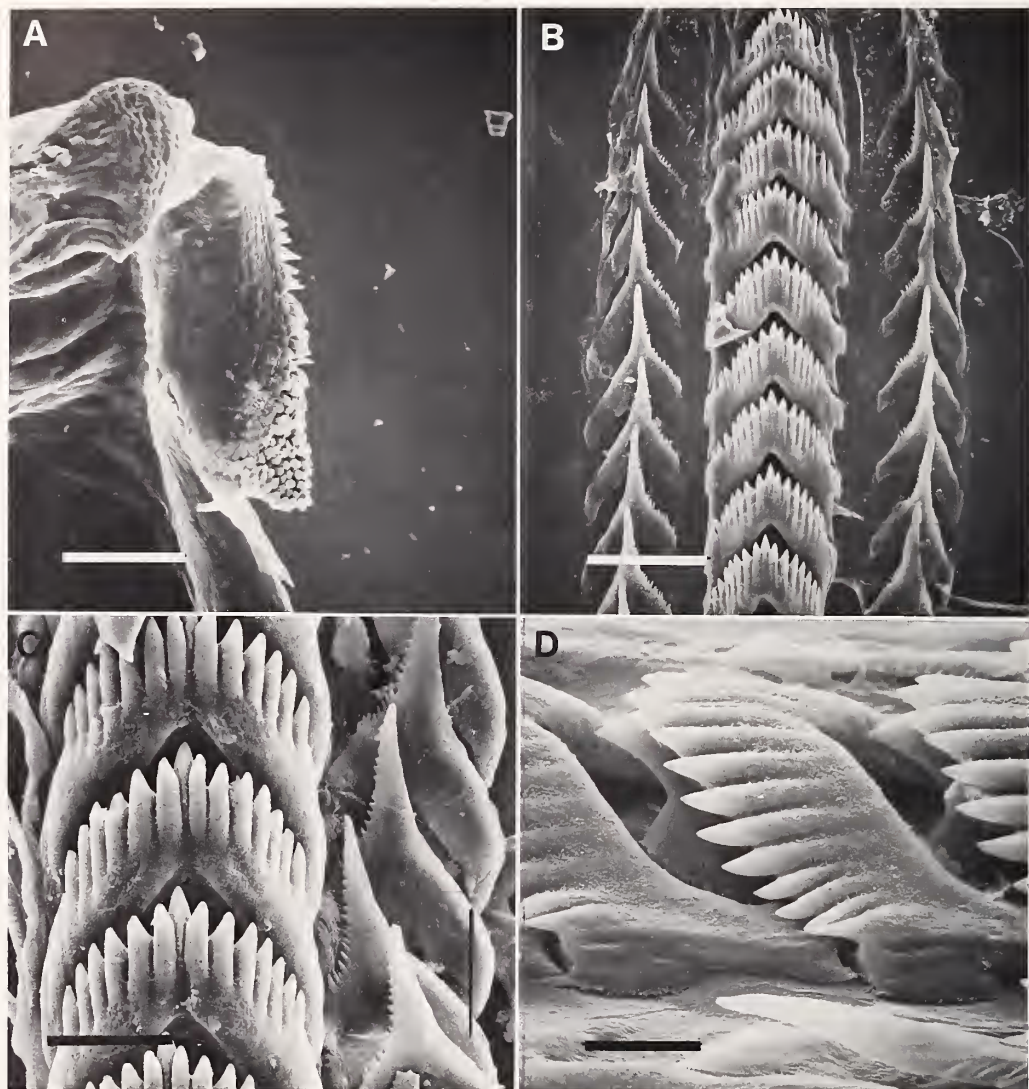


Figure 22

Flabellina delicata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Masticatory border, Madang, Papua New Guinea, scale = 40 μ m. B. Entire width of radula of holotype, Madang, Papua New Guinea, scale = 40 μ m. C. Entire width of radula, Aliwal Shoals, South Africa, scale = 20 μ m. D. Lateral view of rachidian teeth of holotype, Madang, Papua New Guinea, scale = 10 μ m.

communication). Determination of its relationship to other members of the genus requires further study and elaboration of the original description.

Flabellina delicata Gosliner & Willan,
sp. nov.

(Figures 1G, 21–23)

Coryphellina sp.: GOSLINER, 1987:114, fig. 224.

Distribution: *Flabellina delicata* is known from Papua New Guinea (present study) and from Natal, South Africa (GOSLINER, 1987, and present study).

Etymology: The epithet *delicata* refers to the elongate, graceful body form of this species.

Type material: Holotype: California Academy of Sciences, CASIZ 070999, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 30.5 m (maximum) depth, 11 February 1988, T. M. Gosliner.

Paratypes: One specimen, CASIZ 071000, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 10.4 m depth, 19 February 1988, T. M. Gosliner. One specimen, South African Museum, Cape Town, SAM A35719, dissected, Aliwal Shoals, off Scottburgh, Natal, South Africa, 12.2 m depth, 2 May 1982, T. M. Gosliner.

