

The Genus *Flabellina* Voigt, 1834 (Mollusca: Opisthobranchia) from Bahía de Banderas (Pacific Coast of Mexico) with Ecological Observations, the Description of a New Species, and the Redescription of *Flabellina cynara*

Sandra Millen¹ and Alicia Hermosillo²

¹ Department of Zoology, University of British Columbia, Vancouver, B.C., Canada, V6T 1Z4; Email: millen@zoology.ubc.ca; ² Universidad de Guadalajara, Centro Universitario de Ciencias Biológicas y Agropecuarias, Las Agujas, Zapopan, Jalisco, México; Email: alicia_hg@prodigy.net.mx.

Bahía de Banderas is located halfway down the Pacific coast of Mexico. Six sympatric species of the genus *Flabellina* have been found there, *F. cynara* (Marcus and Marcus, 1967), *F. telja* Marcus and Marcus, 1967, *F. bertschi* Gosliner and Kuzirian, 1990, *F. marcusorum* Gosliner and Kuzirian, 1990, *F. vansyoci* Gosliner, 1994 and *F. fogata* sp. nov., which is described here. The body color of *F. fogata* is semi-transparent red with a darker red digestive tract, the ceratal cores are bright fiery red with white opaque spots; rhinophores are irregularly and weakly annulate. The ecology of the six sympatric species was also studied with emphasis on seasonal patterns and habitats. This paper describes *Flabellina fogata*, its relationship with sympatric species and how it is distinguished from similar *Flabellina* species. In addition, new information on the anatomy of the incompletely described species, *Flabellina cynara* is given.

KEYWORDS: *Flabellina*, Flabellinidae, sympatric species, eastern Pacific, nudibranchs.

Resumen

Bahía de Banderas se localiza en la parte central de la costa del Pacífico mexicano. Seis especies simpátricas del género *Flabellina* se han encontrado ahí: *F. cynara* (Marcus y Marcus, 1967), *F. telja* Marcus y Marcus, 1967, *F. bertschi* Gosliner y Kuzirian, 1990, *F. marcusorum* Gosliner y Kuzirian, 1990, *F. vansyoci* Gosliner, 1994 y *F. fogata* sp. nov. descrita en este artículo. El color del cuerpo de *F. fogata* es rojo a blanco semi-transparente con un tracto digestivo más oscuro; los centros de los ceratas son rojo fuego con puntos opacos blancos; los rinóforos son irregular y débilmente anulados. La ecología de las seis especies simpátricas se estudió con énfasis en los patrones temporales y hábitat. En este artículo se describe *Flabellina fogata*, su relación con las especies simpátricas y cómo se distingue de otras especies de *Flabellina* similares. Adicionalmente, se da nueva información de la especie *Flabellina cynara* cuya descripción original es incompleta.

PALABRAS CLAVE: *Flabellina*, Flabellinidae, especies simpátricas, nudibranchs, Pacífico este.

Bahía de Banderas has been the subject of studies about the diversity of opisthobranch faunal composition (Sphon and Mulliner 1972; Bertsch et al. 1973; Ferreira and Bertsch 1975; Bertsch 1978, 1980; Bertsch and Kerstitch 1984). Hermosillo-González (2003) reported over 20 new dis-

tributional records for the bay. New species have recently been described for the area (Hermosillo and Valdés 2005; Gosliner and Bertsch 2004; Dayrat 2005). The composition is therefore well known but numerous species remain undescribed.

The family Flabellinidae has received considerable attention in the past 30 years (Miller 1971; Kuzirian 1979; Gosliner and Griffiths 1981; Gosliner and Kuzirian 1990; Gosliner and Willan 1991; Gosliner 1980, 1994). The phylogenetic and systematic relationships of the Flabellinidae have been examined by Gosliner and Kuzirian (1990) and from their analysis, it is apparent that the genus *Flabellina* contains numerous, morphologically diverse species. The morphological characteristics include a triserrate radula with a denticulate rachidian tooth and laterals; strong jaws, corners of the foot (propodial tentacles) are present and the anus is pleuroproct in position. This genus has varied rhinophore shapes and usually bright body and ceratal colors. There are over 54 species of this genus described for all temperate and tropical seas, and they are present in a variety of habitats: reefs, rocks, and sandy bottoms where hydroids are present.

There are 14 described species of the genus *Flabellina* known for the eastern Pacific (Berhens and Hermosillo 2005). Of these, eight have been reported in Mexico (Hermosillo et al. 2006). During monthly surveys for a three-year period, six species were found regularly in 10 representative localities within Bahía de Banderas: *F. bertschi* Gosliner and Kuzirian, 1990; *F. cynara* (Marcus and Marcus, 1967), *F. fogata* sp. nov., *F. marcusorum* Gosliner and Kuzirian, 1990, *F. telja* Marcus and Marcus, 1967 and *F. vansyoci* Gosliner, 1994. The seasonal variation, feeding and spawning of these species are presented. In this paper, we describe a new species *F. fogata* sp. nov. and provide a redescription with additional information on the anal position, radula, and reproductive systems of the sympatric species *Flabellina cynara* (Marcus and Marcus, 1967).

MATERIALS AND METHODS

Bahía de Banderas is located on the west coast of Mexico, in the states of Jalisco and Nayarit. Its large surface, over 1000 km², makes it the largest bay on the mainland Pacific coast of Mexico. Punta Mita and Cabo Corrientes, 42 kilometers apart, delimit Bahía de Banderas to the north and south, respectively. It has 115 km of coastline (Fig. 1). Bahía de Banderas is located in the intermediate zone from 18° to 28°N between the colder waters from the north, where the seasonal thermal variations are rather large, and the warmer waters from the south, where the variations are small.

Ten localities were monitored monthly from February 2002 to April 2005. Observation, survey, and collecting were done by SCUBA diving in the shallow subtidal (between the depths of 1 and 25 meters) with immersions of 75 to 150 minutes. Temperature and rainfall were monitored and a Kruskal-Wallis test was done to determine the presence of any significant seasonality.

Species observed were photographed *in situ* with a Nikon Coolpix 995 digital camera in an Aquatica housing, utilizing an onboard YS-30 Sea&Sea strobe and an INON slave strobe. For small specimens, a 5× wet lens was used. All were later photographed in an aquarium using a

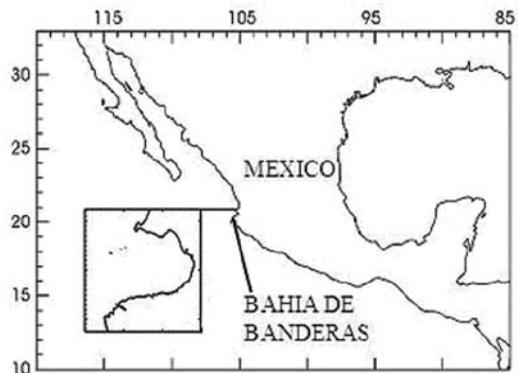


FIGURE 1. Map of Mexico with insert of Bahía de Banderas on the Pacific coast.

Nikon Coolpix 995 digital camera with two INON strobes; with white balance set to bright daylight. The color plate was prepared using Adobe Photoshop® 7.0, but the colors of the photographs were not corrected.

The specimens were relaxed in a 7% magnesium chloride solution in freezing sea water and preserved in 70% ethanol. We dissected the specimens by making a right lateral incision from back to front just above the foot. The internal features were examined and drawn using a dissecting microscope with a *camera lucida* attachment. The buccal mass was removed and placed in 10% sodium hydroxide until the radula and jaws were isolated from the surrounding tissue. The radula and jaws were then rinsed in water, dried, and mounted for examination. Scanning electron micrographs were made with a Hitachi S-4700FE SEM. Notes on the external features of the living animals were taken in the field under a dissecting microscope or a 10× magnification loupe.

SEASONAL WEATHER PATTERNS AT BAHÍA DE BANDERAS

Because of its tropical nature, the landmass around Bahía de Banderas does not have the four typical climatic land seasons but only two, at least which are obvious: (a) rainy season during the summer (June–November) and (b) dry season (December–May). The water temperature undergoes dramatic changes throughout the year, with the lowest temperatures in April and highest ones in September and August (approximately 17.7 to 30°C). The month with highest recorded rainfall is August with an average of 46.6 cm (average annual rainfall for the bay is 149.6 ± 16.3 cm).

