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TWO NEW SPECIES OF FLABELLINIDAE (OPISTHOBRANCHIA: AEOLIDACEA) FROM BAJA CALIFORNIA

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ABSTRACT: Two new species of Flabellina are described from Baja California. Flabellina bertschi sp. nov. is widely distributed within the Gulf of California from Puerto Peñasco to the area north of La Paz. Flabellina marcusorum sp. nov. has been found on the Pacific and Gulf coasts of Baja California, as well as the coast of Brazil. This species was originally recorded from Brazil as Coryphellina rubrolineata O'Donoghue, 1929. However, when compared with Indo-Pacific material of F. rubrolineata, the presently described species is consistently distinct in its internal and external morphology. A preliminary phylogeny of the Flabellinidae supports the maintenance of Flabellina as a single, large, diverse genus.

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INTRODUCTION

The opisthobranch gastropod fauna of the Pacific and Gulf of California coasts of México has been extensively studied for much of the twentieth century (e.g., MacFarland 1924; Baker and Hanna 1927; Marcus and Marcus 1967; Keen 1971; Bertsch and Ferreira 1974; Bertsch 1977, 1978a, b, c; Gosliner and Behrens 1985). Although approximately 150 different species have been recorded from the region, many new records and taxa remain to be added to the fauna.

Seven species of the aeolidacean family Flabellinidae have been recorded from the Pacific coast of Baja California and the Gulf of California. The flabellinid nudibranch Flabellina rubro-

lineata (O'Donoghue, 1929), originally described from the Red Sea, has subsequently been reported from Japan (Baba 1949) and Australia (Willan and Coleman 1984). Marcus and Marcus (1961, 1970) recorded specimens of this species (as Corvphellina O'Donoghue, 1929) from the coast of Brazil and from Sonora, México. Recent investigations within the Gulf of California and from the Pacific coast of Baja California have yielded specimens of Flabellina Voigt, 1834, that are identical in their external morphology to material described by the Marcuses from México and Brazil. These animals are consistently different from Indo-Pacific specimens of F. rubrolineata (O'Donoghue) and are here described as a new species.

Other investigations into the opisthobranch fauna of the Gulf of California have yielded specimens of a second undescribed species of flabellinid, which is also described in this paper. This species has been collected from several different localities within the Gulf of California. Its anatomy is described and compared to other closely allied species.

DESCRIPTIONS

Flabellina bertschi sp. nov.

(Figs. 1A, 2, 3)

Flabellina telja Er. Marcus and Ev. Marcus, 1967:223, in part, specimen from Puerto Peñasco, collected by Mary Anne Hill, 18 June 1966.

TYPE MATERIAL.—Holotype, California Academy of Sciences, San Francisco, CASIZ 066760, in tide pool, among hydroids on *Sargassum* sp., Puerto Peñasco, Sonora, México, 23 July 1975, Hans Bertsch and P. Cook. Five paratypes, CASIZ 066761, same date and locality as holotype. One dissected paratype, CASIZ 066762, same date and locality as holotype. One paratype, CASIZ 066763, collected from hydroids on vertical wall, San Diego Reef (25°12'N, 110°42'W), s.e. of Isla San Diego, Gulf of California, México, 13 m depth, 24 July 1985, T. M. Gosliner.

DISTRIBUTION. – Flabellina bertschi is known within the Gulf of California from Puerto Peñasco, south to Isla San Diego.

ETYMOLOGY. — This species is named for our friend and colleague, Hans Bertsch, who first noted that this appears to be an undescribed species. Hans has contributed considerably to our knowledge of the Panamic molluscan fauna.

DESCRIPTION. – External morphology. The living animals (Fig. 1A) are thin and elongate (8– 12 mm long). The body color is translucent white with an overlaying opaque white pigment on the distal two-thirds of the rhinophores and oral tentacles. The opaque white pigment covers most of the dorsal surface of the animal, except for an area of translucence immediately posterior to the rhinophores. Each translucent ceras contains a central red to red-brown digestive diverticulum and terminates in a large, opaque white cnidosac.