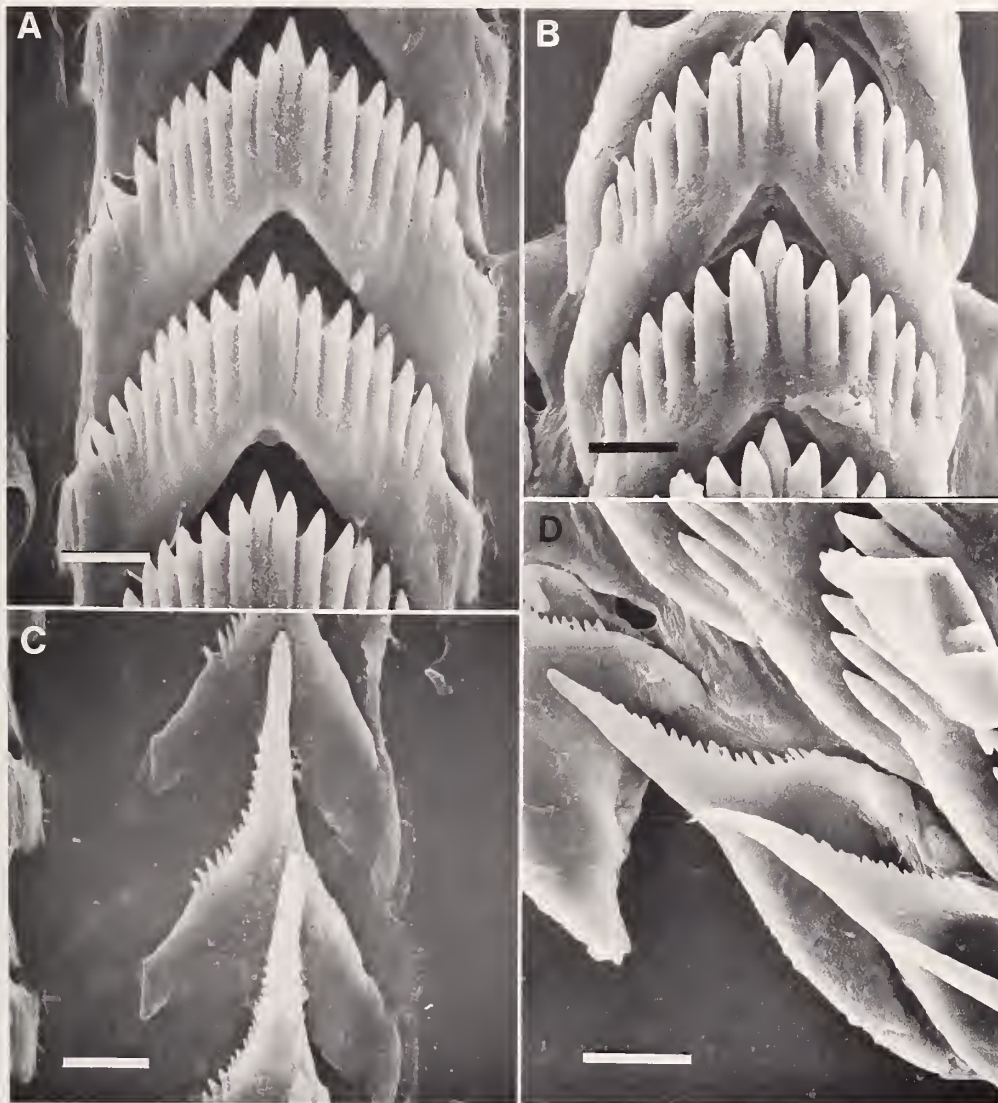


Figure 23

Flabellina delicata Gosliner & Willan, sp. nov., scanning electron micrographs, scales = 10 μm . A. Dorsal view of rachidian teeth of holotype, Madang, Papua New Guinea. B. Dorsal view of rachidian teeth, Aliwal Shoals, South Africa. C. Lateral teeth of holotype, Madang, Papua New Guinea. D. Lateral teeth, Aliwal Shoals, South Africa.

External morphology: The living animals (Figure 1G) are 15–20 mm in length. The general body color is deep reddish purple. Generally, the oral tentacles are a deeper purple than the rest of the body. The rhinophores are deep red throughout. The cerata are translucent white basally, with the opaque white digestive gland giving the cerata an overall white appearance. Near the middle of each ceras, an opaque white transverse band is present on its surface. More distally, the ceras is again translucent and a golden-yellow-orange enlarged portion of the digestive gland is visible. A subapical transverse ring of translucent purple is present just below the translucent white apex.

The body is narrow and delicate in appearance (Figure

21A). The notal brim is slightly expanded at the base of the cerata, but is otherwise reduced. The oral tentacles are slender and elongate, terminating at an acute apex. The rhinophores (Figure 21B) are elongate and slender with approximately 30 well-separated papillae on their posterior surface. The rhinophores terminate at an acute apex. The tentacular foot corners are elongate and acutely pointed. The numerous cerata are slender and cylindrical throughout their length (Figure 21E). The cerata are arranged in distinct, well-separated clusters. The precardiac cluster contains 3 or 4 distinct rows with 1–6 cerata per row. The postcardiac clusters are arranged in 5–8 horse-shoe-shaped arches. The anteriormost arch contains 6–10

Table 3.

Morphological variation in *Flabellina*. 0 = ancestral; 1-3 = derived states; 9 = missing data.