A Kruskal-Wallis analysis for water temperatures and rainfall demonstrated that there were actually three significantly different ($p < 0.05$) climactic seasons within the bay (Fig. 2): (a) a dry-cold season (DC) February, March, April and May, during which the water temperature is the lowest (17.7 to 23.3°C) and there is little or no rainfall; (b) a wet-hot (WH) season

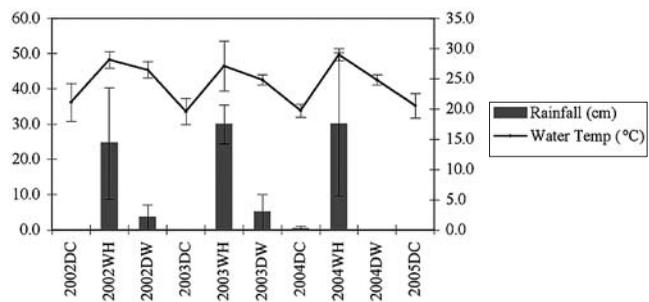


FIGURE 2. Water temperature and rainfall for Bahía de Banderas during the study period.

August, September and October, with high water temperatures (26.6 to 30°C) and monsoon-like rain, and (c) a dry-warm (DW) season in the months of November, December and January, when the rainy season is over or almost over and the water temperature remains warm (23.3 to 27.7°C). This pattern was observed consistently during the period of study (April 2002 to April 2005).

FLABELLINID DISTRIBUTION AND ABUNDANCE AT BAHÍA DE BANDERAS

Table 1 shows the accumulated abundance of each species observed from April 2002 to April 2005 in each of the 10 surveyed localities. Four of the six sympatric species constitute over 89% of the total of individuals of *Flabellina* recorded in Bahía de Banderas: *F. bertschi*, *F. cynara*, *F. marcusorum* and *F. telja*. These four species were present in all the survey sites. *Flabellina marcusorum* and *F. telja* are the most abundant species and together represent 63.9% of the individuals. They can occur in different localities and seasons possibly because both species appear to feed on several species of athecate hydroids, and this feeding flexibility may have enabled them to extend their feeding over a longer period. *Flabellina marcusorum* is consistently the most abun-

dant throughout its known geographic distribution (Camacho-García et al. 2005; Hermosillo et al. 2006).

FLABELLINID SEASONAL PATTERNS

We used the number of individuals registered by hour of search (individuals/hour) to determine which species showed a seasonal pattern, testing with Kruskal-Wallis for significance. When a significant

difference was found, a box-whisker plot and a multiple range test were used to find the groupings. The graph (Fig. 3) indicates species abundance and average water temperature (°C). A significant seasonal pattern ($p < 0.05$) was found for three of the species: *F. marcusorum*, *F. telja* and *F. vansyoci*. No pattern was observed ($p > 0.05$) for the other three: *F. bertschi*, *F. cynara* and *Flabellina fogata*. Prey was always athecate hydroids, usually attributable to the genus *Eudendrium*. Differences in shape and polyp color allowed the species to be readily distinguished in the field, but they were not formally identified because of the lack of expertise in the area.

Flabellina marcusorum exhibits an increase in abundance during WH, and diminishes in DW, with lowest abundance in DC and repeating the increase in WH. This means an increase in abundance occurs when water temperatures rise abruptly (approximately 5°C between May and June).

Flabellina telja was very abundant in 2002 and the first two seasons of 2003. Table 2 shows that the numbers diminished significantly during the rainy season (WH) and remained low in the rest of the study area. Iguana and Majahuitas were the sites with the greatest abundance of this species at the beginning of the study, both sites are close to rivers and streams. The rapid real estate

TABLE 1. Abundance of the six species of *Flabellina* in Bahía de Banderas.

	Amarradero	Pared	Torres	Iglesias	Majahuitas	Iguana	Arcos	Lindomar	Viuda	Escondido	Total individuals	Abundance accum.	% Abundance	% Accumulated
<i>F. marcusorum</i>	171	144	137	219	197	140	197	90	464	23	1782	1782	35.7	
<i>F. telja</i>	30	18	82	121	257	411	210	211	24	45	1409	3191	28.2	63.9
<i>F. bertschi</i>	6	66	54	21	26	27	279	29	215	9	732	3923	14.7	78.6
<i>F. cynara</i>	0	11	13	3	5	6	64	172	241	39	554	4477	11.1	89.7
<i>F. vansyoci</i>	0	87	0	0	1	0	1	4	199	88	380	4857	7.6	
<i>F. fogata</i>	0	1	10	0	0	1	125	0	0	0	137	4994	2.7	
Totals	207	327	296	364	486	585	876	506	1143	204	4994			
%	4.1	6.5	5.9	7.3	9.7	11.7	17.5	10.1	22.9	4.1				

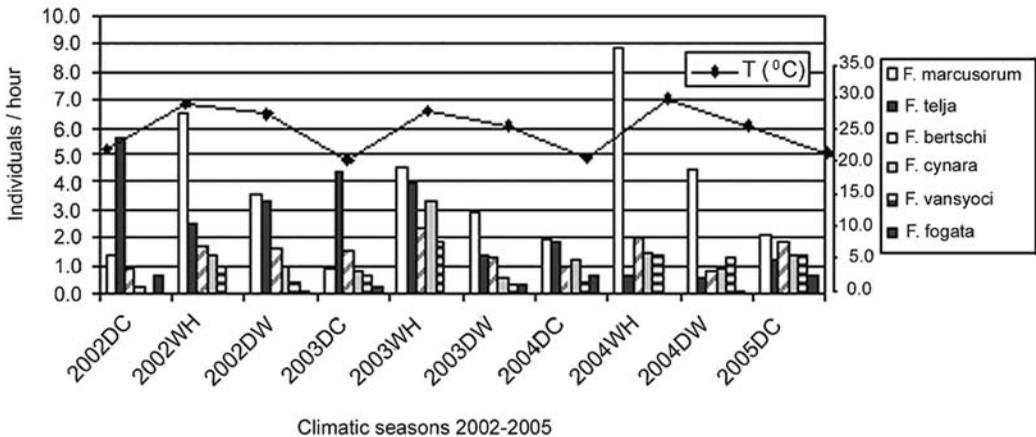


FIGURE 3. Abundances (individuals/hour) of *Flabellina marcusorum*, *Flabellina telja*, *Flabellina bertschi*, *Flabellina cynara*, *Flabellina vansyoci* and *Flabellina fogata*. Water temperature in °C.

TABLE 2. Natural history observations of the species of *Flabellina* in Bahía de Banderas.

	<i>F. marcusorum</i>	<i>F. telja</i>	<i>F. vansyoci</i>	<i>F. bertschi</i>	<i>F. fogata</i>	<i>F. cynara</i>
Known distribution	Gulf of California to Ecuador; Caribbean	Gulf of California to Galápagos	Gulf of California to Panamá	Southern California to Panamá	Bahía de Banderas	Gulf of California to Panamá
Distribution within Bahía de Banderas	10 sites	10 sites	Viuda, Pared, Escondido.	10 sites	Arcos	All except Amarradero
Type of spatial distribution	Usually solitary	Usually solitary	Gregarious	Gregarious	Gregarious	Usually solitary
Seasonal pattern	Yes, summer	Yes, winter	Yes, summer	No	Yes, winter	No
Depths	Shallow subtidal, below 1 m	Intertidal, shallow subtidal	Shallow subtidal, below 3 m	Subtidal below 10 m	Subtidal, below 15 m	Subtidal, below 4 m
Swimming capability	No	Yes, laterally bending the body	No	No	No	Yes, rowing its cerata
Prey	Athecate hydroid with white tentacles, purple-blue hydranths	Various species of athecate hydroids	<i>Eudendrium</i> sp. (bright orange)	<i>Eudendrium</i> sp. (red-orange) and others	<i>Eudendrium</i> sp. (red-orange)	Various species of athecate hydroids (including <i>Tubularia</i>)
Prey specific	No	No	Yes	No	Yes	No
Color of egg mass	Rose pink	Light pink	Rose pink	White	Orange	White

development in the south of the Bay (between old Vallarta and Cabo Corrientes, which encompass these sites) has resulted in deforestation and an increase in sediments being carried down to the ocean by runoff and rivers, particularly during the rainy season. These sediments suffocate filter feeding animals, such as hydroids. It is possible that the hydroid favored by *Flabellina telja* is more susceptible and the diminished numbers of *F. telja* could indicate that this hydroid has not recovered in these locations.

