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Coeloplana waltoni, a new species of minute benthic ctenophore (Ctenophora: Platyctenida) from south Florida

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Abstract.—A minute and abundant species of benthic ctenophore is described, resurrected from an unpublished manuscript of Frederick M. Bayer (deceased). It is an ectosymbiont of octocorals in south Florida. Members of the ctenophoran order Platyctenida were unknown from American waters until 1945, when specimens from Miami, Florida were reported by F. G. Walton Smith and referred to the genus *Coeloplana*. That species subsequently was found in Jamaica, and Rankin (1956) described it under the new generic name *Vallicula*. A second species of creeping ctenophore was found in the 1960s and rediscovered in 2011, living as an ectosymbiont on octocorals in the coastal waters near Miami. This species belongs to the original genus *Coeloplana* and is here described as *Coeloplana waltoni*, new species. This description is based on specimens examined by F. M. Bayer in the 1960s and additional material from collections obtained in 2012–2013. Critical differences between *C. waltoni* and *Vallicula multiformis* are noted, based on recently collected specimens of the latter in Biscayne Bay, Miami, Florida.

Keywords: ectosymbiont, Florida, platyctenid ctenophore, subtropical western Atlantic

In 1880, the Russian zoologist A. Kowalevsky reported the discovery of a remarkable planariform ctenophore from the Red Sea, to which he gave the name *Coeloplana metschnikowii*. In the ensuing 70 yr, additional species of these peculiar creeping ctenophores were discovered in various parts of the Indo-Pacific region, in particular, Japan and Southeast Asia, and several related genera were described. These are *Ctenoplana* Korotneff (1886), which retains vestiges of ctenes in the adult stage and is able to swim as well as to creep in the manner of *Coeloplana*; *Gastrodes* Korotneff (1888) (because of its double homonymy, i.e., with two previously named taxa bearing this name, it was later renamed *Gastra* Stechow, 1921, see also Stechow 1923), an internal parasite in salps which is so modified that it was at first not recognized as a ctenophore; *Tjalfiella*, a sessile form living upon the pennatulid *Umbellula* off Greenland and first reported by Mortensen (1910); *Planoctena*, from Southeast Asian waters, a genus extremely close to *Ctenoplana*, established by Dawydoff (1936); the remarkable *Lyroc-*

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teis from Japan, a giant among the Platyctenida, first found in 1896 but formally named by Komai (1941) who recognized its true affinities; and, finally, the curious genus *Savangia*, which has six tall, tuberculate aboral papillae and resembles a nudibranch mollusk, described from the China Sea by Dawydoff (1950). It is noted that *Gastrodes* and *Gastra* are not listed in Mills (1998); however, in Mills' updated log (2014) *Gastrodes komai* Dawydoff, 1937 is listed as a junior synonym of *Lampea komai* (Dawydoff, 1937).

No representatives of the Platyctenida were known from American waters until 1945, when some translucent, creeping, flatworm-like animals collected from seawater aquaria at Miami by W. H. Sutcliffe, Jr., were recognized by F. G. Walton Smith (1945), Marine Laboratory (now Rosenstiel School of Marine and Atmospheric Science), University of Miami, and reported as a species of *Coeloplana*. These metazoans proved to be abundant in Biscayne Bay, living on algae and colonies of the arborescent ctenostome bryozoan *Zoobotryon*. Regrettably, no opportunity to study them in detail presented itself, and the species remained undescribed systematically until 1956 when J. J. Rankin (1951, 1956) published an account of some specimens found in Jamaica. For these, she established the new genus *Vallicula*, based upon the shape of the tentacular sheaths, nature of the aboral papillae, presence of oral grooves, and position of the body when detached from the substrate and floating freely. There is no doubt of the identity of the Jamaican animals when compared with those reported from Florida (Walton-Smith 1945). The new species described herein, by virtue of its smooth aboral surface, seems more similar to the original *Coeloplana* than do any of the species subsequently ascribed to this genus.

Materials and Methods

This description of a new species of *Coeloplana* is based on two sets of collections, the first studied by F. M. Bayer in the 1960s, and a second series of collections obtained in 2012 and 2013. The early collection examined in this study (USNM 52454) contains several specimens adhering to octocoral branches from Soldier Key, upper Florida Keys. This collection was made by F. M. Bayer on 10 October 1960 and was fixed in Bouin's solution; it is in excellent condition. Recent collections (2012–2013) have followed the conditions and provisions outlined in the Special Activity License (No. SAL-12-1365-SR), Florida Fish and Wildlife Conservation Commission.

Branch clippings from various octocoral species inhabiting the upper Florida Keys and off Dania Beach, Florida were cut with scissors underwater to lengths of 10–20 mm. Bayer's (1961) monograph was used to identify octocoral species. Sampling was confined to the higher peripheral branches of colonies in order to minimize injury. Each branch was sealed in a water-filled polypropylene bag and transferred to a 20-liter bucket. The bag mouths were opened to facilitate circulation. The branches were then transported to the laboratory under continuous aeration where they were examined microscopically. Live animals collected off Dania Beach (22 July 2013) were observed and photographed with a Leica MZFLIII dissecting microscope fitted with a Carl Zeiss camera attachment. Three video clips showing full body views of the ctenophore (MVI_0780), close up views of symbiotic flatworms (MVI_0784), and a clip of a specimen moving slowly over an octocoral host (MVI_0791) are available as supplementary material. Specimens were carefully removed with forceps in order to avoid damage or collected while floating freely at the water's surface. Specimens were relaxed for 2 h in isotonic $MgSO_4$ and

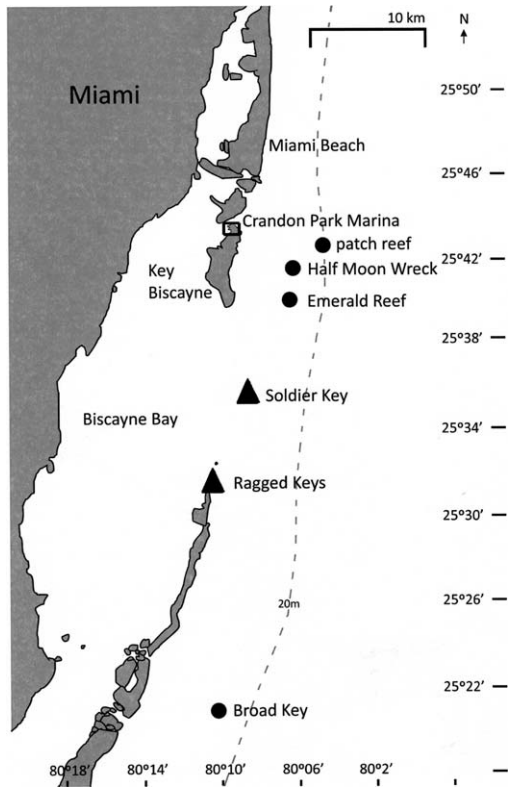

Fig. 1. Map of upper Florida Keys showing collection sites of *Coeloplana waltoni*. Triangles = 1960s, circles = 2012–2013. *Vallicula multiformis* was collected at Crandon Park Marina, Key Biscayne (open rectangle).