Species	ceratal peduncles	preanal cerata	rhinophores	anus	oral glands	central cusp	receptaculum seminis	bursa copulatrix	foot corners	reproductive system
ancestor	1	0	0	2	1	2	0	0	1	0
<i>affinis</i>	2	0	1	2	1	2	1	0	1	0
<i>albomarginata</i>	1	0	2	2	1	2	0	2	1	0
<i>babai</i>	2	1	1	2	1	2	0	2	1	0
<i>baetica</i>	1	0	2	2	1	2	0	2	1	0
<i>bertschi</i>	1	0	0	2	1	2	0	2	1	0
<i>bicolor</i>	2	2	1	2	1	3	1	0	1	0
<i>bilas</i>	2	2	1	2	1	2	1	1	1	0
<i>delicata</i>	1	0	2	2	1	2	0	1	1	1
<i>engeli</i>	2	1	1	2	1	2	0	2	1	0
<i>exoptata</i>	1	0	2	2	1	2	0	2	1	1
<i>funeka</i>	2	0	1	2	1	2	0	0	1	0
<i>isshitana</i>	2	0	1	2	1	9	0	0	1	0
<i>marcusorum</i>	1	0	2	2	1	2	0	0	1	1
<i>pedata</i>	1	0	0	2	1	2	0	2	1	0
<i>pellucida</i>	1	0	0	2	1	2	0	0	1	0
<i>poenicia</i>	1	0	2	2	1	2	9	9	1	9
<i>riwo</i>	2	2	1	2	1	3	2	1	1	0
<i>rubrolineata</i>	1	0	2	2	1	2	0	1	1	1
<i>rubropurpurata</i>	2	0	1	2	1	2	0	0	1	0
<i>telja</i>	2	0	1	2	1	2	0	0	1	0
character number	1	2	3	4	5	6	7	8	9	10

cerata. More posterior arches contain fewer cerata. The posteriormost arch contains 1-3 cerata. The gonopore is situated ventral to the posterior 2 rows of the precardiac ceratal cluster. The pleuroproct anus is situated in the interhepatic space, ventral to the edge of the notum. The nephroproct is immediately anterodorsal to the anus.

Buccal mass: The buccal mass is small relative to the rest of the body. The narrow ducts of the paired oral glands emanate from the anterior portion of the buccal mass. The jaws (Figure 21C) are broad and ovoid. The masticatory border (Figure 22A) bears 5 or 6 rows of small denticles. The outermost row bears the longest denticles.

The radular formula is $31 \times 1 \cdot 1 \cdot 1 \cdot$ in two specimens examined. The rachidian teeth (Figures 22B-D, 23A, B) are broad with short lateral limbs. There are 6-9 elongate, acute denticles on either side of the elongate central cusp. The central cusp is depressed below the level of the adjacent denticles (Figure 22D). The lateral teeth (Figure 23C, D) are triangular with a relatively broad base. The primary cusp is narrow and elongate. There are 15-18 minute denticles along most of the inner margin of the laterals.

Reproductive system (Figure 21D): The narrow preampullary duct curves and widens into the saccate ampulla. The ampulla curves, narrows, and divides into the oviduct and vas deferens. The short oviduct joins with the two receptacula seminis, which are approximately equal in size. The oviduct continues for a short distance and enters

the albumen gland. The albumen and membrane glands are adjacent to each other and are much smaller than the voluminous mucous gland. From the entrance of the oviduct into the female gland mass, the vaginal duct continues distally towards its own aperture adjacent to the penis. The vagina gives rise to a small bursa copularix immediately prior to exiting at the vaginal pore. The vas deferens is short and straight and appears to be prostatic nearest the ampulla. It is uniform in diameter for most of its length and is contiguous with the simple, unarmed penial papilla.

Discussion: By means of its unique color pattern, *Flabellina delicata* can be distinguished from other members of the genus with papillate rhinophores. Its notal brim is more reduced than *F. rubrolineata*, as in *F. marcusorum* and *F. exoptata*. The papillae on the rhinophores are fewer in number and sparser in arrangement than in the other species that possess papillae. The postcardiac ceratal clusters are arranged in horseshoe-shaped arches as in *F. rubrolineata* and *F. marcusorum* rather than in linear rows as in *F. exoptata*. However, *F. delicata* has more cerata per cluster than do the other species.

The rachidian radular teeth of *Flabellina delicata* are broader relative to their length than in *F. rubrolineata*, *F. marcusorum*, or *F. exoptata*. Only *F. exoptata* and *F. delicata* have numerous denticles on the cutting edge of the lateral teeth.