The rhinophores are smooth, without ornamentation, and are up to 2.5 mm in length. The oral tentacles are approximately as long as the rhinophores. The cylindrical cerata are of uniform diameter throughout most of their length. They (Fig. 2A) are arranged in discrete clusters that are inserted on slightly pedunculate mounds of notal tissue. The anteriormost cluster on either side is most pronounced in its elevation from the notum. The left and right anterior branches of the digestive tract each contain three or four rows of cerata with 1–4 cerata per row. The posterior digestive branch contains up to six clusters of cerata, each containing 1–3 rows of cerata. Each row is composed of 1–3 cerata. The anteriormost cluster contains more rows of cerata, with more cerata per row. The density of both rows per cluster and cerata per row decreases posteriorly.

The genital apertures are located on the right side of the body ventral to the first and second or second and third ceratal rows. The pleuroproctic anus is situated within the interhepatic space, below the notum, immediately anterior to the anteriormost cerata of the right digestive branch. The nephroproct is located immediately anterodorsal to the anus. The anterior border of the foot (Fig. 2B) bears elongate foot corners that are held perpendicular to the longitudinal body axis, when the animal is actively crawling. The foot narrows posteriorly and terminates in an acutely pointed tail.

Buccal cavity. The thin, ovoid jaws (Figs. 2C, 3A) occupy much of the muscular buccal mass. They bear several rows of minute denticles on their elongate masticatory margin. From the anterior end of the buccal mass, a pair of elongate, highly digitate oral glands extends posteriorly within the laterally elevated tissue of the notum. The posterior limit of the glands is at the anteriormost cluster of cerata of the posterior digestive branches. A pair of elongate strap-like salivary glands joins the posterior end of the buccal mass near its junction with the esophagus. The triseriate radula, also contained within the buccal mass, has a formula of $24-31 \times 1.1.1$, in five specimens examined. The rachidian teeth (Fig. 3C, D) bear 6-8 elongate denticles on either side of the elongate central cusp. The central cusp is depressed ventrally below the level of the adjacent denticles. The teeth are broadly curved and deeply incised posteriorly. The posterior limbs of each tooth terminate in a posteriorly extended tubercle. The lateral teeth (Fig. 3B) are broadly triangular and bear an elongate primary denticle. The inner masticatory margin bears 9-11 irregular denticles.

Reproductive system. The arrangement of organs (Fig. 2D) is androdiaulic. The narrow preampullary duct expands into the ampulla and divides into the oviduct and vas deferens distally. The oviduct immediately expands into the



FIGURE 1. Living animals. A. Flabellina bertschi sp. nov., photograph of holotype. B. Flabellina marcusorum sp. nov., photograph of a paratype specimen from San Diego Reef, Baja California Sur, México.



FIGURE 2. Flabellina bertschi sp. nov. A. Lateral view of holotype showing arrangement of cerata, a = anus; ga = genital aperture; n = nephroproct; pc = pericardial hump; r = rhinophore, scale = 1 mm. B. Ventral view of holotype, scale = 1 mm. C. Jaw, scale = 0.2 mm. D. Reproductive system, alb = albumen gland; am = ampulla; me = membrane gland; mu = mucous gland; od = oviduct; pe = penis; pr = prostate; rs = receptaculum seminis, scale = 0.5 mm.

two ovoid lobes of the receptaculum seminis. The oviduct again narrows and enters the albumen gland, situated between the larger membrane and mucous glands. The vas deferens expands into a simply curved prostatic portion that terminates in the indistinct, conical penial papilla, which is devoid of any armature. The nidamental and penial apertures are united into a short common genital atrium. A bursa copulatrix is absent in the three specimens examined.

DISCUSSION. – Flabellina bertschi is sympatric with five other species of Flabellinidae: Flabellina telja Marcus and Marcus, 1967; F. stohleri Bertsch and Ferreira, 1974; F. iodinea (Cooper, 1863); and F. cynara (Marcus and Marcus, 1967). All possess perfoliate rather than smooth rhinophores. Flabellina marcusorum has strongly papillate rhinophores. None of these species has a white body with red cerata.