preserved in 70% and 95% ethanol or fixed in 2% glutaraldehyde in 0.05 M sodium cacodylate buffered sea water. The alcohol-preserved specimens would be suitable for molecular analysis. Site locations and additional information for recent collections of *Coeloplana waltoni* and *Vallicula multiformis* are contained in Figure 1 and Table 1. The sites of two collections of *C. waltoni* made near the pier at Dania Beach, about 30 km north of Miami Beach, are not shown in Figure 1.

Abbreviations: UMML, University of Miami Marine Laboratory (now the Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami); USNM, United States National Museum (now the National Museum of Natural History (NMNH), Smithsonian Institution.

Systematics

Order Platyctenida Bourne, 1900

Family Coeloplanidae Willey, 1896

Diagnosis.—Creeping or sessile ctenophores, ctene rows absent in adults. Tentacles, with tentilla, retractable into sheaths. Meridional canals branched and anastomosed. Pharynx permanently everted; statocyst present and aboral; body length <6 cm.

Coeloplana Kowalevsky, 1880

Diagnosis.—With the features of the family and often with a high host specificity. May or may not have an oral groove; can form temporary chimneys.

Coeloplana waltoni, new species

Figs. 2–6

Material examined.—*Coeloplana waltoni*. **1960s**: The following information is taken from F. M. Bayer's unpublished manuscript. Several specimens living on the gorgonian *Eunicea palmeri* Bayer, 1961 collected at Soldier Key, Biscayne Bay, Florida, 10 Oct 1960, by F. M. Bayer, fixed in Bouin's. One specimen prepared as a whole-mount on a slide. Twelve specimens, up to 4 mm in length, preserved in ethanol (USNM 52454). Several specimens living on various gorgonians, including *Eunicea palmeri* Bayer, 1961, *Eunicea tourneforti* Milne Edwards & Haime, 1857, *Plexaurella dichotoma* (Esper, 1791), Ragged Keys, Biscayne Bay, Florida, Sep 1964, collected by F. M. Bayer, J. J. McClelland, and Samuel Stout; fixed in Bouin's. Four prepared as a whole-mount on one slide; one serially sectioned. Paratypes. Several specimens living on various gorgonians, Ragged Keys, Biscayne Bay, Florida, Sep 1964, collected by John A. Jones and R. J. Daly; preserved in formalin. Paratypes. Several specimens living on gorgonians,

Table 1.—Benthic ctenophore collection information, *Coeloplana waltoni* and *Vallicula multiformis* Rankin, 1956, southeast Florida, 2012–2013. Numbers (*n*) of individuals denote those found on one to three, 10–20 cm-long branches of microhabitat. Values in brackets under Microhabitat denote wet settled volumes of algae sampled.

Date	Species	*n*	Microhabitat	Location	Latitude, Longitude
18 Feb 2012	*Coeloplana waltoni*	30	*Gorgonia ventalina* Linnaeus, 1758	Broad Key	25°20′01.96″N, 80°12′25.17″W
	C. waltoni	35	*Plexaura homomalla* (Esper, 1792)		
	C. waltoni	11	*Pseudoplexaura porosa* (Houttuyn, 1772)		
11 May 2012	–	0	*Pseudopterogorgia acerosa* (Pallas, 1776)	Emerald Reef	25°39′27.95″N, 80°07′43.34″W
	C. waltoni	>48	*Eunicea tourneforti* Milne Edwards & Haime, 1857		
	–	0	*Pseudopterogorgia acerosa*		
	–	0	*Pseudopterogorgia hystrix* Bayer, 1961		
	C. waltoni	1	*Gorgonia ventalina*		
24 Oct 2012	*Vallicula multiformis*	3	*Acanthophora spicifera* + clumps unidentified macroalgae [6 liters, 0.4 liters]	Crandon Park Marina	25°43′32.07″N, 80°09′19.04″W
16 Nov 2012	–	0	*Pterogorgia* sp.	Patch Reef	25°43′35.28″N, 80°05′46.6″W
	–	0	*Plexaurella nutans* (Duchassaing & Michelotti, 1860)		
	–	0	*Eunicea laciniata* Duchassaing & Michelotti, 1860		
	–	0	*Eunicea calyculata* (Ellis & Solander, 1786)		
	–	0	*Gorgonia ventalina*		
16 Nov 2012	–	0	*Pterogorgia* sp.	Half Moon Wreck	25°43′38.61″N, 80°08′04.08″W
	C. waltoni	11	*Eunicea laciniata*		
20 Feb 2013	*V. multiformis*	10	Filamentous green algae, *Enteromorpha* sp. [6 liters]	Crandon Park Marina	25°43′32.07″N, 80°09′19.04″W
27 Feb 2013	*V. multiformis*	2	Filamentous green algae, *Enteromorpha* sp. [2.5 liters]	Crandon Park Marina	25°43′32.07″N, 80°09′19.04″W
20 Mar 2013	*V. multiformis*	1	Clumps of unidentified algae	Crandon Park Marina	25°43′32.07″N, 80°09′19.04″W
12 Apr 2013	–	0	*Pseudopterogorgia bipinnata* (Verrill, 1864)	Half Moon Wreck	25°43′38.61″N, 80°08′04.08″W
	–	0	*Pseudopterogorgia acerosa*		
	–	0	*Pseudoplexaura porosa*		
	–	0	*Eunicea succinea* (Pallas) forma *plantaginea* (Lamarck, 1815)		
14 May 2013	*C. waltoni*	3	*Plexaura flexuosa* Lamouroux, 1821	Dania Beach	26°03′30.0″N, 80°06′31.5″W
	C. waltoni	12	*Muriceopsis flavida* (Lamarck, 1815)		
	C. waltoni	3	*Eunicea palmeri* Bayer, 1961		
22 Jul 2013	–	0	*Plexaurella nutans*	Dania Beach	26°03′25.7″N, 80°06′32.4″W
	–	0	*Gorgonia ventalina*		
	C. waltoni	3	*Muricea muricata*		
	C. waltoni	4	*Eunicea succinea*		
	C. waltoni	4	*Eunicea calyculata*		
	C. waltoni	6	*Muriceopsis flavida*		