The reproductive system of *Flabellina delicata* is most similar to *F. rubrolineata*. Both species have a reduced bursa

Table 3
Continued.

lateral teeth	number of laterals	rhino-phoral papillae	ceratal groups	rhino-phores	penial warts	denticles on lateral	notal brim	prostate	anterior liver arch	receptaculum seminis
0	1	0	0	0	0	0	0	0	0	0
0	1	0	0	1	0	0	1	1	0	0
0	1	1	0	0	0	0	0	0	0	1
0	1	0	0	2	0	0	1	0	0	0
1	1	1	0	0	0	0	0	0	1	0
0	1	0	0	0	0	0	0	0	0	1
0	1	0	0	2	0	0	1	0	0	0
0	1	0	0	2	0	0	1	0	0	0
0	1	2	0	0	0	1	1	0	1	1
0	1	0	0	2	0	0	1	0	0	0
0	1	2	1	0	0	1	1	0	1	1
0	1	0	0	1	0	0	1	1	0	0
1	1	0	0	1	0	0	1	1	0	0
0	1	2	0	0	0	0	1	0	1	1
0	1	0	0	0	0	0	0	0	0	1
1	1	0	0	0	0	0	0	0	0	0
0	1	2	0	0	0	0	0	0	1	9
0	1	0	0	2	0	0	1	0	0	0
0	1	2	0	0	0	0	0	0	1	1
0	1	0	0	2	0	0	1	0	0	0
0	1	0	0	2	1	0	1	0	0	0
11	12	13	14	15	16	17	18	19	20	21

copulatrix. However, the vas deferens is shorter and straighter in *F. delicata* than in *F. rubrolineata*.

Three other distinct species have sparsely papillate rhinophores, *Flabellina albomarginata* Miller, 1971, *F. baetica* Garcia Gomez, 1984, and *Flabellina* sp. 1 (GOSLINER, 1987). These species differ from the above-mentioned taxa in several significant regards. The papillae on the rhinophores are less well developed, the cerata are arranged in simple crowded rows (except in *F. baetica*), and the reproductive system is diaulic rather than triaulic.

DISCUSSION

The phylogenetic and systematic relationships of the Flabellinidae have recently been examined by GOSLINER & KUZIRIAN (1990). From their analysis, it is apparent that the genus *Flabellina* contains numerous, morphologically diverse species. Included in the genus are some of the most primitive aeolids, such as *F. islandica* (Odhner, 1937), as well as intermediate and highly derived taxa. They concluded that the most highly derived taxa formed two distinct clades. All of the taxa included in the present study are members of these two clades. In members of both of these clades, digitate oral glands and a depressed central cusp of the rachidian tooth are present. The first of these clades includes taxa with cerata elevated on distinct peduncles and densely annulate or perfoliate rhinophores. The second clade contains taxa with a bilobed receptaculum

seminis, and most members of this clade also possess papillae ornamenting the posterior face of the rhinophores.

In order to examine further the phylogeny of members of these two clades of derived flabellinids, the morphology of the taxa described here was examined and the morphology of previously described flabellinids was reviewed and, in several cases, re-examined. Eight additional characters, not included in the previous study, were examined here. These data are compiled in Table 3.

Character Polarity

Twenty-one characters of 20 taxa were included. The polarity of these characters was determined using outgroup comparison of less derived flabellinids (see GOSLINER & KUZIRIAN, 1990). The basis for determining polarity of these features is discussed below. The sequence of characters is identical to that presented in Tables 3 and 4.

1. Ceratal peduncles: Outgroups of flabellinids and species of *Notaeolidia* have the cerata arranged in linear rows. These rows emerge from epithelial tissue that is at the same level as the rest of the notum. In more derived taxa, the ceratal clusters emerge from stalked clusters, which are well elevated from the notum. These may contain compound ceratal clusters or simple ones.

2. Preanal ceratal rows: Species of less derived flabellinids, including all of the taxa not included in this study (outgroup taxa), have several rows of cerata anterior to

Table 4
Coding for characters in Table 3.

1. ceratal peduncles	1 = low	2 = elevated	
2. preanal cerata	0 = 3-4 rows	1 = 2 rows	2 = one row
3. rhinophores	0 = simple	1 = ringed	2 = papillate
4. anus	1 = posterior	2 = interhepatic	
5. oral glands	0 = absent	1 = present	
6. central cusp	2 = depressed	3 = elevated	
7. receptaculum seminis	0 = semiserial	1 = serial	2 = absent
8. bursa copulatrix	0 = stalked	1 = reduced	2 = absent
9. foot corners	0 = rounded	1 = tentacular	
10. reproductive system	0 = diaulic	1 = triaulic	
11. lateral teeth	0 = denticulate	1 = smooth	
12. number of laterals	0 = more than 1	1 = 1	
13. rhinophoral papillae	0 = short	1 = elongate	
14. ceratal groups	0 = all arches	1 = posterior rows	
15. rhinophores	0 = no rings	1 = annulate	2 = perfoliate
16. penial warts	0 = absent	1 = present	
17. lateral denticles	0 = few	1 = many	
18. notal brim	0 = present	0 = absent	
19. prostate	0 = uniform	1 = constricted	
20. anterior liver arch	0 = absent	1 = present	
21. receptaculum seminis	0 = single	1 = bilobed	

the anus, which form a distinct ceratal cluster. In some derived species that have cerata elevated on peduncles, the number of anterior ceratal rows is reduced. In the most highly derived species (e.g., *Flabellina bicolor*, *F. riwo*, and *F. bilas*), there is only a single ceratal row per peduncle in both the preanal and postanal ceratal clusters.

3. Rhinophores: In most ancestral flabellinids the rhinophores are simple, without any ornamentation. GOSLINER & KUZIRIAN (1990) have shown that this appears to be the case in the least derived members of the family. Ornamented rhinophores have evolved independently within different lineages of the family. Within the more highly derived members of the family studied here the rhinophores may be simple, ringed (annulate or perfoliate), or papillate. The simple condition is considered to represent the ancestral state. Ringed and papillate rhinophores have probably both evolved directly from simple ones, though the sequence of changes is uncertain. Owing to the lack of certainty of the evolutionary sequence of derived states, this character is treated as unordered in the present analysis.