Flabellina bertschi is similar to two western Atlantic species in its external morphology. Fla-

bellina dushia (Marcus and Marcus, 1963) has smooth rhinophores, a whitish body, and orangebrown cerata, but it lacks an area of translucence posterior to the rhinophores, which characterizes all specimens of F. bertschi examined in this study. More significantly, the lateral radular teeth of F. dushia are thinner with a more acutely pointed cusp. Nothing is known about the reproductive anatomy of F. dushia. Flabellina verta (Marcus, 1970) also has smooth rhinophores, a whitish body, and brown digestive gland. However, it has opaque white lines on the oral tentacles that join and pass between the rhinophores, which are absent in F. bertschi. Its radula has only half as many rows of teeth as F. bertschi. Also, the reproductive system of F. verta lacks a receptaculum seminis, but has a bursa copulatrix adjacent to the genital atrium. In F. bertschi, there is a bilobed receptaculum seminis, but a bursa copulatrix is absent.

The only other described species that are known to possess a bilobed receptaculum seminis but lack a bursa copulatrix are *F. pedata* (Montagu, 1815) (see Schmekel and Portmann 1982: fig. 7.50e) and *F. albomarginata* (Miller, 1971). In *F. pedata* the body color is purple rather than white. In *F. albomarginata* the rhinophores are covered with small tubercles, and an opaque white line is present around the margin of the foot.

Flabellina marcusorum sp. nov.

(Figs. 1B, 4, 5)

- Coryphellina rubrolineata O'Donoghue, 1929:798; Marcus and Marcus 1961:224, figs. 1–10 (misidentification); Marcus and Marcus 1970:210, fig. 81 (misidentification).
- *Flabellina telja* Marcus and Marcus, 1967:223; Ferreira and Bertsch 1972:414, fig. 1 (misidentification); Kerstitch 1989: 66, fig. 154 (misidentification).

TYPE MATERIAL. – Holotype, California Academy of Sciences, San Francisco, CASIZ 066151, San Diego Reef (25°12'N, 110°42'W), s.e. of Isla San Diego, Gulf of California, México, 13 m depth, 24 July 1985, T. M. Gosliner. Paratypes, CASIZ 066152, six specimens, same date and locality as holotype. Paratypes, CASIZ 066153, two specimens, one dissected, Los Islotes (24°36'N, 110°24'W), Gulf of California, México, 10 m depth, 20 May 1985, Lynne Dunne.

OTHER MATERIAL. – Fifteen specimens, CASIZ 066154, Sayulita (20°52'N, 105°29'W), Nayarit, México, intertidal, 24 Jan. 1975, Gary McDonald. Three specimens, CASIZ 066155, two dissected, São Sebastião, Brazil, Eveline Marcus. One specimen, Arroyo San Carlos, Isla Cedros, Baja California, México, 4 m depth, 31 Dec. 1985, Hans Bertsch.

DISTRIBUTION. - Flabellina marcusorum has been collected from the Atlantic coast of Brazil



FIGURE 3. Flabellina bertschi sp. nov. Scanning electron micrographs of radula of a specimen from Puerto Peñasco. A. Masticatory border of jaw, scale = $10 \ \mu m$. B. Rachidian and lateral teeth, scale = $4 \ \mu m$. C, D. Rachidian teeth, scale = $4 \ \mu m$.



FIGURE 4. Flabellina marcusorum sp. nov. A. Lateral view, a = anus; ga = genital aperture; n = nephroproct; pc = pericardial hump; r = rhinophore, scale = 2 mm. B. Ventral view, scale = 1 mm. C. Rhinophore, scale = 0.5 mm. D. Jaw, scale = 0.2 mm. E. Reproductive system, alb = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; pe = penis; pr = prostate; rs = receptaculum seminis; v = vagina, scale = 1 mm.

(Marcus and Marcus 1961). On the Pacific coast of México, it has been found from Isla Cedros south to Sayulita, Nayarit (present study). Within the Gulf of California, it is known from San Agustín, Sonora, south to Los Islotes, north of La Paz, Baja California Sur.