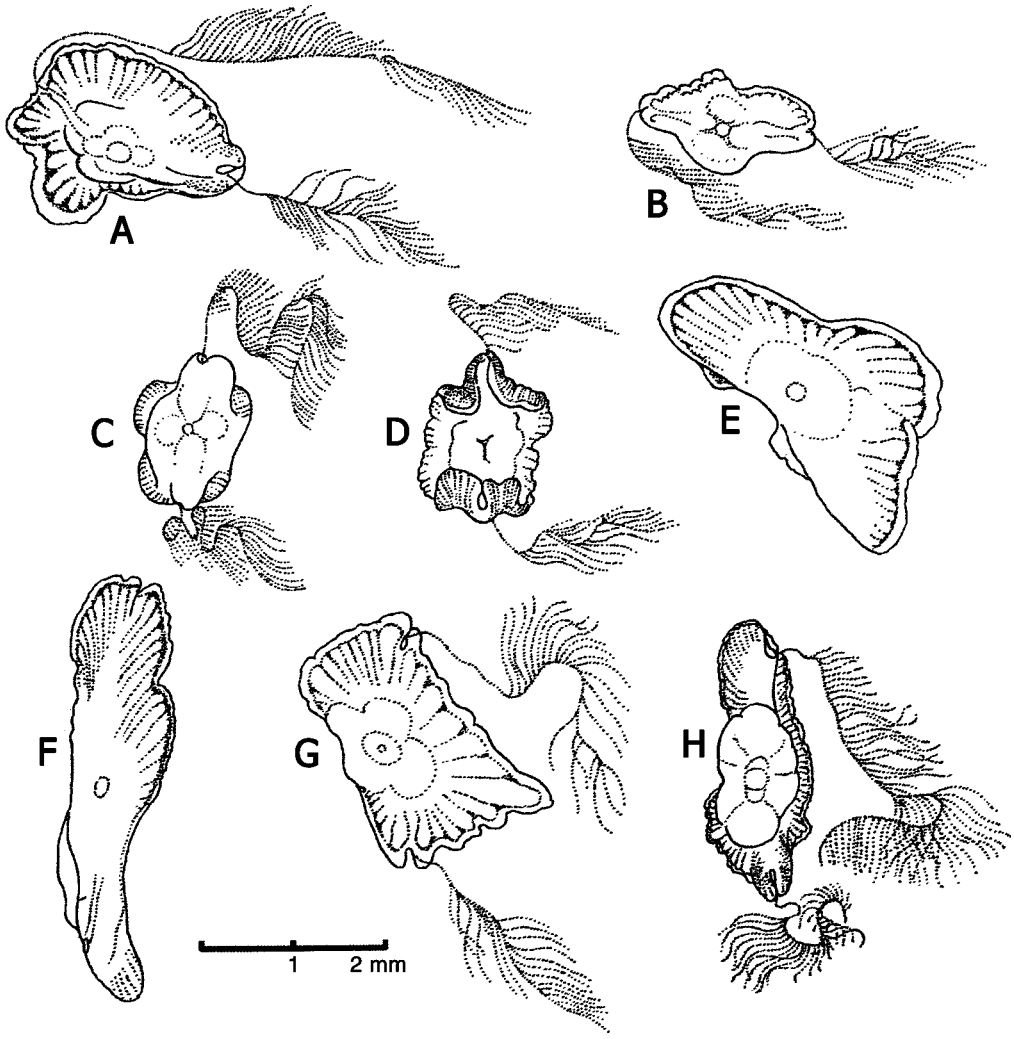

Fig. 2. *Coeloplana waltoni*. Live animal outline sketches. A, attached and resting; B–D, floating free; E–H, attached and creeping. Centrally located statocyst is visible in aboral views (A–C, E–G), the mouth is visible in D, H. The long pinnate tentacles are visible in A–D, G, H. Drawings by F. M. Bayer.

Ragged Keys, Biscayne Bay, Florida, 22 Oct 1964, collected by R. J. Daly and R. E. Gore; preserved in Zenker's.

2012–2013: Re-examination of specimens collected at Soldier Key, Florida (USNM 52454). Several specimens living as ectocommensals on *Muriceopsis flavida* (Lamarck, 1815), 2–3 m depth off Dania Beach, 22 Jul 2013, collected by J. Levy and B. Coffman. One specimen selected as the holotype (USNM 1222176). Two specimens selected as paratypes (USNM 1222177). Several specimens living as ectocommensals on *Muriceopsis flavida*, 2–3 m depth off Dania Beach, 14 May 2013, collected by B. Coffman. Two specimens, slides A and B, paratypes (USNM 1222178). Several specimens living as ectocommensals on *Muriceopsis flavida*, 2–3 m depth off Dania Beach, Florida, 14 May 2013, collected by B. Coffman. Three specimens selected as paratypes (UMML 9.1). One specimen from *Muriceopsis flavida*, 2 m depth, off