4. Anus: In the Notaeolidiidae and less derived members of the Flabellinidae the anus is situated in the pleuroproctic position, and is located in the posterior half of the body. In more derived taxa, the anus is situated near the middle of the most anterior postanal ceratal cluster. In all of the taxa examined here, the anus is situated within the interhepatic space, which represents the most derived condition within the family.

5. Oral glands: GOSLINER & KUZIRIAN (1990) suggested that an absence of oral glands represents the ancestral state

within the Flabellinidae, because oral glands are also absent in the Notaeolidiidae. Most primitive members of the Flabellinidae lack oral glands, with the exception of *Flabellina salmonacea* (Couthoy, 1838), which has a pair of ventral pyriform oral glands. In all of the taxa studied here, the oral glands are highly ramified, are found dorsally, and extend to the bases of the preanal ceratal cluster. Even in cases where the glands were not specifically described, such as in *Flabellina ischitana* Hirano & Thompson, 1990, they are evident in photographs of the living animal (HIRANO & THOMPSON, 1990:fig. 1).

6. Central cusp of the rachidian teeth: All of the less derived members of the Flabellinidae possess rachidian teeth of the radula with a central cusp that is above, or at the same level as, the adjacent denticles. This feature is especially evident when the teeth are viewed laterally. In almost all derived species, the central cusp is depressed below the level of the adjacent denticles. In two species examined in this study, *Flabellina riwo* and *F. bicolor*, the central cusp is elevated. This is considered to be a secondarily derived reversal of the depressed cusp within the in-group studied here. This assumption is based upon the highly derived nature of all other aspects of the morphology of these species.

7. Receptaculum seminis: EDMUNDS (1970) described two forms of the receptaculum seminis in aeolid nudibranchs. A serial arrangement has two distinct ducts entering the receptaculum, while a semiserial configuration has only a single duct entering the receptaculum. Edmunds considered the former to be the ancestral condition within the aeolids. This appears to be the case in *Notaeolidia*

(WÄGELE, in press), and was considered to represent the ancestral condition within the Flabellinidae (GOSLINER & KUZIRIAN, 1990). The majority of more derived species of flabellinids have a semiserial receptaculum. Some of the derived members studied here also possess a serial receptaculum. This is considered to be a secondarily derived reversal to a serial receptaculum from a semiserial condition. In one instance, in *Flabellina riwo*, the receptaculum is entirely absent. This is considered to be a further modification of the secondarily derived serial configuration.

8. Bursa copulatrix: The presence of a stalked bursa is considered to represent the ancestral state in the Aeolidacea (EDMUNDS, 1970). This plesiomorphic condition exists in the majority of the Flabellinidae (GOSLINER & KUZIRIAN, 1990). In other taxa, the bursa may be reduced in size and sessile, or it may be entirely absent. Both of these arrangements are considered derivations of the primitive state. It is difficult to place the derived states in a linear configuration, because loss of the bursa may not require reducing the bursa prior to loss. For this reason this character is treated as unordered.

9. Foot corners: A simply rounded anterior end of the foot is present in *Notaeolidia* (WÄGELE, in press) and in two primitive species of *Flabellina* (GOSLINER & KUZIRIAN, 1990), *F. islandica* and *F. salmonacea*. Possession of tentacular foot corners represents a derived state within the Flabellinidae. This apomorphic condition is present in all of the taxa examined in this study.

10. Reproductive system: GHISELIN (1966) argued that, in opisthobranchs, an androdiaulic reproductive system preceded a triaulic arrangement of organs. The vast majority of flabellinids have an androdiaulic reproductive system. However, a few species, which are highly apomorphic in other aspects of their anatomy, have a triaulic arrangement of reproductive organs. This is considered to represent an apomorphic feature within the flabellinids, and appears to be the case throughout the Opisthobranchia.

11. Lateral teeth: In species of *Notaeolidia* (WÄGELE, in press) and in most species of *Flabellina*, the lateral radular teeth bear a series of denticles along their inner edge. In a few species of *Flabellina* studied here, the laterals are smooth and entirely devoid of denticles. In *F. ischitana*, a few reduced denticles may be present or entirely lacking in different individuals (HIRANO & THOMPSON, 1990). The absence of denticles on the lateral teeth is considered to represent a derived feature within *Flabellina*.

12. Number of lateral teeth: In species of *Notaeolidia* (WÄGELE, in press) there is a variable number (3–5) of lateral radular teeth on either side of the rachidian. In *Flabellina islandica* there are two rows of laterals on either side of the rachidian. In the remainder of *Flabellina* species, there is only a single lateral tooth on either side of the rachidian. This is considered the derived state within the genus.

13. Rhinophoral papillae: In some species of Flabellinidae, Facelinidae, and Aeolidiidae, the posterior surface of the rhinophores bears numerous papillae. It is clear that this condition has arisen independently within these lineages of aeolids and represents a derived feature within each of these families. Within the Flabellinidae, some taxa have simple rounded papillae while others have elongate digitiform ones. On a functional basis, more elongate papillae probably arose from simply rounded ones. The derived condition provides greater surface area for chemosensory reception.