ETYMOLOGY. – This species is named for Ernst Marcus and Eveline du Bois Reymond Marcus, who first recorded this species (as *Coryphellina rubrolineata*) from Brazil and the Gulf of California.

DESCRIPTION. - External morphology. The living animals (Fig. 1B) are 7-30 mm in length. The general body color is translucent rose pink. The oral tentacles, foot corners, rhinophores are rose basally, with purple pigment in their middle, and opaque white present on the apical portion. The oral tentacles have a wide band of purple, while the cerata bear only a narrow ring between the pink and white pigments. The pigment on the apices of the cerata may be yellowish rather than white, in some specimens. The rhinophores bear more purple pigment on their posterior face, where it covers most of the surface of the papillae. The anterior face of the rhinophores bears less purple pigment. The posterior end of the foot is also purple with an opaque white line or spot on its posterodorsal end. The digestive gland within the cerata is the same rose color as the rest of the body.

The rhinophores (Fig. 4C) are elongate (approximately 4 mm in length) and conical. They each bear approximately 100 long papillae on their posterior face. The papillae are approximately 0.5 mm in length and are arranged in somewhat indistinct rows, covering the middle two-thirds of the rhinophores. The oral tentacles are thin and elongate, tapering to a rounded apex. They are longer than the rhinophores.

The cerata are cylindrical and rounded apically immediately distal to the ovoid cnidosac. Within each ceras is a thin core of digestive gland that fills a variable portion of the diameter of the ceras. The cerata are arranged in distinct groups (Fig. 4A). Only the anterior cluster is slightly elevated from the notum. The anterior, precardiac cluster contains 3–5 rows of cerata on either side of the animal, with 2–4 cerata per row. The postcardiac cerata are arranged in 6–8 groups per side of the body. Generally, each group contains a pair of tightly packed rows with 2–4 cerata per row. Only the posteriormost 1–2 rows are unpaired and consist of a single row. The gonopore is situated on the right side of the body, ventral to the third and fourth ceratal rows of the precardiac cluster. The pleuroproctic anus is situated at the posterior end of the interhepatic space, just anterior to the first postcardiac ceratal row. The nephroproct is immediately anterodorsal to the anus.

The foot (Fig. 4B) is grooved anteriorly and possesses elongate, tentacular foot corners. Posteriorly, it tapers gradually to a narrow tail.

Buccal cavity. The buccal mass is short and muscular. Extending from the anteroventral portion of either side of the buccal mass is a large digitate oral gland, which extends into the widened portion of the notum in the region of the precardiac cerata. Within the buccal mass is a pair of large chitinous jaws (Fig. 4D). They are ovoid with an elongate masticatory margin (Fig. 5A). The margin bears several rows of denticles with 20-24 denticles on the outer row. The radular formula is $27-34 \times 1.1.1$. in six specimens studied. The rachidian teeth (Fig. 5B, C) are simply arched with 5-8 triangular denticles on either side of the elongate central cusp. The central cusp is approximately the same width as the adjacent denticles but is depressed ventrally from their level. The lateral teeth (Fig. 5B, D) are triangular in shape with a broad base extending towards the outer edge. There is a single prominent, acutely pointed apex. On the inner margin of the tooth is a series of 4-12 triangular denticles.

At the posterior limit of the buccal mass, near its junction with the esophagus, is a pair of elongate salivary glands that extend posteriorly on the dorsolateral surface of the stomach.

Reproductive system. The arrangement of reproductive organs is essentially triaulic (Fig. 4E). The ovotestis is a diffuse aggregation of distinct follicles. The female acini are distinct. The narrow preampullary duct widens into an ampulla consisting of two convolutions. The postampullary duct again narrows and passes between the lobes of the albumen and membrane glands. After a short distance it divides into the oviduct and vas deferens. After a short distance the oviduct joins a pair of receptacula seminis. The more proximal receptaculum is the larger of the two. The oviduct again narrows, and a short distance later enters the nidamental glands. At this branching point, a distinct, narrow vaginal duct continues towards the genital apertures. Imme-