Flabellina vansyoci has its greatest abundance in the WH season. *Flabellina vansyoci* is strictly a specialist, only found feeding and living on one ramified atecathe hydroid, likely a *Eudendrium* sp., with bright orange polyps, which has a stable population throughout the year but a very localized presence. The presence of *F. vansyoci* is limited to the three sites where the hydroid is found: Escondido, Viuda and Pared.

For *Flabellina fogata* a clear, but not statistically significant ($p > 0.05$), seasonal pattern is observed, with no individuals recorded during DW. Their presence is recorded during DC (when the temperature is about 19°C) and diminishes at the beginning of WH, when the water temperature increases. The cycle is clearly defined, however the relative abundances were too small to show a statistical difference. This species seems to have a fast growth because sexually mature adults are observed even at the beginning of the cycle and only a few small juveniles are found. This fast growth has been reported previously for aeolids. Rudman (1979) relates this to species feeding on transitional prey, in this case one which is present only during the colder water months (DC). The fast growth of a large population allows the egg-laying to proceed while the food source is still available.

SPECIES DESCRIPTIONS

The key morphological features of the six sympatric species of the genus *Flabellina* observed regularly in Bahía de Banderas are listed in Table 3.

Family Flabellinidae Voight, 1834***Flabellina* Voight, 1834**TYPE SPECIES: *Flabellina affinis* (Gmelin, 1791) by monotypy.***Flabellina fogata* Millen and Hermosillo, sp. nov.**

Figures 4A, 5, 6.

ETYMOLOGY.— The word *fogata* means bonfire in Spanish and is given to this species because of its fiery red cerata.

MATERIAL EXAMINED.— HOLOTYPE: Los Angeles County Museum, LACM 30347, Los Arcos, Bahía de Banderas, Jalisco, Pacific coast of Mexico, 22 May, 2004, depth 19 m on hydroids collected by A. Hermosillo. PARATYPES: California Academy of Sciences, CASIZ 175007, 2 specimens, Los Arcos, Bahía de Banderas, 27 April, 2002, depth, 17 m on hydroids, collected by S. Millen. OTHER MATERIAL EXAMINED: 3 specimens, Los Arcos, Bahía de Banderas, 27 April, 2002, depth, 17 m on hydroids, collected by S. Millen.

EXTERNAL MORPHOLOGY.— This species is long and slender, slightly higher than wide and has a living length up to 15 mm (Fig. 4A). A typical preserved specimen measured $6 \times 2 \times 2.3$ mm ($l \times w \times h$). There is a small notal brim in the area of ceratal insertions which is discontinuous in the cardiac region. The rhinophores are irregularly and weakly annulate, with approximately 9 annulations, appearing knobby in preserved specimens. Rhinophores are cylindrical, gradually tapering to a blunt apex and measure up to 2.3 mm long. The body color of living animals is semi-transparent red to almost translucent white with a darker red digestive tract. The rhinophores and oral tentacles are the same as the body; the rhinophores are slightly darker towards their bases.

The ceratal cores are bright fiery red and terminate in pale, translucent white cnidosacs (Figs. 4A, 5B). The outer surface is translucent red, including over the cnidosacs. Spots of opaque white pigment are scattered evenly along the entire lengths of the cerata. The density of spots varies. The cerata are up to 1.5 mm long, cylindrical with pointed tips; they are inserted in clusters along the well-developed, notal brim (Fig. 5A). The anterior cluster contains 12–20 cerata in four to five rows that bifurcate ventrally. The post-cardiac clusters contain fewer cerata, in two arch-like bifurcating rows in the first few clusters, posteriorly there is one row. The rows never have more than four cerata. There are 4–7 posterior clusters with very small gaps between each cluster. Because the clusters bifurcate towards the outside, the cerata are almost continuous ventrally.

The head (Fig. 5C) is small and round with a small mouth. It is slightly narrower than the foot. The oral tentacles extend from the anterior-lateral corners and are parallel to the oral surface. The tentacles are short, stout and flattened ventrally, up to 0.75 mm in length, shorter than the length of the rhinophores.

The foot (Fig. 5C) is bilabiate and thickened anteriorly with a wide anterior notch and short, thick propodial tentacles. The foot is narrower than the body with a well-developed flange and ends in a short, bluntly tapered trailing portion.

The genital aperture (Fig. 5A) is located under the middle of the first ceratal cluster. The pleuroproctical anal opening is on a small conical papilla under the 1st or 2nd cerata of the first post-cardiac cluster. The renal opening is slightly in front of the anus and posterior in the inter-hepatic space.

DIGESTIVE SYSTEM.— The mouth has two small posterior-lateral clusters of labial glands. There are small pedal glands on the foot. There is a smooth cuticle over a small muscular ring in front of the jaws. There are no oral glands. The buccal mass is slightly longer than wide, oval and wider posteriorly. The radular sac projects a small distance posteriorly from the buccal mass. The jaws are pale yellow. The jaw shape (Fig. 5D) is a broad triangle with a small dorsal flange and

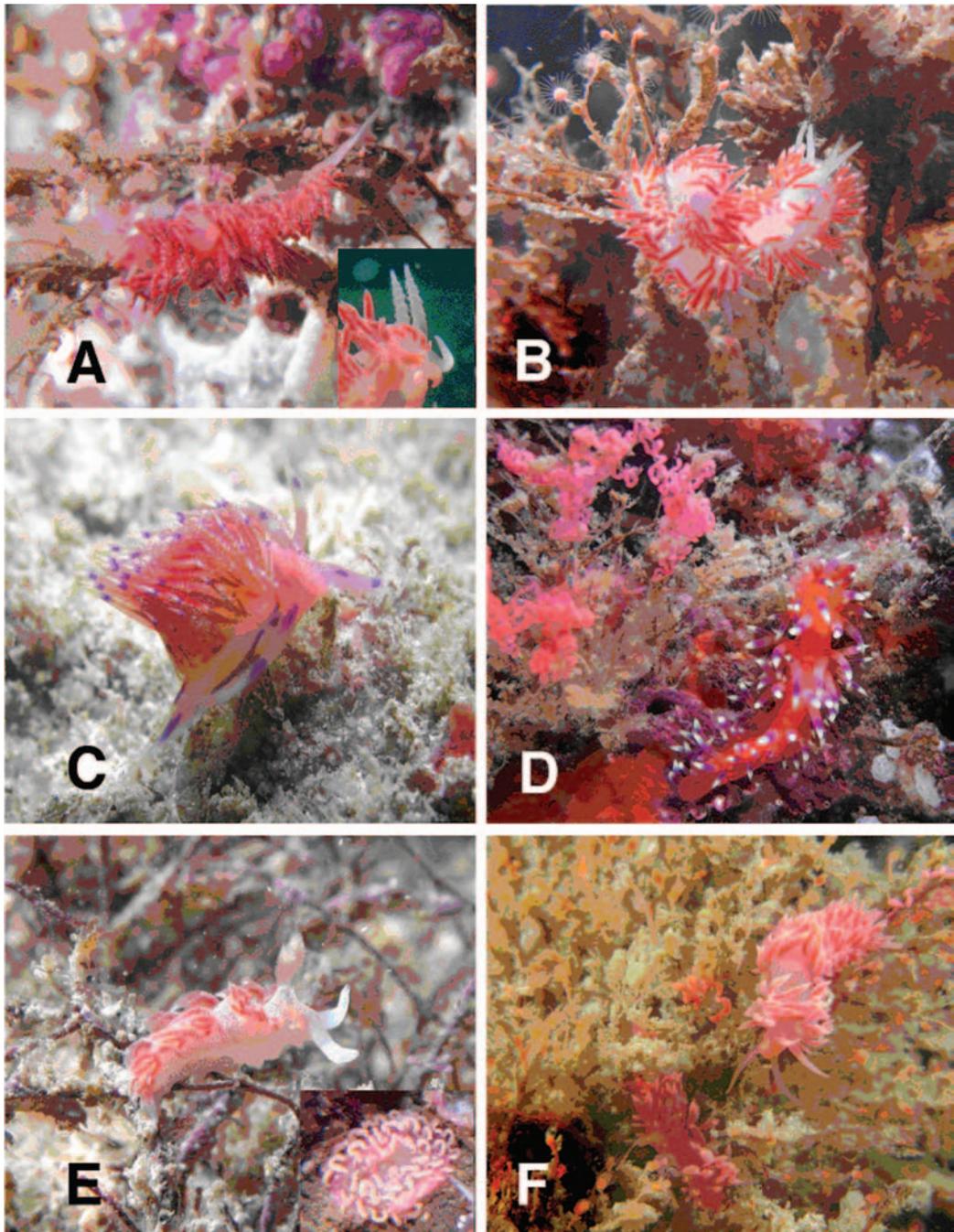


FIGURE 4. Living animals from Bahía de Banderas. A. *Flabellina fogata* sp. nov. Insert shows close up of head. B. *Flabellina bertschi*. C. *Flabellina cynara*. D. *Flabellina marcosorum* and spawn. E. *Flabellina telja*. Insert shows spawn mass. F. *Flabellina vansyoci* and spawn.