14. Ceratal groups: In a few species of flabellinids, the cerata are arranged in horseshoe-shaped arches, in a fashion similar to that described for the Favorininae (see EDMUNDS, 1970). A reduction of the postanal arches to linear rows represents a derived condition found only in *Flabellina exoptata*.

15. Rhinophoral rings: Most opisthobranchs utilize their rhinophores as their primary chemosensory organs. The Flabellinidae and other aeolidacean taxa include species with smooth and ornamented rhinophores. Smooth rhinophores provide less sensory surface area and are considered to represent the ancestral condition, based on functional criteria. The least derived members of Flabellinidae, Eubranchidae, Tergipedidae, and Aeolidiidae have smooth rhinophores. In derived species, the rhinophores are generally ornamented with either papillae (see above), well separated annulations or densely packed lamellae (perfoliate rhinophores). All of these conditions exist within the Flabellinidae. Judging from the cladogram presented by GOSLINER & KUZIRIAN (1990), it appears that annulate rhinophores originated several times within the family. Perfoliate rhinophores are present only in members of one of the most highly derived clades, that which includes *Flabellina bicolor* and its relatives (Table 1). The sister group of this clade includes *F. affinis*, and contains taxa with annulate rhinophores. The ancestors to these two clades had smooth rhinophores. It is clear that, within the Flabellinidae, both the annulate and perfoliate states are derived, but it is uncertain as to whether either condition is derived from the other. Functional arguments would suggest that perfoliate rhinophores would provide greater surface area than do annulate ones. From this perspective, it is hypothesized that perfoliate rhinophores are derived from annulate ones.

16. Penial papillae: Among members of the Flabellinidae, the presence of wartlike papillae on the penial papilla is limited to *Flabellina telja*. This state is not known in aeolidacean out-groups of flabellinids and represents a derived condition.

17. Denticles on lateral teeth: As discussed above, the taxa studied here include species with denticulate and smooth lateral teeth, and it has been concluded that denticulate teeth represent the ancestral condition. Two species of flabellinids with papillate rhinophores, *Flabellina*

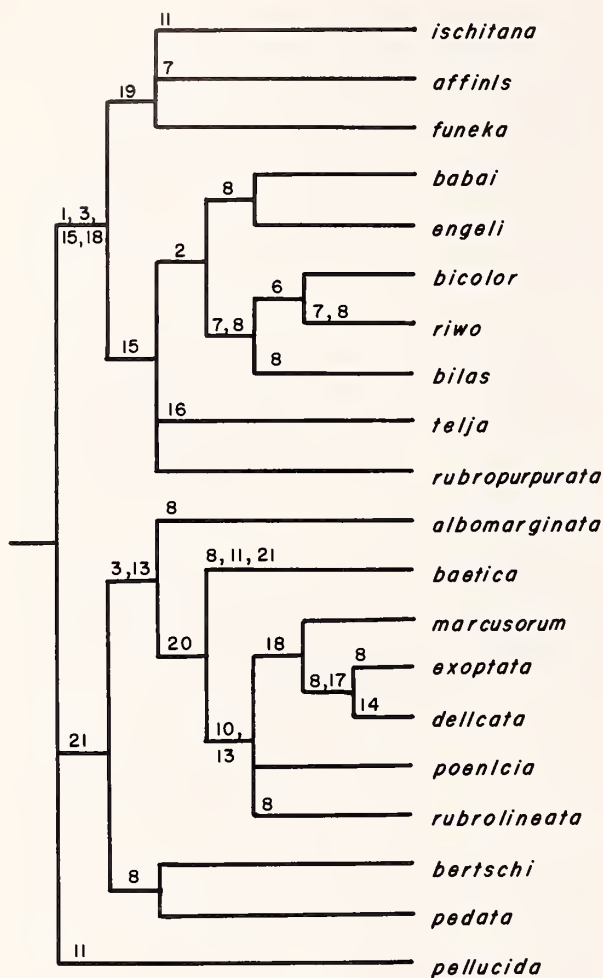


Figure 24

Cladogram depicting phylogeny of highly derived flabellinids included in this study.

exoptata and *F. delicata*, have more numerous denticles than other members of their clade or than in out-groups of flabellinids. Therefore, lateral teeth with multiple denticles are considered derived from teeth with few denticles.

18. Notal brim: The presence of a distinct rim of tissue along the dorsolateral margins of the body has been considered as a plesiomorphic feature within the Aeolidacea (ODHNER, 1939). In the least derived flabellinids, a continuous notal brim is present. In more derived flabellinids, the notal brim is interrupted, and in the most derived taxa the brim is entirely absent. In the clade of flabellinids studied here, the notal brim is either partially or entirely reduced. The latter is considered derived within the in-group.

19. Prostate: In almost all flabellinids, the prostate is of uniform diameter throughout its length. In *Flabellina af-*

finis, *F. funeka*, and *F. ischitana*, there is a constriction of the prostate near its distal end. This is considered a derived feature within this clade.