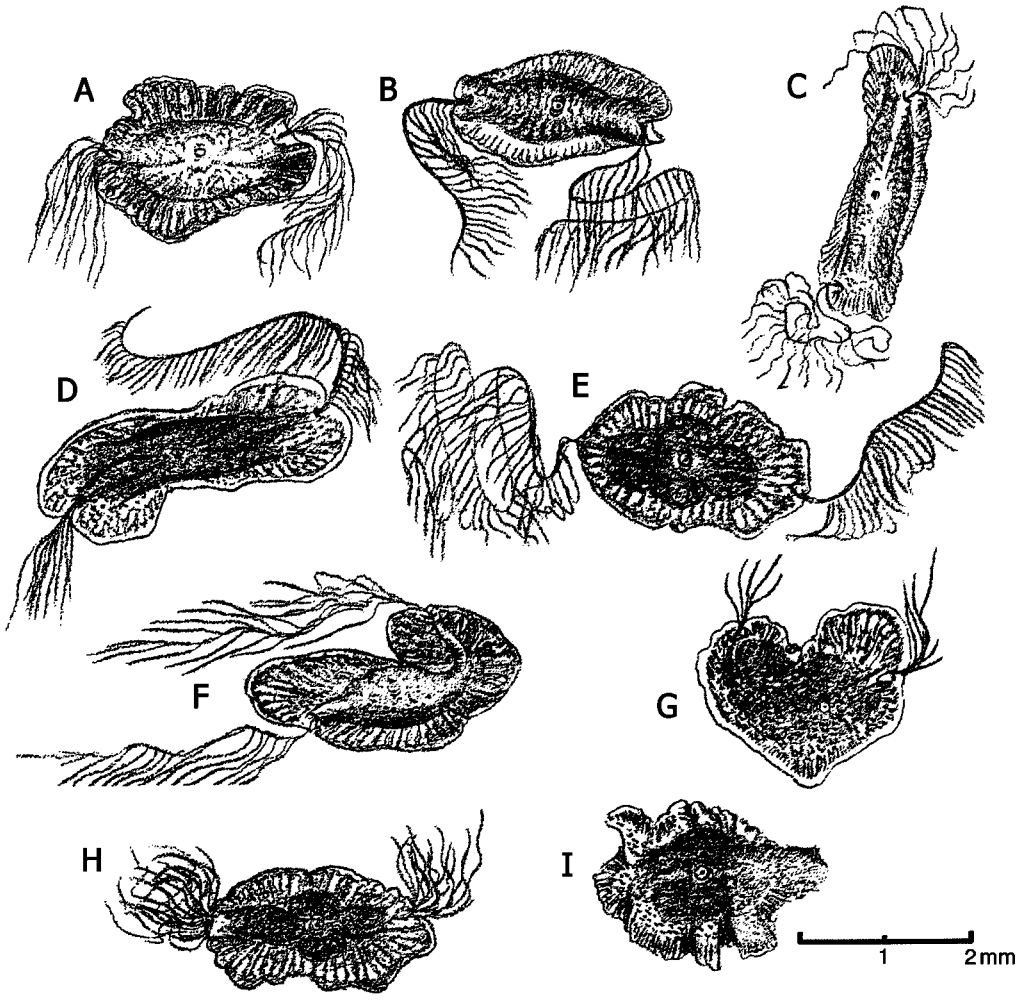

Fig. 3. *Coeloplana waltoni*. Aboral views of live specimens with tentacles in various degrees of extension (A–F) and retraction (G–I), and illustrating the disposition of pigmentation. Smooth, non-papillate upper surface and mid-body thickening along tentacular axis are evident. Drawings by F. M. Bayer.

Dania Beach, Florida, 14 May 2013, collected by B. Coffman; serial longitudinal sections, slides A4 and A5, paratype (UMML 9.2).

Other material examined.—*Vallicula multiformis* Rankin, 1956. **2012–2013**: Crandon Park Marina, Biscayne Bay, Florida, mixed macroalgal assemblages (*Acanthophora spicifera* predominant), suspended from boat slips, 0.1–0.4 m depth, collected by J. Levy and P. W. Glynn, 24 Oct 2012, one specimen selected for study (UMML 9.4); 20 Feb 2013, *Enteromorpha* sp. predominant, collected by J. Levy, 8 specimens selected for study (UMML 9.3). Site location and numbers of specimens collected are noted in Figure 1 and Table 1.

Description.—The newly designated holotype and paratype specimens collected in 2012–2013, both living and preserved individuals, were compared critically with F. M. Bayer's original description and illustrations in his unpublished manuscript of material examined in the 1960s with additional new information noted.

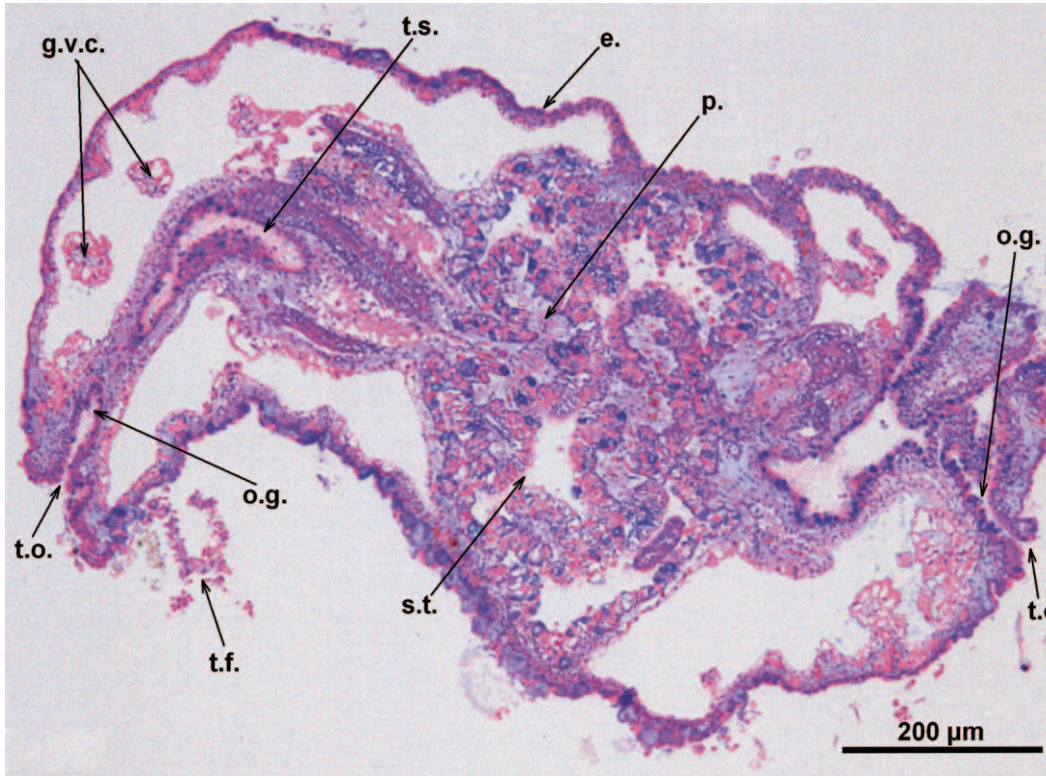

Fig. 4. *Coeloplana waltoni*. Histological longitudinal section, 3 µm, stained with hematoxylin and eosin. Abbreviations: e, epidermis; g.v.c., gastrovascular canals; o.g., oral groove; p., pharynx; s.t., stomach; t.f., tentacular filament; t.o., opening of tentacular sheath; t.s., tentacular sheath.

