

The Genus *Colpomenia*
Derbès et Solier (Phaeophyta)
in the Gulf of California

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and *James N. Norris*



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ABSTRACT

Wynne, Michael J., and James N. Norris. The Genus *Colpomenia* Derbès et Solier (Phaeophyta) in the Gulf of California. *Smithsonian Contributions to Botany*, number 35, 18 pages, 11 figures, 1976.—Four species of the brown algal genus *Colpomenia* Derbès et Solier (Scytosiphonales) are recognized as occurring within the Gulf of California: *C. sinuosa* (Roth) Derbès et Solier, *C. tuberculata* Saunders, *C. ramosa* Taylor, and *C. phaeodactyla*, new species. Some of the specimens interpreted by Dawson (1944) as *Rosenvingea intricata* are now referred to *C. ramosa* Taylor. Although recorded from the Pacific coast of Baja California, *C. ramosa* has not yet been reported within the Gulf. Interrelationships of the species complex of *Colpomenia* with related genera such as *Iyengarina* Boergesen, *Rosenvingea* Boergesen, and *Scytosiphon* C. Agardh are discussed.

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Contents

	<i>Page</i>
Introduction	1
Key to <i>Colpomenia</i> Species in the Gulf of California	2
1. <i>Colpomenia sinuosa</i> (Roth) Derbès et Solier	2
2. <i>Colpomenia phaeodactyla</i> , new species	5
3. <i>Colpomenia tuberculata</i> Saunders	8
4. <i>Colpomenia ramosa</i> Taylor	11
Discussion	13
Ecological Observations	15
Literature Cited	17

The Genus *Colpomenia* Derbès et Solier (Phaeophyta) in the Gulf of California

Michael J. Wynne
and *James N. Norris*

Introduction

Three distinctive morphological forms of *Colpomenia* Derbès et Solier within the Gulf of California, Mexico, have been recognized by previous authors (Setchell and Gardner, 1924; Dawson, 1944, 1966) as representing separate forms of a single variable species, *C. sinuosa* (Roth) Derbès et Solier: f. *sinuosa*, f. *deformans* Setchell and Gardner, and f. *tuberculata* (Saunders) Setchell and Gardner. According to Dawson (1944) the latter also included f. *expansissima* Setchell and Gardner. Under its various guises *Colpomenia* collectively forms a dominant element of the intertidal winter and spring flora of the Gulf of California. Field and microscopic studies, however, have led the present authors to conclude that the *Colpomenia* complex in the Gulf includes four distinctive species, separated by morphological, anatomical, and habitat differences. The variable appearance of these species of *Colpomenia* raises problems of distinguishing them from related genera of the family Scytosiphonaceae. This paper, then, analyzes certain of the generic delimitations within the family.

Specimens studied are deposited in the herbaria of the following institutions: United States Na-

tional Herbarium, Smithsonian Institution (US); University of Michigan (MICH); University of California, Berkeley (UC); University of Texas at Austin (TEX); University of Arizona, Tucson (ARIZ); Universidad Autónoma de Mexico (MEXU); Allan Hancock Foundation Herbarium, University of Southern California (AHFH); and the Gilbert Morgan Smith Herbarium, Hopkins Marine Station of Stanford University, Pacific Grove, California (GMS). Collection numbers of J. N. Norris carry the prefix JN- and refer to his field notebooks. Specimens were collected by him unless otherwise noted; those collected by Katina E. Bucher are noted as KB.

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Michael J. Wynne, Department of Botany, The University of Texas at Austin, Texas 78712. James N. Norris, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Drs. M. M. Littler, F. R. Fosberg, and B. Simpson for their comments on the ecological observations.

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For the opportunity to participate on the R/V *Dolphin* cruise to the northern Gulf of California, JN thanks Dr. William Fenical, Chief Scientist, Scripps Institution of Oceanography. He is also grateful to the scuba diving and collecting assistance of Katina Bucher, Dr. Howard Sleeper, Mark Helvey, George Boehlert, and David Moore. Thanks are due to Drs. Richard S. Felger, Mark M. Littler, Richard Evans Schultes, Andrew T. Weil, and Nicholas P. Yensen, Diane Littler, James Woessner, and William Wheeler for generously sharing their collections. Finally, we thank Katina Bucher for her help throughout this study and assistance in processing the specimens studied.

Key to *Colpomenia* Species in the Gulf of California

1. Thalli consisting of clustered finger-like sacs arising from a common prostrate holdfast; wall of sacs thin, delicate, usually less than 100 μm thick 2. *C. phaeodactyla*
Thalli not consisting of such finger-like sacs; thalli ranging from spherical, balloon-like shapes to irregularly shaped, prostrate or sessile expanses; thallus wall thicker, firmer, exceeding 200 μm in thickness 2
2. Thalli with irregular lobed branches, forming a spreading adherent clump 4. *C. ramosa*
Thalli smooth or tuberculate but lacking definite branches, forming sessile expanses or globose sacs 3
3. Thalli with tuberculate, warty surface, of a crisp, rigid texture; thickness exceeding 0.5 mm, often about 1.0 mm; plurilocular organs up to 25 μm long 3. *C. tuberculata*
Thalli with smooth or convoluted surface, but never tuberculate or rigid; thickness 0.3–0.5 mm; plurilocular organs 40 μm or more long 1. *C. sinuosa*

1. *Colpomenia sinuosa* (Roth) Derbès et Solier

FIGURES 1, 2a,b, 11a

Ulva sinuosa Roth, 1806:327, pl. 12a–c.