FIGURE 5. Flabellina marcusorum sp. nov. Scanning electron micrographs. A. Masticatory border of a specimen from San Diego Reef, Baja California Sur, México. B. Rachidian and lateral teeth of specimen from São Sebastião, Brazil. C. Rachidian tooth of specimen from São Sebastião, Brazil. D. Lateral tooth of specimen from San Diego Reef, Baja California Sur. Scales = 10 μm.

diately prior to emptying into its own genital pore, it joins with a large saccate bursa copulatrix. The bursa is thin walled and short stalked. The nidamental glands comprise the bulk of the reproductive system. The mucous gland is by far the largest portion, while the albumen and membrane glands are smaller. The nidamental glands empty via their own gonopore, ventral to the vaginal and penial apertures. The vas deferens is initially quite narrow and expands into a smooth prostatic portion, which is slightly convoluted. The vas deferens enters the short penial sac at its distal end. The penial papilla is tubular and thin with a slightly flared apex. There is no armature associated with the penial papilla.

DISCUSSION. – Flabellina marcusorum was originally described from Brazil (Marcus and Marcus 1961) as Coryphellina rubrolineata O'Donoghue, 1929. Marcus and Marcus (1970) also misidentified specimens from the Gulf of California as C. rubrolineata. Flabellina marcusorum has also been misidentified as Flabellina telja Marcus and Marcus, 1967 by Ferreira and Bertsch (1972) and Kerstitch (1989). The latter species differs from F. marcusorum in having perfoliate rather than papillate rhinophores, and in several other major details of its external and internal anatomy.

Flabellina marcusorum and F. rubrolineata differ in several consistent aspects of their coloration. In Flabellina rubrolineata there is a middorsal and a pair of lateral red or purple lines along the length of the animal (O'Donoghue 1929; Baba 1955, pl. 13, fig. 37; Abe 1964, pl. 30, fig. 107; Willan and Coleman 1984, fig. 133; Tan, Pai, and Hsha 1987, fig. 52). These observations are confirmed by examination of specimens of F. rubrolineata from Aldabra Atoll and Madang, Papua New Guinea, in this study. Occasionally, the red or purple lines may be interrupted as in the case of the specimen illustrated by Willan and Coleman, but are present in all material observed. In F. rubrolineata the rhinophores are opaque white basally with apical purple pigment. The body color is a much deeper rose in F. marcusorum, and longitudinal lines are never present on the body. The rhinophores are purplish basally with an opaque white apex, the reverse of the colors in F. rubrolineata.

The number of radular rows and denticles on the radular teeth varies considerably in both species (Table 1). However, the shape of the rachidian teeth differs consistently between the two species. In *Flabellina marcusorum* the indentation of the posterior end of the tooth extends deeply, almost to the basal portion of the central denticles (Marcus and Marcus 1961; Fig. 5B, C). In *F. rubrolineata* (Fig. 6A–C), the indentation is rounded and does not extend as far forward, leaving a triangular chitinous area between the indentation and the basal portion of the denticles. The lateral teeth of *F. rubrolineata* (O'Donoghue 1929:fig. 219d; Fig. 6D) bear a series of striations along the middle of their outer edge, which are absent in all specimens of *F. marcusorum* that have been examined.

In their description of Flabellina marcusorum from Brazil, Marcus and Marcus (1961, as Coryphellina rubrolineata) depicted the reproductive anatomy in detail. Their specimens had a large spherical bursa copulatrix, but no receptaculum seminis. Our examination of Brazilian specimens provided by Eveline Marcus and from material collected from the Pacific coast of México indicates that all specimens do possess a bilobed receptaculum seminis near the branching of the oviduct. In addition, the reproductive system is entirely triaulic in all the material we examined. The only aspect of the reproductive anatomy of F. rubrolineata that has been described was the presence of an unarmed penis (O'Donoghue 1929). However, Dr. Kikutaro Baba provided dissection notes of a specimen of F. rubrolineata from Japan, and we dissected specimens from Papua New Guinea. Both species possess a triaulic arrangement of organs and two proximally situated receptacula seminis; however, their anatomy differs from that of F. marcusorum in two significant regards. The prostate of F. marcusorum is more elongate and convoluted than in F. rubrolineata. More importantly, the bursa copulatrix is small and sessile in F. rubrolineata, while it is well developed and stalked in F. marcusorum.