Animals of small size, at most about 5 mm in greatest length when fully extended and creeping, usually 2–3 mm when attached and passively resting (Fig. 2A), and only 1.5–2.0 mm when detached and floating free (Fig. 2B–D). When the animal is attached to a smooth surface and resting, the outline is roughly oval, longer in the tentacular axis, but the shape is extremely fluid, changing momentarily by

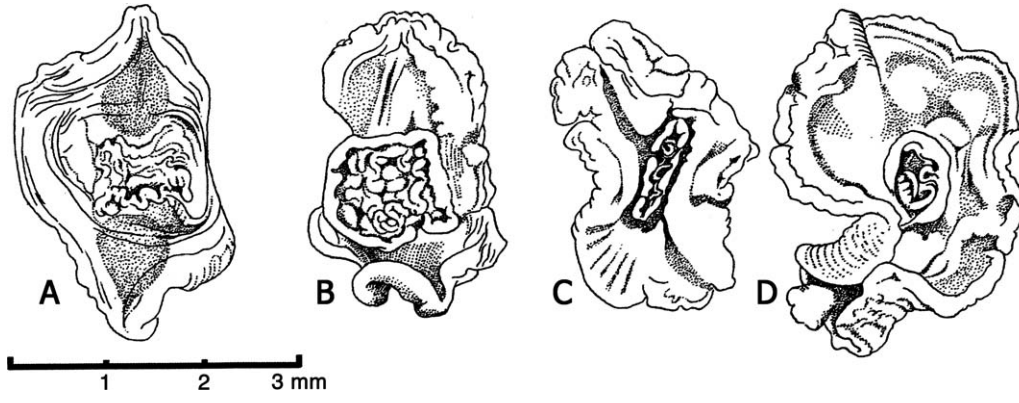

Fig. 5. *Coeloplana waltoni*. A–D, oral views of mouth and pharyngeal folds. Drawings by F. M. Bayer.

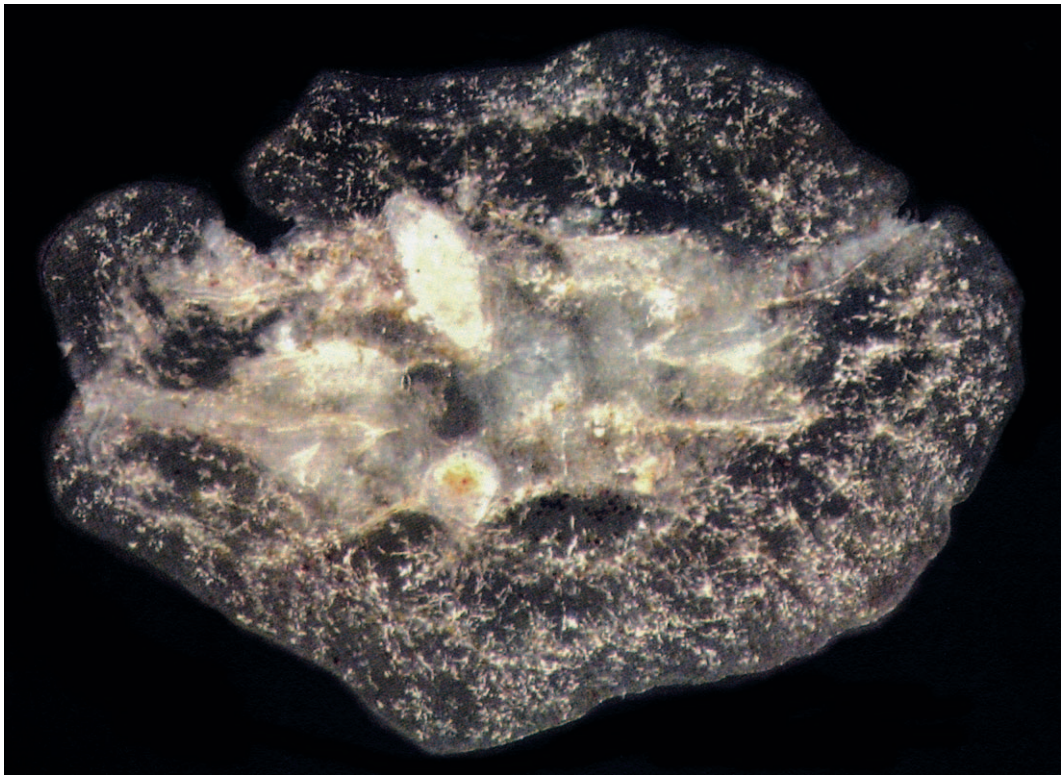

Fig. 6. *Coeloplana waltoni*. Aboral view of living free-floating specimen (~ 2 mm length). Collected off Dania Beach, 22 July 2013.

local advances and retractions of the margin. When creeping, the outline becomes quite elongated and flatworm-like (Fig. 2E–H), and in this condition the greatest length is diagonal to the tentacular axis, as the animals rarely advance with the tentacular margin foremost; usually a point to one side of the tentacular aperture leads. In this state, the width of even the largest specimens may be as little as 0.5 mm. With the exception of the aboral sense organ, which forms a small central protuberance, the aboral surface is entirely smooth and completely lacking aboral papillae or "dorsal tentacles." The body is thickest in the central region over the stomach and pharynx, and along the tentacular sheaths, so there is a slightly raised elongated bulge situated in the tentacular axis (Fig. 3A–I). The tentacle sheaths are pyriform and open to the exterior at a slight notch in the margin that can, however, be pulled back some distance from the edge of the animal (Figs. 2–4). The tentacles are long – twice to three times the diameter of the body – and serially pinnate; however, portions of the distal tip are readily autotomized, which together with their great motility, makes it almost impossible to obtain meaningful measurements of their length from living material. The apical sense organ is well developed and clearly visible with low magnification as a pale central spot. Under higher power, the statolith can be clearly viewed and appears to be in constant rapid vibration. The sense organ closes by contraction of the margin in an iris-like fashion; however, closure rarely occurs, and then only momentarily. Because of several irregular marginal lobulations or foldings, the aperture is not circular. The

functional mouth is roughly circular, bounded by oral folds, and capable of great distension. If the entire oral surface of the animal is considered the everted outer pharynx, as in *Vallicula* (Rankin 1956:61), the mouth represents the opening of the inner pharynx. There seem to be distinct "oral grooves" along the tentacular axis (Fig. 4) as observed in *Vallicula*. The wall of the inner pharynx, exposed when the mouth is open, is thrown into numerous irregular convolutions called pharyngeal folds (Figs. 4, 5A–D). The canal system is much simpler than in *Vallicula* and other species of *Coeloplana*. It is composed of simple spacious subdivisions of the meridional canals that radiate outward from the stomach to the margin, reminiscent of the organization in the parasitic burrowing form of *Lampea* found in salps (= *Gastrodes* Korotneff, 1888, = *Gastra* Stechow, 1921). The canals are in such close proximity that there are apparently no connecting canals but only openings through the walls between adjacent canals. In life, the animals are translucent (not transparent). Some individuals display a pale yellowish green tint (Fig. 6), whereas others are yellowish brown and darker in the central area over the stomach and along the tentacular sheaths. There is a fine irregular reticulation of white on all individuals, and most of them also have brown pigment granules, which in some are coalesced to form a reticulation somewhat coarser than the white pattern.