anterior articulatory knob. There is a well-developed masticatory flange bearing 2–5 rows of denticles, although only the outer row is well developed (Figs. 5D, 6A). The radula consists of 20–26 rows of teeth with the formula (1.1.1). The rachidian teeth (Figs. 5E, 6B) have a deeply incised base, long undepressed cusp and 5–7 denticles per side. The lateral teeth (Figs. 5E, 6B) are large, broad triangles with incised bases, slightly shorter on the inner edge. The inner edge is slightly curved and bears 11–17 denticles running from near the base almost to the tip.

The salivary glands are long and strap-like, orange in color and lie on either side of the stomach. They have a narrow duct, which enters the buccal bulb on either side of the ventral esophagus. The tubular esophagus is short, thin-walled, and wide. It enters a long, oval stomach. The right anterior hepatic duct has short branches, which bifurcate at the tips. The left anterior hepatic duct leaves the stomach slightly anterior to the right and has fewer cerata. The posterior hepatic duct runs ventral to the ovotestis. The short intestine curves down and up to a large anal papilla.

NERVOUS SYSTEM.— The central nervous system consists of large, fused cerebro-pleural ganglia lying close together. There are long stalks to large rhinophoral ganglia located in the bases of the rhinophores. The large eyes are almost sessile. The statocysts are large. The pedal ganglia are oblong, slightly smaller than the cerebropleurals and attached with a longer commissure. The oval buccal ganglia lie a short distance apart beneath the esophagus. They have small gastro-esophageal ganglia.

REPRODUCTIVE SYSTEM.— The reproductive system is illustrated in Figs. 5F, 6C–D. The ovotestis forms continuous clusters posterior to the stomach. The female ancini are peripheral to the larger male ancini. The latter are joined by small collecting ductules and eventually unite to form a hermaphroditic duct. This duct enlarges into an ampulla with one and a half coils. The

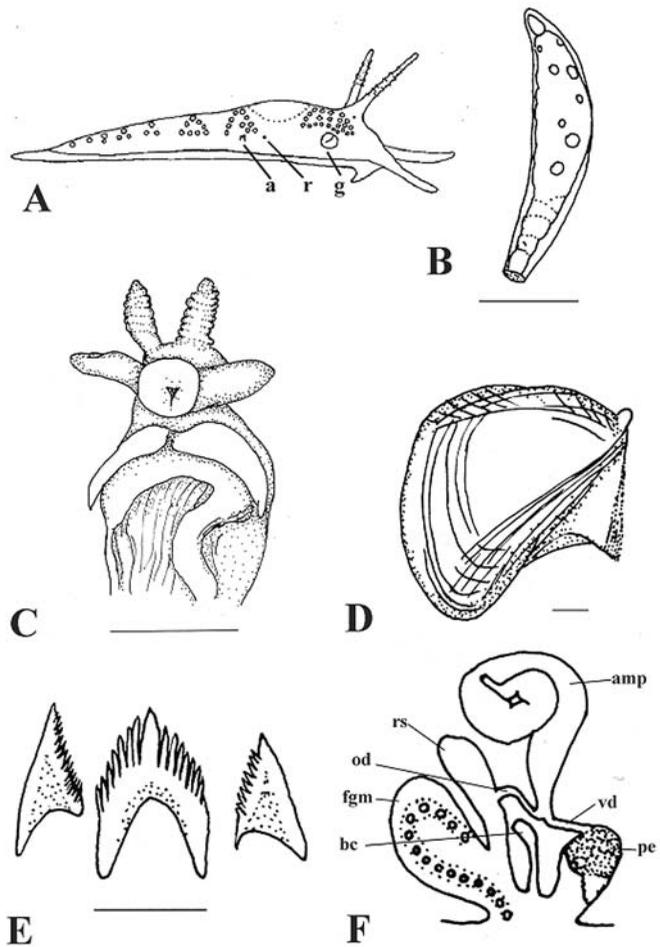


FIGURE 5. *Flabellina fogata* sp. nov. A. Right lateral view showing position of ceratal insertions. Stylized drawing. Key: a, anus; g, genital apertures; r, renal opening. B. Ceras showing opaque white spots. Scale bar = 0.5mm. C. Ventral view of head and foot. Scale bar = 1mm. D. One jaw. Scale bar = 0.1 mm. E. One row of radular teeth. Scale bar = 50 μ m. F. Stylized drawing of reproductive system. Key: amp, ampulla; bc, bursa copulatrix; fgm, female gland mass; od, oviduct; rs, receptaculum seminis; pe, penis; vd, vas deferens.

ampulla bifurcates into an oviduct and a vas deferens. The oviduct enters an elongate, serially arranged seminal receptacle. The distal oviduct enters the female gland mass at the albumen gland. There is a small, separate, long-stalked bursa copulatrix. The female gland mass has a large, creamy mucous gland, a white membrane gland and a central, granular albumen gland. The vas deferens is short and narrow. It enters a large penial bulb containing a bulbous, penis with glands proximally. Distally the muscular penis flares into a small disk and bears a row of short papillae (Fig. 6D). The male and female atria join a short distance before their common exit.

DISCUSSION OF *FLABELLINA FOGATA*.— Using the character set developed by Gosliner and Kuririan (1990), *Flabellina fogata* is a moderately derived flabellinid having external plesiomorphic features of a well-developed notal brim, and posterior anal placement. The cerata are in clusters, a moderately derived condition and the rhinophores have annulations. Internal plesiomorphic features are the lack of oral glands, presence of many rows of jaw denticles and a level rachidian cusp, although the latter is reduced in size from the elongate plesiomorphic condition. The reproductive system is apomorphic in that it has a stalked proximal bursa, a short vas deferens and a discoid penis containing proximal penial glands (Gosliner and Kuzirian 1990). This reproductive system is similar to that of *Flabellina trilineata* (O'Donoghue, 1921), which has annulate rhinophores and three white lines and *F. verta* (Marcus, 1970), which has smooth rhinophores. These two species, the former from the eastern Pacific, the latter from the Caribbean, appear to be close to this new species as are the eastern Pacific species *F. verrucosa* (Johnson, 1832) and *F. cooperi* (Cockereell, 1901) which have a similar leaf-like penis with papillae (personal observation). The bright red-orange body, combined with irregular rhinophoral annulations, distinguishes *Flabellina fogata* from these species and combined with the reproductive structures, from all other *Flabellina* species worldwide.