20. Anterior liver arch: In primitive members of the Flabellinidae and other aeolids, the cerata are arranged in simple linear rows. In a few derived flabellinids, the rows of cerata are elevated on a cushion that forms an arch-shaped expansion. This represents a derived state. As noted above, in *Flabellina exoptata* the postanal arches are secondarily reduced to form single linear rows.

21. Receptaculum seminis: In most species of flabellinids, the receptaculum seminis is a semiserial structure consisting of a single spherical or pyriform sac (see character 7 above). In some species studied here, the receptaculum consists of two distinct lobes. A bilobed receptaculum is considered to represent the apomorphic state.

In order to examine further the phylogeny of the taxa studied here, these morphological data were analyzed using PAUP (Phylogenetic Analysis Using Parsimony version 2.41 by David Swofford). All characters were treated as ordered, with the exceptions of the ornamentation of the rhinophores and the elaboration of the bursa copulatrix. The phylogeny of these highly derived Flabellinidae is presented here (Figure 24).

GOSLINER & KUZIRIAN (1990) argued that the cladogram they presented had implications for the systematics of the Flabellinidae. Exclusion of *Flabellina* and *Coryphella* from *Coryphella* as distinct genera rendered *Coryphella* a paraphyletic taxon. Paraphyletic taxa are untenable in modern phylogenetic classification. Therefore, all species were contained within the single genus *Flabellina* on the basis of priority. The present analysis demonstrates that maintenance of the traditionally accepted confines of *Coryphella* makes the genus polyphyletic as well as paraphyletic.

The cladogram presented here is one of two most parsimonious cladograms. The other cladogram contains *Flabellina riwo* and *F. bilas* as sister taxa. These two taxa are the sister taxon of *F. bicolor*. The alternative hypothesis presented in Figure 24 was chosen since it required only one transformation of the depressed central cusp of the rachidian tooth to an elevated one. Instead, we hypothesize that the reduction of the bursa copulatrix occurred twice in these three taxa. The bursa copulatrix has been known to be reduced or lost in several other lineages.

Several unresolved trichotomies are presented. Further examination of the highly derived flabellinids studied here and the inclusion of other undescribed taxa may facilitate the revision of the phylogenetic hypotheses presented.

GOSLINER & KUZIRIAN (1990) noted that there is a distinct correlation between the phylogeny and biogeography of the Flabellinidae. Virtually all of the plesiomorphic taxa are found in polar or cold temperate oceans. More derived taxa are generally found in temperate wa-