Habitat.—*Coeloplana waltoni* live as commensals on various species of shallow-water gorgonians. In the 1960s, they were found on several species in the genera *Eunicea*, *Plexaurella*, and *Muricea*, and the incidence of infestation in some localities was almost 100%. In fact, on the several occasions when collections were made, every gorgonian examined was found to host these ctenophores. Specimens were found from September through May in the 1960s and more recently during the fall and winter months, and in July, suggesting year round occurrence. More recently (2012–2013) gorgonian hosts included species of *Eunicea*, *Gorgonia*, *Pseudoplexaura*, *Pseudopterogorgia*, *Plexaura*, and *Muriceopsis* (Table 1). The highest numbers of *C. waltoni*, i.e., >48 individuals, were found on *Eunicea tourneforti* collected at Emerald Reef. *Gorgonia ventalina* and *Plexaura homomalla* at Broad Key also hosted numerous ctenophores, totaling 30 and 35 individuals, respectively. Multiple short branches (4–13 cm in length) of an individual of *Plexaura flexuosa* collected at Soldier Key on 10 October 1960 (USNM 52454) still contain 12 individuals of *C. waltoni* firmly attached to the coenenchyme. Relatively large numbers also were collected from *Eunicea laciniata* at the Half Moon Wreck site (11 individuals) and from *Muriceopsis flavida* off Dania Beach (18 individuals). When abundant on any given host colony, the ctenophores became crowded and were often in contact.

Etymology.—Named in honor of F. G. Walton Smith, founder of the Rosenstiel School of Marine and Atmospheric Science, who first recognized the occurrence of benthic ctenophores in American waters.

Behavior.—The ctenophores creep slowly on the surface of the gorgonian rind and are usually very close to the polyps. Often they are found encircling the calyces of the polyps, even extending into the mouth. The translucent body, with its flecks of white and brown pigment, blends with the surface of the gorgonian, which is sprinkled with white where spicules show through the epidermis and also with brownish or purplish pigment spots. The ctenophores are extremely difficult to see in situ and can be found only by close examination of the living gorgonian submerged in seawater. Unlike specimens of *Coeloplana bocki*, which Komai (1922) removed from their alcyonacean hosts by means of a pipette, individuals of *Coeloplana waltoni* adhere tightly to the gorgo-

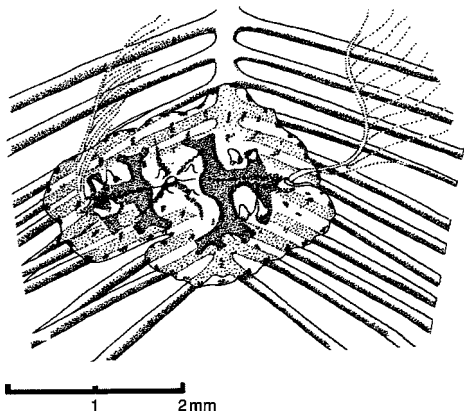

Fig. 7. *Vallicula multiformis* Rankin. Resting on unidentified host. Three clusters of papillae visible, one around apical organ and one behind each tentacular aperture. Drawing by F. M. Bayer.

nian and can be dislodged only by carefully lifting them off with fine-pointed forceps. The oral surface often assumes a concave shape, which may aid in forming a suction cup-like seal. They are rather firm and elastic and suffer no damage if handled gently. They produce quantities of sticky mucus that aids in clinging tightly to gorgonians living in swift currents. This mucus apparently is secreted by the highly glandular epithelium that contains both clear and granular cells, closely resembling the epidermis of *Coeloplana mitsukurii* and *Lyrocteis imperatoris* (Komai 1922:pl. 4, fig. 1; Komai 1942:fig. 4A). Once detached from the host, the copious adhesive mucus of *C. waltoni* makes the animals very difficult to dislodge from the forceps. When unattached, they assume a "floating phase" (Fig. 6; video clip MVI_0780) similar to that described in *Vallicula* by Rankin (1956:58). Although it is presumably the chief, if not the only, means of moving from one host to another, it is not known whether this "phase" is ever voluntarily assumed by *Coeloplana*, as it is by *Vallicula*. Unlike *Vallicula*, *Coeloplana* does not fold itself lengthwise along the tentacular axis but instead hollows the oral surface and folds the margins inward on either side of the tentacular apertures (Fig. 2D). In this condition, the animals usually trail their tentacles, possibly as a flotation device and/or to catch in the branches of any gorgonian that might serve as a new host. If stimulated by moving water, the creeping animals also stream their tentacles in a food-catching attitude. They readily eat young nauplii of *Artemia* in the laboratory, so it seems likely that their natural food consists of minute zooplankters and the abundant copepods that live as epizoites on the surface of the gorgonians.

Comparisons.—It is unlikely that *Coeloplana waltoni* could be confused with *Vallicula multiformis* (Figs. 7, 8), which is the only other platyctene reported from the western Atlantic region. Its small size (one-third to one-quarter that of *Vallicula*), smooth aboral surface, simple, sac-like tentacle sheaths, simple canal system, and translucent (rather than transparent) quality, render *C. waltoni* quite distinct. The habitat of *C. waltoni*, occurring on shallow water gorgonians, is quite limited. *Vallicula* has never been found living upon gorgonians but occurs generally among algae, on the bryozoan *Zoobotryon*, and on other fouling organisms, or under stones (Marcus 1957). *Vallicula* has been collected only in the boat harbor of the Crandon Beach Marina, where there is limited water motion, turbid conditions, and low light penetration.

Coeloplana sophiae Dawydoff, 1938 is the only other species in the genus known to associate with a gorgonian [*Solenocaulon jedanensis* in the South China Sea (Dawydoff 1938)]. Also, *Coeloplana waltoni* is markedly different from *C. sophiae* in color and morphology. The latter is brick red with white flecks, and possesses numerous distinctively arranged dorsal papillae, and a unique median oral groove extending along the entire length of the oral surface and ascending aborally to the tentacular sheaths.