There are 14 described species of *Flabellina* known from the eastern Pacific (Behrens and Hermosillo 2005), all are markedly different from *Flabellina fogata*. Only five species have known distributions that overlap that of *F. fogata* (Table 3, Fig. 2). *Flabellina marcorum* has a purple-pink body with darker purple cerata with yellow cnidosacs. The rhinophores of this species are so distinct it cannot be confused with any other sympatric species: red colored, heavily papillate in the back and smooth in the front. *Flabellina bertschi* has red cerata like *F. fogata*, but the body is opaque white, the rhinophores are smooth, white colored and it is a small sized animal. *Flabellina vansyoci*, *F. telja*, *Flabellina cynara* and *F. fogata* have white spots on cerata and body, but these species can be easily separated from each other. *Flabellina vansyoci* can be reddish instead of its more usual rose-pink to purple and it also has white spots on the cerata, although the spots are larger, congested ones rather than fine dots. *Flabellina vansyoci* also has rugose markings on the rhinophores and the cerata are in clusters. Externally *Flabellina vansyoci* and *F. fogata* can be separated by the location of the anus, which is in the middle of the inter-hepatic space in *F. vansyoci* and posterior, under the first or second post-hepatic ceras in *F. fogata*. These two species can also be distinguished by their cnidosacs, which are translucent white in *F. fogata* and pink in *F. vansyoci*. Internally the radulae differ in that *F. vansyoci* has a depressed central cusp while *F. fogata* has an elevated cusp. *Flabellina fogata* lacks the large, compound oral glands found in *F. vansyoci*, which are visible as lateral white granulations in living animals. In the reproductive system, *F. vansyoci* has a trialuic system with two seminal receptacles and no bursa copulatrix, while *F. fogata* has a dialuic system with one seminal receptacle and a stalked bursa copulatrix. *Flabellina telja* is pale pink, has bulbous, heavily perfoliate rhinophores, thin, elongate oral tentacles, and bears white spots on the body as well as the cerata. *Flabellina cynara* is salmon-pink colored but unlike *F. fogata* it bears distinct purple markings on the foot, oral tentacles, and rhinophores; which are white and heavily perfoliate, and the cerata in the middle of the dorsum are longer than the

length of the animal and are on elevated peduncles.

There are nine, non-sympatric *Flabellina* species which can occur in the eastern Pacific. Eight of them lack white spots on the cerata. *Flabellina amabilis* Hirano and Kuzirian, 1991 is white with red-orange cerata and white cnidosacs but the rhinophores are smooth. *Flabellina japonica* (Volodchenko, 1937) and *F. islandica* (Odhner, 1937) also have smooth rhinophores

and continuous, not clustered, cerata. *Flabellina verrucosa* has verrucose rhinophores. *Flabellina trilineata* (O'Donoghue, 1921) has annulate rhinophores but can be distinguished by the three white lines on the body and stronger annulations on the rhinophores. *Flabellina triophina* (Bergh, 1894) has weakly annulate rhinophores, but a more elongate head and continuous cerata. *Flabellina iodinea* (Cooper, 1862) has heavily perfoliate rhinophores and cerata on pedicles. The dramatic purple, orange and red coloration is very different from *Flabellina fogata*. *Flabellina pricei* (MacFarland, 1966) has perfoliate rhinophores, cerata on pedicles and grey-white and yellow coloration that cannot be confused with *Flabellina fogata*. Only *Flabellina cooperi* has fine white spots on the cerata, but it has verrucose rhinophores and green ceratal cores that clearly distinguish it from the annulate rhinophores and red cerata of *F. fogata*.

All species with annulate rhinophores found worldwide, have recently been discussed by Millen and Hamann (2006). All species are clearly distinct from *Flabellina fogata*, the closest being *F. trilineata* from the Pacific, which has been discussed, and *F. dana* Millen and Hamann, 2006 from the Caribbean. *Flabellina dana* has a white body with a large opaque white mid-notal stripe and white sides. It lacks opaque white spots on the cerata and has a bulbous, tapering penis without glands (Millen and Hamann 2006; Millen 2007).

NATURAL HISTORY.— Known only in Bahía de Banderas, México at a limited number of sites, primarily Los Arcos (Table 1). It occurs at depths of 15–20 m. in small numbers, usually in the dry-cold season (Fig. 3). It appears to feed only on one species of *Eudendrium* with red-orange polyps (Table 2) upon which it lays a highly convoluted string of pink eggs, one per capsule. The spawn and prey hydroid are photographed in Hermosillo et al. (2006, sp. #188, pg.16).

Flabellina bertschi Gosliner and Kuzirian, 1990

Figure 4B.

MATERIAL EXAMINED.— 1 specimen, Los Arcos, Bahía de Banderas, Jalisco, 26 April 2002, collected by S. Millen, rock wall on hydroids.

REMARKS.— We found that the external morphology of the present material agrees with the original description except that a small, discontinuous notal brim was found and only the anterior cluster of cerata appeared to be raised. Internally this species was as described. The penis was small and conical within an elongate, glandular sheath.

NATURAL HISTORY.— This species is found from southern California to Panama and through-

TABLE 3. External characteristics of the six species of *Flabellina* from Bahía de Banderas.

Species	Rhinophores	Ground color	Color of cerata	Living size (mm)
<i>F. marcusorum</i>	Red, papillate posteriorly	Bright pink	Pink, purple and yellow	Up to 20
<i>F. telja</i>	Yellow or brown, perfoliate	Light pink, white spots	Brownish pink	Up to 24
<i>F. vansyoci</i>	Pink, verrucose	Rose pink	Rose pink, white spots	Up to 15
<i>F. bertschi</i>	White, smooth	White	Reddish pink, white tip	Up to 8
<i>F. fogata</i>	Translucent orange, annulate	Translucent orange	Red with white spots	Up to 15
<i>F. cynara</i>	White with purple tips, perfoliate	Pink with purple markings	Salmon and purple, white spots	Up to 12

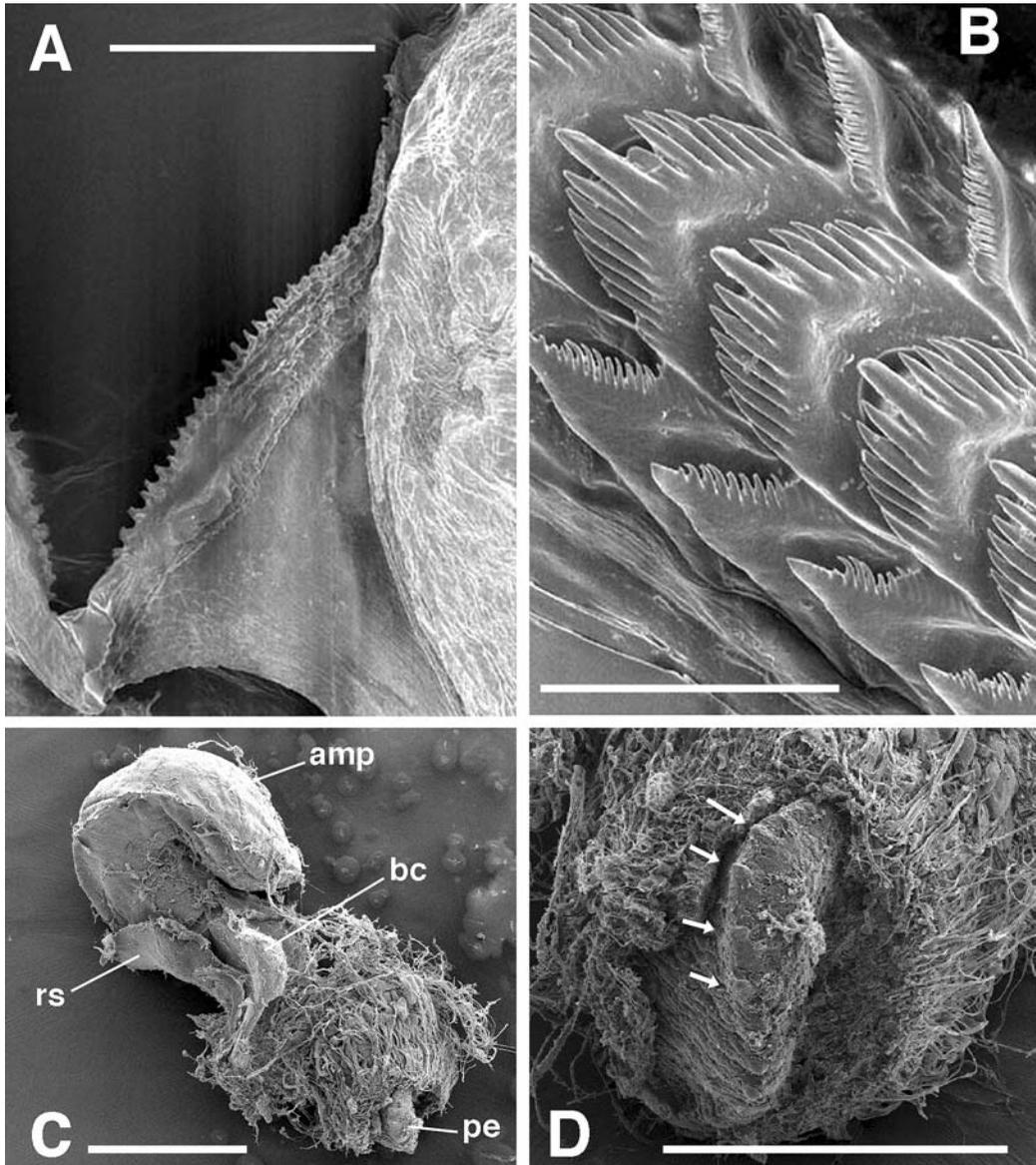


FIGURE 6. Scanning electron micrographs of *Flabellina fogata* sp. nov. A. Masticatory flange of a jaw. Scale bar = 100 μ m. B. Radular teeth. Scale bar = 50 μ m. C. Reproductive system. Scale bar = 500 μ m. Key: amp, ampulla; bc, bursa copulatrix; rs, receptaculum seminis; pe, penis. D. Close up of the penis, arrows indicate papillae. Scale bar = 300 μ m.