Generic Division within the Flabellinidae

The genus *Coryphellina*, with *C. rubrolineata* as the type species, was placed in synonymy with *Coryphella* (Miller 1971). More recently Gosliner and Griffiths (1981) considered *Coryphella*, including *Coryphellina*, as a junior synonym of *Flabellina*. This view has been generally adopted

		Caratal		Denticles	Decentracijum	Durron		
	Color	arrangement	Radular formula	rachidian	seminis	copulatrix	Locality	Reference
F. rubrolineata	3 longitudinal ver- million or crimson	6-8 groups	30–32 × 1.1.1.	6-7	1	I	Red Sea	O'Donoghue 1929
F. rubrolineata	mid-dorsal lines 3 longitudinal red lines, cerata with	5 rows 5 arches	30 × 1.1.1.	7–9	bilobed	I	Japan	Baba 1955, per- sonal communi-
F. rubrolineata	purple bands 3 longitudinal red- dish purple lines,	3 rows 4 arches	30 × 1.1.1.	68	bilobed	minute	Papua, New Guinea	cation present study
	body variously colored							
F. marcusorum	body orange, rhino- phores & cerata with purple & opaque white	3 rows 7 arches	27 × 1.1.1.	5-8	absent, bilobed in pres- ent ma- terial	elongate stalk	Brazil	Marcus 1961, present study
F. marcusorum	body pink orange, tentacles, cerata rhinophores with purple rings	11 groups	34 × 1.1.1.	7	1	I	Gulf of Cal- ifornia	Marcus and Mar- cus 1970
F. marcusorum	body pink, oral tenta- cles, rhinophores & cerata with pur- ple & opaque white	3–5 rows 6–8 double rows	31 × 1.1.1.	6-8	bilobed	elongate stalk	Pacific Mexico, Gulf of California	present study

TABLE 1. Comparative morphology of Flabellina rubrolineata and F. marcusorum.

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FIGURE 6. Flabellina rubrolineata (O'Donoghue, 1929). Scanning electron micrographs of specimen from Madang, Papua New Guinea. A. Dorsal view of half-row of radula. B. Dorsal view of rachidian tooth. C. Ventral view of rachidian tooth. D. Lateral tooth. Scales = $10 \ \mu m$.

TABLE 2. Morphological diversity in Flabellina.

	peduncles	cerata	rhinophores	anus	oral glands	central cusp	receptaculum seminis	bursa copulatrix	foot corners	reproductive system	lateral teeth	number of laterals	rhinophoral papillae
hypothetical													
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0
affinis	2	2	1	2	1	2	1	0	1	0	0	1	0
albomarginata	1	1	2	2	1	2	2	1	1	0	0	1	1
alisonae	2	2	3	2	1	1	1	0	1	0	0	1	0
babai	2	2	3	2	1	2	1	1	1	0	0	1	0
bertschi	1	1	0	2	1	2	2	1	1	0	0	1	0
browni	0	1	0	1	0	1	1	0	1	0	0	1	0
capensis	0	1	0	1	0	1	1	0	1	0	0	1	0
cynara	0	1	3	0	0	1	0	0	1	0	2	1	0
dushia	0	1	0	2	9	2	9	9	1	9	0	1	0
engeli	2	2	3	2	1	2	1	0	1	0	0	1	0
falklandica	0	0	0	0	9	1	9	9	1	9	0	1	0
funeka	2	2	1	2	1	2	1	0	1	0	0	1	0
fusca	0	0	1	1	0	1	1	0	1	9	0	1	0
gracilis	1	1	0	1	0	1	1	0	1	0	0	1	0
iodinea	1	2	3	1	0	1	3	0	1	0	2	1	0
islandica	0	0	0	1	0	0	0	0	0	0	0	0	0
lineata	0	1	0	1	0	1	1	0	1	0	0	1	0
marcusorum	1	2	2	2	1	2	2	1	1	1	0	1	2
nobilis	0	0	0	0	0	1	1	0	1	0	0	1	0
ornata	2	2	3	2	1	1	1	0	1	0	0	1	0
pedata	1	1	0	2	1	2	2	1	1	0	0	1	0
pellucida	1	1	0	2	1	2	2	1	1	0	1	1	0
poenicia	1	2	2	2	9	2	9	9	1	0	0	1	1
pricei	1	1	1	1	1	2	9	0	1	0	1	1	0
rubrolineata	1	2	2	2	1	2	2	0	1	1	0	1	2
salmonacea	0	0	0	0	2	0	3	0	0	0	0	1	0
telja	2	2	3	2	1	2	1	0	1	0	0	1	0
trilineata	1	1	1	1	1	1	1	0	1	0	0	1	0
verrucosa	0	0	0	1	0	1	1	0	1	0	0	1	0
verta	0	1	0	2	9	1	0	1	1	0	0	1	2
species 1	1	2	2	2	1	2	2	1	1	1	0	1	2
species 2	1	2	2	2	1	1	1	0	1	0	0	1	0