Relationships.—The characteristics of this new species seem clearly to support

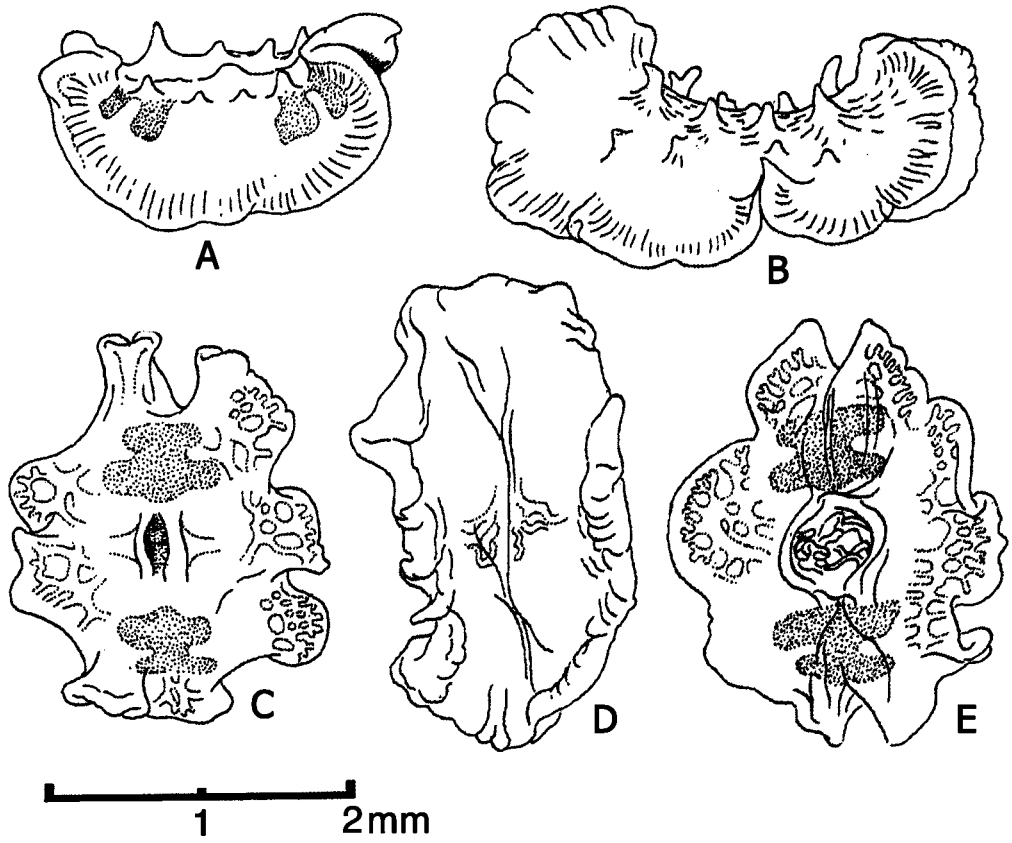

Fig. 8. *Vallicula multiformis* Rankin. Major papillae visible in lateral-aboral views (A, B), and mouth and pharyngeal folds in oral views (C–E). Drawings by F. M. Bayer.

its placement in the original genus *Coeloplana*, rather than in *Vallicula* as conceived by Rankin (1956). The defining characteristics of the latter genus are its "anchor shaped" tentacular sheaths, variable number and position of aboral papillae, presence of "food grooves" along the tentacular axis leading from the margin to the pharyngeal opening, and occurrence of a "floating phase" in which the animal folds itself lengthwise along the tentacular axis, turns up (aborally) the openings of the tentacular sheaths to form short "chimney-like" structures. Also, *Vallicula* is able to drift in the plankton. Although specimens collected in Florida appear to be the same as those found in Jamaica by Rankin (1956) and in Brazil by Marcus (1957), the present observations and interpretations differ sufficiently from theirs to raise some doubt about the status of *Vallicula*. A form like the "floating phase" of *Vallicula* also occurs in *Coeloplana waltoni* and may be widespread in *Coeloplana*. In spite of intensive plankton sampling around the Miami area where both genera are abundant, neither has been taken in the plankton.

In all of the material of *Vallicula* from Florida, the aboral papillae seem to have a rather consistent distribution, and regardless of their retractility, do not change position. The major papillae commonly occur in three groups of four: one group around the apical organ, and one behind each tentacular opening (Fig. 7); sometimes the tentacular openings are flanked by two papillae instead of four (Fig. 8A,

B), and additional laterally-placed papillae have also been observed (Fig. 8B). Smaller projections may appear along the gastrovascular canals, and these are so small that they can be fully retracted.

The anchor-shaped tentacular sheaths, suggested as characteristic of *Vallicula* (Figs. 7, 8A, C, E), probably are not limited to *V. multiformis*. A similar configuration in *Coeloplana bocki* is suggested in illustrations published by Komai (1922:pl. 2, fig. 1). *Coeloplana scaberiae* also has large tentacular sheaths with varying cross-bar development, not so elaborately branching, but similar to *Vallicula* in some specimens (Matsumoto & Gowlett-Holmes 1996). When exposed, the inner pharynx of *Vallicula*, as in *Coeloplana waltoni*, consists of prominent folds (compare Figs. 4, 5, 8E).

In view of the fact that *Coeloplana metschnikowii* Kowalevsky, 1880, the type species of *Coeloplana*, has no dorsal papillae, and that tentacular sheaths with lateral branches occur in *Coeloplana* and *Vallicula*, the various nominal species should be reviewed and the validity of these characters reappraised. Pending such a review, generic alignment is not disturbed, and the new species herein established is assigned to *Coeloplana*.

Remarks.—Coeloplana waltoni represents a new, minute species of platyctenid ctenophore that exhibits an ectosymbiotic lifestyle. In Matsumoto's (1999) summary of known *Coeloplana* host associations, five species were listed as being associated with marine plants (mainly green, red, and brown algae), six species with echinoderms (echinoids and asteroids), and nine species epizooic on cnidarians. *Coeloplana willeyi* Abbott, 1907 is found on a variety of plants and echinoderms. Of the cnidarian hosts, seven species of *Coeloplana* were associated with alcyonaceans, and one species each with a pennatulid and gorgonian cnidarian. At present, *Coeloplana sophiae* is the only species associated with a gorgonian. It is now possible to add three additional platyctenid-cnidarian associations with the discovery of *Coeloplana anthostella* and *Coeloplana bocki* inhabiting *Dendronephthya* spp. (alcyonaceans) in Korea (Song & Hwang 2010, Song et al. 2011) and *Coeloplana* sp. associated with the aboral surfaces of fungiid corals in Malaysia (Hoeksema et al. 2013). Three species were listed as planktonic. Additional records are *Coeloplana bannwarthi*, inhabiting the echinoid *Diadema* (Eeckhaut et al. 1997), and *Coeloplana willeyi* that adheres to the fronds of the green alga *Caulerpa racemosa* var. *cylindracea* (Cavas & Yurdakoc 2005).