out Bahía de Banderas (Table 1). It occurs at depths of 10 m. or deeper, in great abundance throughout the year, with no significant season, but a slight peak in the wet-hot season (Fig.3). It feeds primarily on a species of *Eudendrium* with red-orange polyps (Table 2) upon which it lays a highly convoluted string of white eggs. The spawn and prey hydroid are photographed in Behrens and Hermosillo (2005, sp. #229, p. 105)

***Flabellina cynara* (Marcus and Marcus, 1967)**

Figures 4C, 7, 8.

MATERIAL EXAMINED.— 2 specimens, Sept 27, 1987 Isla Coronado, Bahía de los Angeles, Baja California, Mexico, collected by H. Bertsch. 3 specimens March 11, 1993, Panama, collected by A. Hermosillo, 2 specimens, May 4, 2002, Los Arcos, Bahía de Banderas, collected by A. Hermosillo. 2 specimens June 13, 2003, Bajo de la Viuda, Bahía de Banderas, collected by A. Hermosillo.

EXTERNAL MORPHOLOGY.— The external anatomy is illustrated by Marcus and Marcus (1967, fig. 71). The preserved animals examined ranged in length from 5–16.5 mm with cerata in the largest specimen up to 12 mm long. The width slightly exceeds the height. The body is wide in front and truncates abruptly into a narrow trailing portion. The rhinophores are perfoliate with up to 29 leaves extending most of their length, meeting at a thin line anteriorly and posteriorly. The cerata are lanceolate with narrow smooth cores and small cnidosacs. They are set onto slightly raised areas with a scalloped outer notal brim. There is one large, sloping pre-cardiac cluster and at least 8 post-cardiac clusters. In a 13 mm animal, the anterior cluster had 9 rows of 2–5 cerata, the posterior clusters had successively fewer rows and cerata per row.

The head is round with a vertical mouth and is narrower than the foot. The oral tentacles are long, lanceolate and only slightly flattened, originating parallel to the oral surface. The tentacles are longer than the rhinophores.

The foot is distinctly separate from the propodial tentacles, which have a bilabiate anterior margin with a wide gap in the upper lip. The split extends the full length of the propodial tentacles, which are slightly shorter than the width of the foot. The foot has a wide flange and abruptly tapers posteriorly into a pointed trailing portion, which has a slight dorsal crest.

The genital opening is posterior beneath the first ceratal cluster. Due to the length of this cluster, the genital opening is just anterior of the mid-part of the body. The renal opening is interhepatic and high on the side. The anus is far posterior, between the second and third post-cardiac clusters. Because of the scalloping nature of the notal flange, the anus appears hidden between the ceratal clusters, although it is located high on the side and not on the notal brim and therefore is pleuroproct in position.

DIGESTIVE SYSTEM.— Labial and oral glands are absent. The buccal mass is short and deep with a round lip disk against the yellowish brown jaws. The long masticatory margin is darker than the jaws. The jaws are as illustrated by Marcus and Marcus (1967, figs. 72–73, p. 222). The long radular sac points downward. Inside there is a thin, dark shelf leading to the infolded, tubular esophagus, which is also dark due to a chitin lining on the interior. The radula (Fig. 7A) had 16–19 rows of teeth. The rachidian teeth have a small elevated cusp and 5–11 denticles per side, with some denticles fused to the central cusp. The shape is as illustrated by Marcus and Marcus (1967, fig. 74). The narrow laterals had between 7 and 16 inner denticles. On some teeth no outer denticles were seen, on others 1–7 tiny denticles were present (Fig. 7B). The small salivary glands are short and sausage shaped. The long esophagus leads to a large, oval stomach. The two anterior hepatic ducts exit far back on the stomach, the posterior hepatic duct runs dorsal to the ovotestis. The intestine is large and long, ending on a small anal cone.

NERVOUS SYSTEM.— The central nervous system has fused cerebro-pleural ganglia with large rhinophoral ganglia located just below the rhinophores. Two nerves leave each ganglia. The eyes are large and almost sessile. The small, oval, pedal ganglia are ventral with a visceral loop. The ganglia are very knobby with large ganglionic clusters, making the statocysts impossible to discern. The buccal commissure is only slightly longer than the visceral loop with two large, close together, buccal ganglia each with a small gastro-esophageal ganglion.

REPRODUCTIVE SYSTEM.— The reproductive system (Figs. 7C–D, 8) consists of an ovotestis

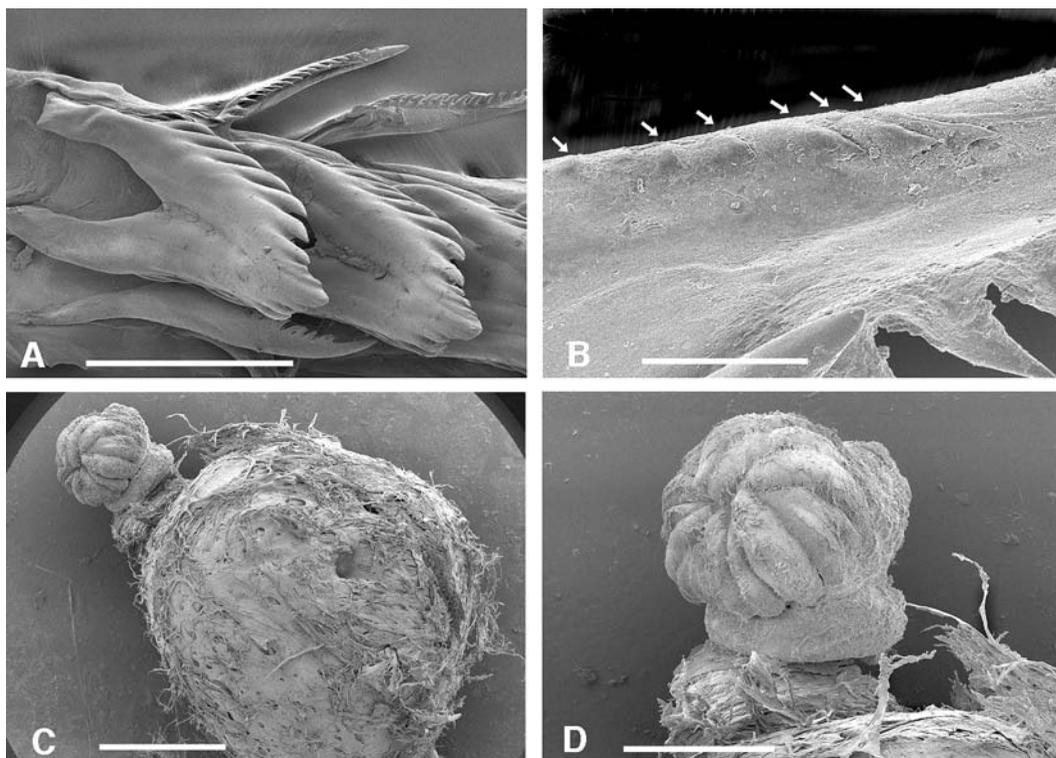


FIGURE 7. Scanning electron micrographs of *Flabellina cynara* (Panama). A. Central and lateral teeth. Scale bar = 200 μm . B. Lateral tooth showing large inner and small outer denticles, indicated by arrows. Scale bar = 20 μm . C. Internal, muscular atrium and everted penis. Atrium has a slice and pinhole on right (dissected specimen). Scale bar = 1 mm. D. Closer view of everted penis and warty preputium. Scale bar = 500 μm .