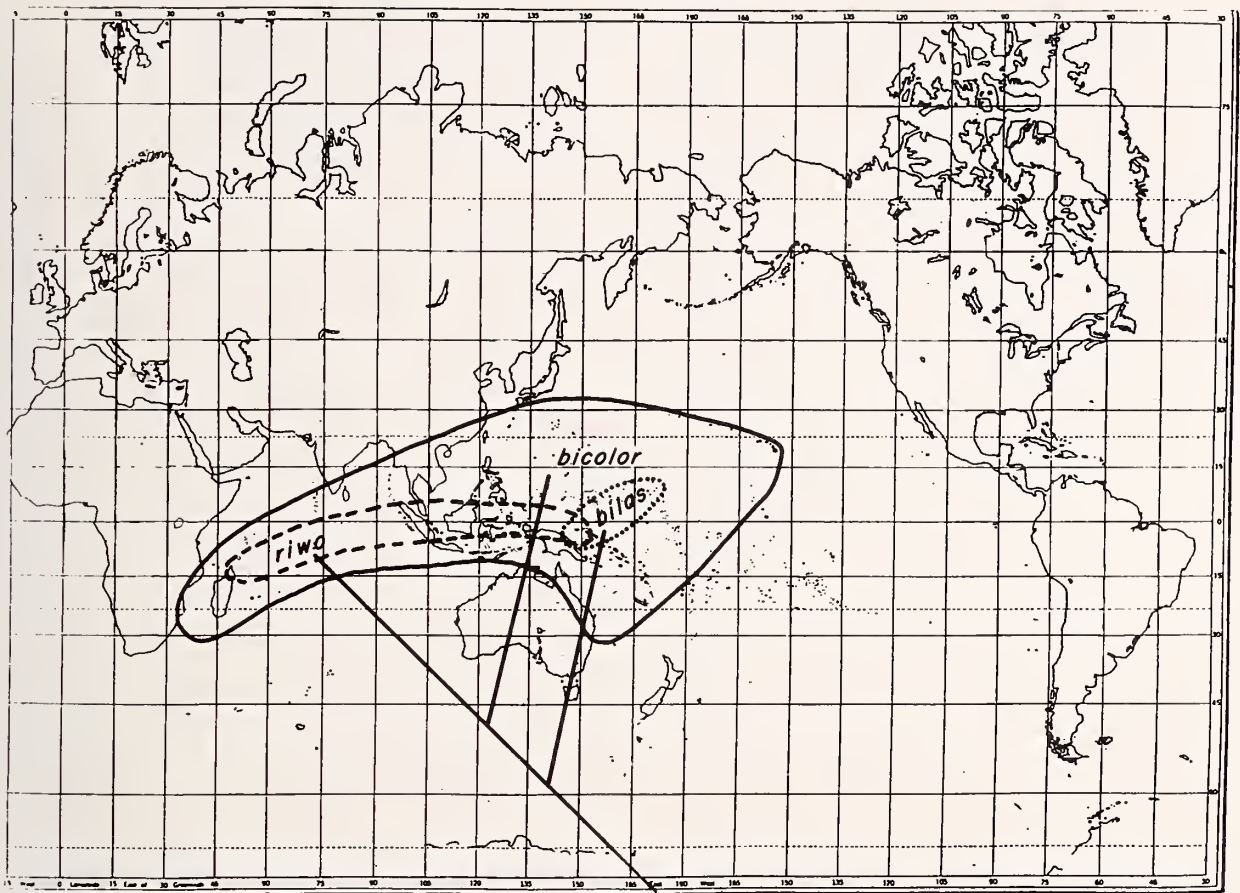


Figure 25

Area cladogram of one clade of flabellinids with perfoliate rhinophores.

ters, and the most derived taxa inhabit subtropical and tropical oceans. Area cladograms are presented for two of the clades studied here (Figures 25, 26). Neither of these examples demonstrates marked geographical separation or vicariance. Subsequent dispersal has swamped the original allopatric distributions at the time of speciation, and many of the species are presently sympatric over much of their ranges. In the one case where vicariance is clearly demonstrable, the separation of *Flabellina marcusorum* populations on either side of the Isthmus of Panama, no discernible morphological differentiation has occurred between allopatric populations (GOSLINER & KUZIRIAN, 1990), despite the fact that they have been separated for approximately 1.6 million years (WOODRING, 1966; ROSEN, 1976).

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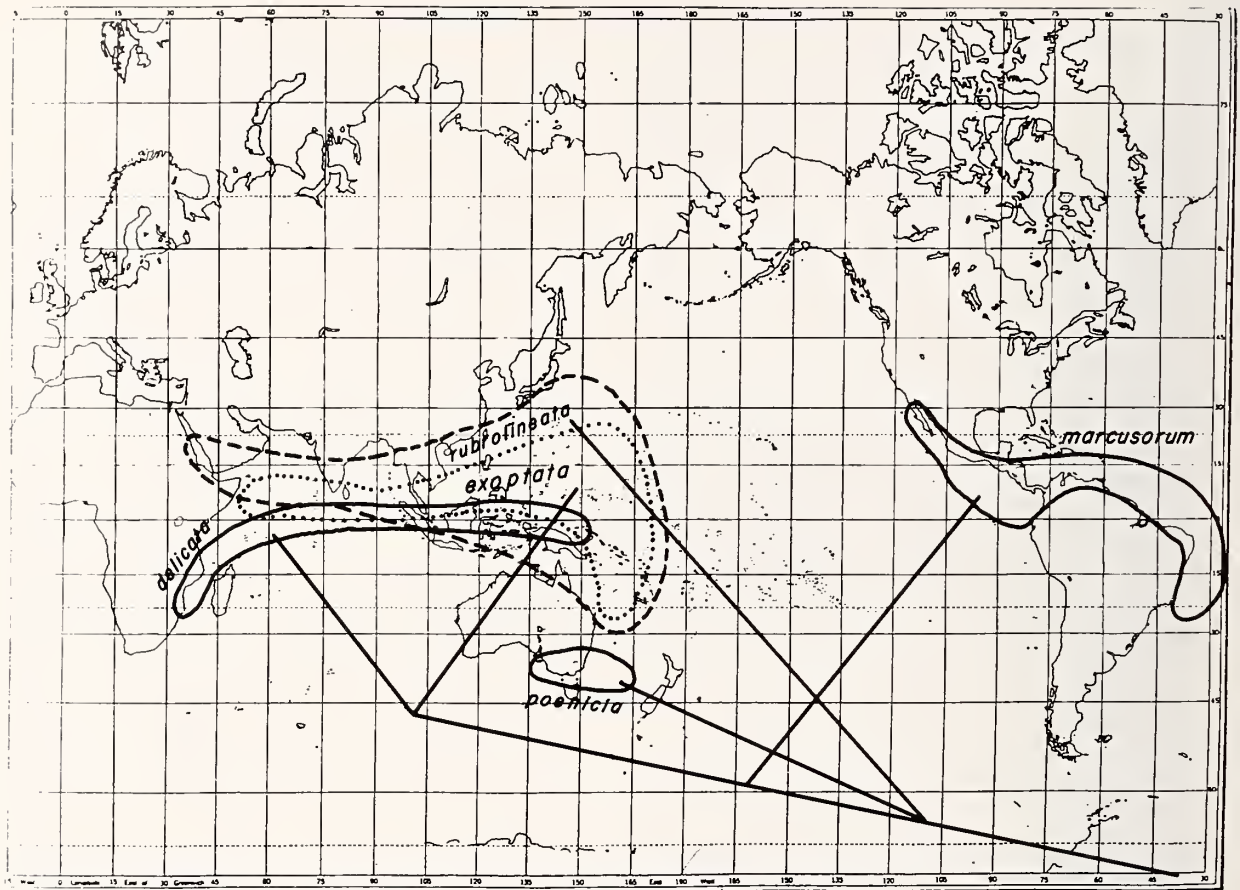


Figure 26

Area cladogram of flabellinids with triaulic reproductive system and papillate rhinophores.

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