Since the gorgonian colonies sampled typically ranged between 0.5 to 1.0 m in height and possessed numerous branches and branchlets, producing a high surface area, it is likely that single colonies could host hundreds if not thousands of individual *Coeloplana waltoni*. Because platyctene ctenophores are capable of both sexual and asexual reproduction (Hyman 1940), Matsumoto & Gowlett-Holmes (1996) hypothesized that these dual reproductive modes could explain their high population numbers. The latter workers noted that a platyctene species in Hawai'i, *Vallicula multiformis*, reaches population densities of over 3000 individuals m^{-2} (C. P. Galt pers. comm.). *Coeloplana scaberiae*, a species described by Matsumoto & Gowlett-Holmes (1996) as inhabiting a brown alga in Australia, attains densities of from one to 50 individuals per alga. These workers found brooded embryos under the margins of 18 of 22 specimens and observed asexual fragmentation. No sign of sexual or asexual reproduction was observed in *C. waltoni* in the present study. Some specimens collected off Dania Beach, however, contained one to two or three unidentified symbiotic flatworms, possibly species of Dalytyphloplanida. These moved freely within the pharynx and stomach and are visible in video clip MVI_0784.

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Literature Cited

Abbott, J. F. 1907. The morphology of *Coeloplana*. Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere 24:41–70.

Bayer, F. M. 1961. The shallow-water Octocorallia of the West Indian region: a manual for marine biologists. Martinus Nijhoff, The Hague, The Netherlands, 373 pp.

Bourne, G. C. 1900. Chapter VII, The Ctenophora. Pp. 1–25 *in* E. R. Lankester, ed., A treatise on zoology. Part II, The Porifera and Coelenterata. Adam & Charles Black, London, United Kingdom.

Cavas, L., & K. Yurdakoc. 2005. An investigation on the antioxidant status of the invasive alga *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman, et Boudouresque (Caulerpales, Chlorophyta). Journal of Experimental Marine Biology and Ecology 325:189–200.

Dawydoff, C. 1936. Les Ctenoplanidae des eaux de l'Indochine française, étude systématique. Bulletin Biologique de la France et de la Belgique 70:456–486.

Dawydoff, C. 1938. Deux Coeloplanides remarquables des eaux indochinoises. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris) 206:1143–1145.

Dawydoff, C. 1950. La nouvelle forme de Cténophores planarisés sessiles provenant de la Mer de Chine Méridionale (*Savangia atentaculata* nov. gen. nov. spec.). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris) 231(17):814–816.

Eeckhaut, I., P. Flammang, C. Lo Bue, & M. Jangoux. 1997. Functional morphology of the tentacles and tentilla of *Coeloplana bannworthi* (Ctenophora, Platyctenida), an ectosymbiont of *Diadema setosum* (Echinodermata, Echinoida). Zoomorphology 117:165–174.

Hoeksema, B. W., Z. Waheed, & A. Alamaru. 2013. Out of sight: aggregations of epizoic comb jellies underneath mushroom corals. Coral Reefs 32:1065.

Hyman, L. H. 1940. The Invertebrates. Part I. Protozoa through Ctenophora. McGraw-Hill, New York, New York, 726 pp.

Komai, T. 1922. Studies on two aberrant ctenophores, *Coeloplana* and *Gastrodes*. Published by the author, Kyoto, Japan, 102 pp.

Komai, T. 1941. A new remarkable sessile ctenophore. Proceedings of the Imperial Academy Tokyo 17:216–220.

Komai, T. 1942. The structure and development of the sessile ctenophore *Lyrocteis imperatoris* Komai. Memoirs of the College of Science, Kyoto Imperial University, Ser. B 17(1):1–36.

Korotneff, A. 1886. *Ctenoplana kowalevskii*. Zeitschrift für Wissenschaftliche Zoologie 43:242–251.

Korotneff, A. 1888. *Cunoctantha* und *Gastrodes*. Zeitschrift für Wissenschaftliche Zoologie 47:650–657, pl. XL.

Kowalevsky, A. 1880. *Coeloplana metschnikowii*. Zoologischer Anzeiger 3:140.

Marcus, E. d. B.-R. 1957. *Vallicula multiformis* Rankin, 1956, from Brazil. Boletim do Instituto Oceanográfico Sao Paulo 7(1–2):87–90.

Matsumoto, G. I. 1999. *Coeloplana thomsoni* sp. nov., a new benthic ctenophore (Ctenophora: Platyctenida: Coeloplanidae) from Western Australia. Pp. 385–393 *in* D. I. Walker & F. E. Wells, eds., The seagrass flora and fauna of Rottnest Island, Western Australia: proceedings of the Ninth International Marine Biological Workshop, held at Rottnest Island, Western Australia, January 1996. Western Australian Museum, Perth, Western Australia.

Matsumoto, G. I., & K. L. Gowlett-Holmes. 1996. *Coeloplana scaberiae* sp. nov., a new benthic ctenophore (Ctenophora: Platyctenida: Coeloplanidae) from South Australia. Records of the South Australian Museum 29:33–40.

Mills, C. E. 1998–present. Phylum Ctenophora: list of all valid species names. Electronic internet document available at <http://faculty.washington.edu/cemills/Ctenolist.html>;. Published by the author, web page established

March 1998, last updated 16 March 2014 (last accessed 25 June 2014).

Mortensen, T. 1910. *Tjalfiella tristoma* n. g., n. sp. A sessile ctenophore from Greenland. Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjbenhavn 17:249–253.

Rankin, J. J. 1951. A new platyctenid ctenophore from Jamaica. Nature 4285:1047.

Rankin, J. J. 1956. The structure and biology of *Vallicula multiformis*, gen. et sp. nov., a platyctenid ctenophore. Journal of the Linnean Society of London, Zoology 43(289):55–71.

Song, J.-I., & S.-J. Hwang. 2010. A new species of genus *Coeloplana* (Ctenophora: Tentaculata: Platyctenida) from Korea. The Korean Journal of Systematic Zoology 26(3):217–221.

Song, J.-I., S.-J. Hwang, S. Lee, & J.-K. Park. 2011. New records of creeping ctenophores, Genus *Coeloplana* (Tentaculata: Platyctenida: Coeloplanidae), from Korea. The Korean Journal of Systematic Zoology 27(1):47–52.

Stechow, E. 1921. Neue Genera und Species von Hydrozoen und anderen Evertebraton. Archiv für Naturgeschichte, Abteilung A 87:248–265.

Stechow, E. 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. Zoologische Jahrbücher, Abteilung für Systematik 47:29–270.

Walton Smith, F. G. 1945. The discovery of *Coeloplana* on American shores. Science 101(2610):17.

Willey, A. 1896. On *Ctenoplana*. Quarterly Journal of Microscopical Science, New Series 39(155):323–342.

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