with large lobes. The peripheral female ancini with solitary eggs are sessile on the sacular male ancini. Each lobe has a small ductule, which joins to form the hermaphroditic duct. The hermaphroditic duct swells into a tubular, highly folded ampulla, then narrows slightly into a post-ampullary duct which distally divides into an oviduct and vas deferens. The narrow oviduct lies on the female gland mass and runs dorsally where two long ducts from tubular receptaculum seminis are inserted. These ducts twist around each other and terminate in two barely enlarged sacs. The oviduct loops ventrally and enters the female gland mass at its entrance to the atrium. The female atrium is large and striated, with an internal shelf-like cushion near its exit and a large chamber behind the cushion. The female gland mass does not have a separate duct but empties into the side of the atrial chamber. It is not large and is highly convoluted. The vas deferens swells a little into a tubular prostatic portion, which is smooth on the outside, although when full of sperm may be irregular in shape. The prostate forms a few loops and enters the large penial atrium. Inside this atrium there is fibrous tissue around the vas deferens, which ends at the base of an attached projection on the atrial wall (Fig. 7C). As the atrium everts, the preputium is folded and warty with a posterior groove leading to the opening of the vas deferens as illustrated by Marcus and Marcus (1967, fig. 75). As it expands, the warty preputium becomes inflated and globular and the posterior opening to the vas deferens everts to form a small, convoluted penial disk (Fig. 7D).

NATURAL HISTORY.— This species is found from the Gulf of California to Panama and throughout Bahía de Banderas (Table 1). It occurs at depths of 4 m. or greater in small numbers

throughout the year, with no significant season, but a slight peak in in the wet-hot season which was pronounced in 2003 (Fig. 3). It feeds on a variety of hydroid species (Table 2). The white spawn mass has been observed but not illustrated.

DISCUSSION OF *FLABELLINA CYNARA*.—

This distinctive species was described from Puerto Peñasco, Sonora, Mexico by Marcus and Marcus (1967). It has since been photographed many times, and its swimming behavior, noted in the original description, has been described in detail by Farmer (1970). Gosliner and Kuzirian (1990) in their cladogram character set added that the anus was posterior and the lateral teeth had both internal and external denticles. Gosliner (1991) in his discussion of a similar species, *F. iodinea* stated that the anus in *F. cynara* was situated in the posterior half of the body. We concur with this; the original description had mistaken the nephroproct for the anus. We also found tiny external denticles on some of the lateral teeth, which are illustrated here for the first time (Fig. 7B).

The general outline of the reproductive system is the same as that compiled by Marcus and Marcus (1967) from serial sections (fig. 75, p. 222). A number of details differ. The irregularity of the prostate is not granular, but only appears so when the contents are not evenly distributed. The warty preputum was not completely everted to show the small disk around the vas deferens, and the duct illustrated by them is actually a groove formed as it exits in a folded state. The long oviduct with its two tubular receptacula is noted here for the first time. The female gland mass is correctly shown as entering a large atrium which has a projecting cushion and a large chamber. This is unusual, but a similar situation is found in at least two other species, *Flabellina iodinea* and *Flabellina triophina* (personal observation). The chamber was interpreted to be a sessile bursa copulatrix by Marcus and Marcus for *F. cynara* and by Gosliner (1991) for *F. iodinea*. It is difficult to know if the striated chamber is homologous to the normal thin walled, balloon-like, bursa copulatrix or if it is simply an area to allow the large, discoid penis found on these three species a place to insert. However, the discoid penis of *Flabellina falklandica* (Eliot 1907) or *F. verrucosa* does not appear to require a similar chamber (personal observation).

***Flabellina marcusorum* Gosliner and Kuzirian, 1990**

Figure 4D.

MATERIAL EXAMINED.— 1 specimen, Majahuitas, Bahía de Banderas, 27 April, 2002, collected by S. Millen. 1 specimen, Los Arcos, Bahía de Banderas, 4 May, 2002, collected by S. Millen. 1 specimen, Los Arcos, Bahía de Banderas, 5 May, 2002, collected by S. Millen.

REMARKS.— The materials examined agrees with the overall species description, however, we observed some color variations. Some specimens are darker, with an orange tint to the overall color.

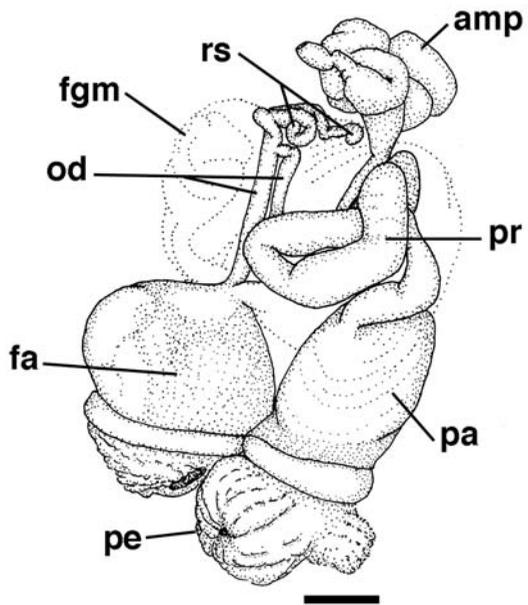


FIGURE 8. *Flabellina cynara* (Panama). Camera lucida drawing of the reproductive system. Scale bar = 0.5 mm. Key: amp, ampulla; fa, female atrium; fgm, female gland mass; od, oviduct; pa, penial atrium; pe, penis; pr, prostatic portion of vas deferens; rs, receptaculum seminis.

In those specimens, the cnidosacs are bright yellow and they have an opaque yellow region on the dorsum. A small notal flange was observed. Internally the anatomy fit the published description. The color pattern leaves no doubt regarding the identity of the species.

NATURAL HISTORY.— This species is found from the Gulf of California to Ecuador, and the Caribbean. It is found throughout Bahía de Banderas (Table 1). It occurs at depths of 1 m. or greater, in large numbers throughout the year, and with a significant seasonal increase in the wet-hot season and decrease in the dry-cold (Fig. 3). It feeds on a variety of hydroid species, but particularly an athecate hydroid with white tentacles and dark purple-blue hydranths (Table 2). The highly convoluted, bright rose-pink spawn mass is illustrated for the first time in Fig. 4D.

Flabellina telja Marcus and Marcus, 1967

Figure 4E.

MATERIAL EXAMINED.— 2 specimens, Majahuítas, Bahía de Banderas, 27 April, 2002, collected by S. Millen. 1 specimen, Islas Marietas, Bahía de Banderas, 29 April, 2002, collected by S. Millen.

REMARKS.— This species was reviewed by Gosliner (1994) and was synonymised with *Flabellina stohleri* Bertsch & Ferreira, 1974. The material we examined agrees with the description of Gosliner (1994). We observed variation in the color of the rhinophores, which can be light yellow, pink or brown. The density of the white spots on the body and cerata also varies among individuals.

NATURAL HISTORY.— This species is found from the Gulf of California to Ecuador and throughout Bahía de Banderas (Table 1). It occurs in the intertidal and shallow subtidal in large numbers throughout the year. There is a significant seasonality, with a peak in the dry-cold season with numbers declining in the wet-hot and dry-wet seasons. Total numbers reduced during the study period (Fig. 3). It feeds on a variety of hydroid species (Table 2). The tightly coiled, light pink spawn mass is illustrated for the first time in the insert in Fig. 4E.

Flabellina vansyoci Gosliner, 1994

Figure 4F.

MATERIAL EXAMINED.— 2 specimens, Paraíso Escondido, Bahía de Banderas, 17 June, 2003, collected by A. Hermosillo.

REMARKS.— The material examined agrees with the species description. A small notal brim was seen on this species.