For all characters 9 = unknown

1.	peduncles	0 = absent, 1 = present, 2 = well elevated
2.	cerata	0 = congested, $1 = $ separate, $2 = $ single groups
3.	rhinophores	0 = simple, 1 = annulate, 2 = papillate, 3 = perfoliate
4.	anus	0 = posterior, $1 = $ middle of cluster, $2 = $ interhepatic space
5.	oral glands	0 = absent, $1 = ramified$, dorsal, $2 = simple$, ventral
6.	central cusp	0 = large, $1 = $ small, $2 = $ depressed
7.	receptaculum seminis	0 = serial, $1 = $ semiserial, $2 = $ bilobed, $3 = $ multilobed
8.	bursa copulatrix	0 = present, 1 = absent
9.	foot corners	0 = rounded, $1 = $ tentacular
10.	reproductive system	0 = diaulic, $1 = $ triaulic
11.	lateral teeth	0 = denticulate, $1 = $ smooth, $2 = $ denticulate on outer edge
12.	number of laterals	0 = 2-3, 1 = 1
13.	rhinophoral papillae	0 = absent, 1 = short, 2 = elongate

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FIGURE 7. Cladogram depicting preliminary phylogeny of Flabellina.

by virtually all opisthobranch systematists. The Flabellinidae is a morphologically diverse assemblage, containing primitive and derived taxa. Subdividing the family into genera is problematic, as there is a continuum of gradually adding derived features, sometimes with poor correlation of these characters. Cladistic analysis, employing Phylogenetic Analysis Using Parsimony (PAUP, by David Swofford), was conducted on all 33 species of Flabellinidae for which adequate morphological data are known, including three undescribed species. Polarity of characters was ascertained by using the Notaeolidiidae as the outgroup of the Flabellinidae. Thirteen characters were considered for 33 taxa. The characters and their distributions are included in Table 2.

Subsequent cladistic analysis produced six equally parsimonious trees of similar configuration and a length of 37 and a consistency index of 0.568, one of which is presented here (Fig. 7). The other five trees differ only in the placement of one or two taxa. All of these cladograms demonstrate that genera such as Flabellina and Corvphellina cannot be maintained without rendering Coryphella paraphyletic. Maintenance of these genera as distinct requires the erection of many new monotypic genera and higher taxa for more primitive members of the family. There are no autapomorphic features to support many of these taxa. This is clearly counterproductive and provides no further resolution of the phylogeny and classification of the Flabellinidae. From this analysis, it is apparent that most plesiomorphic members of the Flabellinidae are restricted to polar environments, with more derived taxa inhabiting temperate and tropical waters. Little adaptive radiation and speciation has occurred within primitive members of the family. Most speciation has occurred in the two clades that possess either perfoliate or papillate rhinophores. Accumulation of morphological data for species that are not well known, including additional undescribed taxa, will provide needed data for future re-evaluation of the generic divisions within the Flabellinidae.

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