NATURAL HISTORY.— This species is found from the Gulf of California to Panama but only in specific sites in Bahía de Banderas. It occurs in the subtidal at depths of 3 m or greater, in large numbers throughout the year. There is a significant seasonality, with a peak in in the wet-hot season and a slight decline in the dry-wet season (Fig. 3). It feeds on a bright orange athecate hydroid species, probably a *Eudendrium* sp., which is only found in isolated colonies in sites with rock walls and high energy. The dark rose-pink spawn mass and hydroid are illustrated in Hermosillo et al. (2006, species # 187, p. 115) and in Fig. 4F.

DISCUSSION

Cladograms of the Family Flabellinidae have been produced by Gosliner and Kuzirian (1990) and Gosliner and Willan (1991). These deal with four of the species of *Flabellina* found in Bahía de Banderas. They consider *Flabellina telja*, *F. marcusorum* and *F. bertschi* to be highly derived, but members of different clades, and *F. cynara* to be moderately derived. *Flabellina cynara* still

has the wider than high body shape adapted to soft bottom habitats but has a more derived reproductive system than basal flabellinids. Based on the characters used by Gosliner and Kuzirian (1990), *Flabellina vansyoci* is a derived species. The four most derived species found in Bahía de Banderas are *F. bertschi*, *F. marcusorum*, *F. vansyoci* and *F. telja*. They lack a notal brim, have oral glands and depressed cusps on the central teeth. *Flabellina telja* has cerata on high pedicles and the clade containing *F. bertschi*, *F. marcusorum* and *F. vansyoci* all have the derived feature of two seminal receptacles as does the more basal *F. cynara*.

Flabellina fogata is moderately derived (personal observation). *Flabellina fogata* has a shortened and wider prostate, as do the more derived species but its clustered cerata, notal brim, elevated cusps on the central teeth and lack of oral glands indicate that it is more basal. It appears to be closest to *F. verrucosa* and *F. cooperi* on the basis of its general anatomy and leaf-like, papillate penis and close to *F. trilineata* due to its penial glands and annulate rhinophores.

ACKNOWLEDGMENTS

The fieldwork for this paper was completed with the support of Roberto Chavez Arce and Buceo Vallartech, ITMAR No. 6, and the Universidad de Guadalajara. We also thank the Department of Zoology and the Bio-Imaging Facility of the University of British Columbia. And, lastly, we gratefully acknowledge the contributions of Hans Bertsch, Kirstie Kaiser, Roberto Chavez, and Pedro Medina for their assistance in the field work and for critical reviews of the manuscript.

LITERATURE CITED

- BEHRENS, D.W., AND A. HERMOSILLO. 2005. *Eastern Pacific Nudibranchs: A Guide to the Opisthobranchs from Alaska to Central America*. Sea Challengers, Monterey, California, USA. 137 pp.
- BERTSCH, H. 1978. The Chromodoridinae nudibranchs from the Pacific coast of America – Part II. The genus *Chromodoris*. *The Veliger* 20:307–327.
- BERTSCH, H. 1980. A new species of *Bornella* from tropical West-America. *Spixiana* 3:33–42.
- BERTSCH, H., A.J. FERREIRA, W.M. FARMER, AND T.L. HAYES. 1973. The genera *Chromodoris* and *Felimida* (Nudibranchia: Chromodorididae) in tropical west America: distributional data, description of a new species, and scanning electron microscopic studies of radulae. *The Veliger* 15:287–294.
- BERTSCH, H., AND A. KERSTITCH. 1984. Distribution and radular morphology of various nudibranchs (Gastropoda: Opisthobranchia) from the Gulf of California, México. *The Veliger* 26:264–273.
- CAMACHO-GARCIA, Y., T.M. GOSLINER, AND A. VALDÉS. 2005. *Field Guide to the Sea Slugs of the Tropical Eastern Pacific*. California Academy of Sciences, San Francisco, California, USA. 129 pp.
- DAYRAT, B. 2005. Advantages of naming a new species under the PhyloCode: an example of how a new species of Discodorididae (Mollusca, Gastropoda, Euthyneura, Nudibranchia, Doridina) may be named. *Marine Biology Research* 1:216–232.
- FARMER, W. 1970. Swimming gastropods (Opisthobranchia and Prosobranchia). *The Veliger* 13:73–89.
- FERREIRA, A.J., AND H. BERTSCH. 1975. Anatomical and distributional observations of some opisthobranchs from the Panamic Faunal Province. *The Veliger* 17:323–330.
- GOSLINER, T.M. 1980. The systematics of the Aeolidacea (Nudibranchia: Mollusca) of the Hawaiian Islands, with descriptions of two new species. *Pacific Science* 33:37–77.
- GOSLINER, T.M. 1991. Four new species and a new genus of opisthobranch gastropods from the Pacific coast of North America. *The Veliger* 34:272–290.
- GOSLINER, T.M. 1994. New records of Flabellinidae (Opisthobranchia: Aeolidacea) from the tropical Americas, with descriptions of two new species. *Proceedings of the California Academy of Sciences*, ser. 4, 48(9):171–183, figs. 1–10.
- GOSLINER, T.M., AND H. BERTSCH. 2004. Systematics of *Okenia* from the Pacific Coast of North America

- (Nudibranchia: Goniodorididae) with descriptions of three new species. *Proceedings of the California Academy of Sciences*, ser. 4, 55(22):414–430.
- GOSLINER, T.M., AND R.J. GRIFFITHS. 1981. Description and revision of some South African aeolidacean nudibranchia (Mollusca, Gastropoda). *Annals of the South African Museum* 84:105–150.
- GOSLINER, T.M., AND A.M. KUZIRIAN. 1990. Two new species of Flabellinidae (Opisthobranchia: Aeolidacea) from Baja California. *Proceedings of the California Academy of Sciences*, ser. 4, 47:1–15.
- GOSLINER, T.M., AND R.C. WILLAN. 1991. Review of the Flabellinidae (Nudibranchia: Aeolidacea) from the Tropical Indo-Pacific, with the descriptions of five new species. *The Veliger* 34:97–133.
- HERMOSILLO-GONZÁLEZ, A. 2003. New distributional records of opisthobranch mollusks for Bahía de Banderas, Mexico (Tropical Eastern Pacific). *The Festivus* 35:21–28.
- HERMOSILLO, A. AND Á. VALDÉS. 2005. Two New Species of Dorid Nudibranchs (Mollusca, Opisthobranchia) from Bahía de Banderas, Pacific Coast of Mexico. *Proceedings of the California Academy of Sciences*, ser. 4, 55:550–560.
- HERMOSILLO, A., D.W. BEHRENS, AND E. RÍOS JARA. 2006. *Opisthobranchios de México. Guía de babosas marinas del Pacífico, Golfo de California y las islas oceánicas*. Dirección de Artes Escénicas y Literatura, Universidad de Guadalajara, Guadalajara, Mexico. Publicación de CONABIO. 143 pp.
- KUZIRIAN, A. 1979. Taxonomy and biology of four New England coryphellid nudibranchs (Gastropoda: Opisthobranchia). *Journal of Molluscan Studies* 45:239–261.
- MARCUS, EV., AND ER. MARCUS. 1967. American opisthobranch mollusks. *Studies in Tropical Oceanography, University of Miami* 6:139–155.
- MILLEN, S.V. 2007. Notes on *Flabellina dana* Millen and Hamann, 2006 from the Caribbean. *Proceedings of the California Academy of Sciences*, ser. 4, 58:241–242.
- MILLEN, S.V., AND J.C. HAMANN. 2006. A new nudibranch species, Genus *Flabellina* (Opisthobranchia: Aeolidacea) from the Caribbean with redescriptions of *F. verta* (Marcus, 1970), and *F. dushia* (Marcus & Marcus, 1963). *Proceedings of the California Academy of Sciences*, ser. 4, 57:925–936.
- MILLER, M.C. 1971. Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the families Flabellinidae and Eubranthidae from New Zealand waters. *Zoological Journal of the Linnean Society of London* 50(4): 311–337.
- RUDMAN, W.B. 1979. The ecology and anatomy of a new species of aeolid opisthobranch mollusk; a predator of the scleractinean coral *Porites*. *Zoological Journal of the Linnean Society of London* 65:339–350.
- SPHON, G.G., AND D.K. MULLINER. 1972. A preliminary list of known opisthobranchs from the Galápagos Islands collected by the Ameripagos Expedition. *The Veliger* 15:147–152.