Colpomenia sinuosa (Roth) Derbès et Solier, 1856:11, pl. 22: figs. 18–20.—Saunders, 1898:164, pl. 32: figs. 7,8.—Setchell and Gardner, 1925:539, pl. 45: figs. 82–86 [with reference to Gulf of California specimens only].—Dawson, 1944:232; 1959:19; 1966:10. [Cf. Misra, 1966:115–6, for synonymy.]

DESCRIPTION.—Thalli (Figure 1) globular or vesicular, becoming irregularly convoluted and expanded with age, reaching a diameter of 14 cm; wall 300–500 μm thick, composed of a surface layer of small pigmented cuboidal cells (Figure 2a) and 4–6 layers of gradually larger, irregularly shaped subcortical and medullary cells; plurilocular organs (Figure 2b) uniseriate (to partially biseriate), about 40 μm in length, clustered in fairly discrete sori often around an invaginated tuft of hairs; paraphyses longer than plurilocular organs, to 55 μm

in length; color golden brown; unilocular sporangia unknown.

TYPE-LOCALITY.—Cadiz, Spain.

HOLOTYPE.—Destroyed at Berlin-Dahlem (according to Dawson et al., 1964).

GULF OF CALIFORNIA DISTRIBUTION.—Growing on rocks and epiphytic on various algae, subtidal (13–16 m depths) to midlittoral levels; throughout the Gulf of California from Puerto Peñasco to Bahía Agua Verde.

GULF OF CALIFORNIA SEASONALITY.—November–April.

DISTRIBUTION.—Common in tropical and subtropical seas throughout the world.

SPECIMENS EXAMINED.—*Gulf of California*. Sonora: Punta Pelicano, vicinity of Puerto Peñasco, 17 Mar 1973, JN-3811 (UC); 19 Apr 1973, JN-3966 (MEXU); 9 Mar 1974, JN-4982 (US), (leg. JN and KB); Feb 1965, Dawson 27558 (ARIZ). Playa Arenosa, vicinity of Puerto Peñasco, 26 Dec 1972, Wynne 3754 (MICH, TEX); 17 Apr 1973, JN-3911 (MICH).

Playa Hermosa, Puerto Peñasco, littoral rock platform and sand areas, 2 Feb 1973, JN-3702 (MICH). Playa Estación, Puerto Peñasco, littoral rock platform and tide pools, Feb 1968, (TEX), (leg. R. Hoshaw); 25 Dec 1972, Wynne 3733

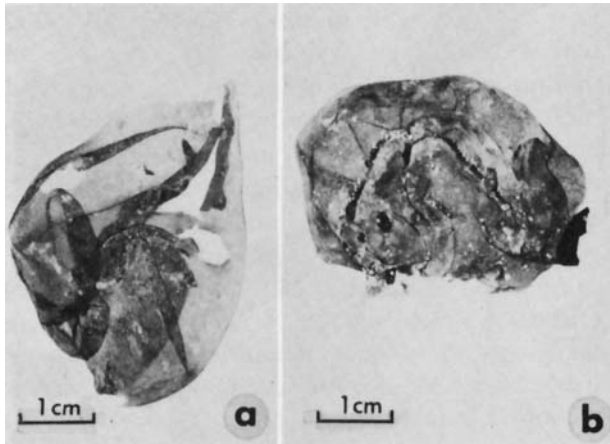


FIGURE 1.—Habits of *Colpomenia sinuosa*: a,b, from Playa Arenosa, Puerto Peñasco (Wynne-3754).

(MICH, TEX); 22 Jan 1973, JN-3621 (US); 25 Nov 1972, JN-3663 (UC), (leg. JN and KB); 4 Feb 1973, JN-3746 (MICH); 4 Mar 1973, JN-3783 (US), JN-3786 (TEX), JN-3801 (MEXU), (leg. JN and KB); 3 Feb 1973, JN-4717 (UC); 18 Jan 1974, JN-4760 (US), (leg. JN and KB); 9 Feb 1974, JN-4929 (UC); 5 Feb 1974, JN-4952 (US) and JN-4956 (ARIZ, MICH, US); 1 Mar 1974, JN-5013 (ARIZ, MICH); 24 Mar 1974, JN-5108 (US), (leg. J. Woessner and W. Wheeler). N side of Punta Lobos, vicinity of Puerto de Lobos, 3 m depth, sand covered rock, 17 Feb 1973, JN-6035 (US), (leg. M. Helvey). W side of Punta Robinson, vicinity of Puerto Libertad, 4.5 m depth, rock reef, 17 Nov 1973, JN-4824 (UC), (leg. JN and KB). Punta Cirio, S of Puerto Libertad, epiphytic on *Sargassum* stipes, W side of cove, 18 Nov 1973, JN-4913 (TEX), (leg. JN and KB). Desemboque de San Ignacio, drift, 3 Apr 1974, JN-5140 (TEX), (leg. R. S. Felger, R. E. Schultes, and A. T. Weil). Isla San Pedro Nolasco, epiphytic on *Sargassum* stipe, NE side of cove, 20 Mar 1974, JN-5206 (GMS), (leg. N. P. Yensen). Baja California: Isla Willard, Bahía San Luis Gonzaga, littoral rocks, 20 Apr 1974, JN-5400 (MEXU, US), (leg. JN and KB). Islas de la Cintura: 3 m depth, E end of Isla Mejía, Puerto Refugio, 23 Apr 1974, JN-5681 (AHFH), leg. JN and KB). Isla Angel de la Guarda, low littoral rocks, NE shore of Puerto Refugio, 23 Apr 1974, JN-5787 (MICH, US).

REMARKS.—Blackler (1964) differentiated the two

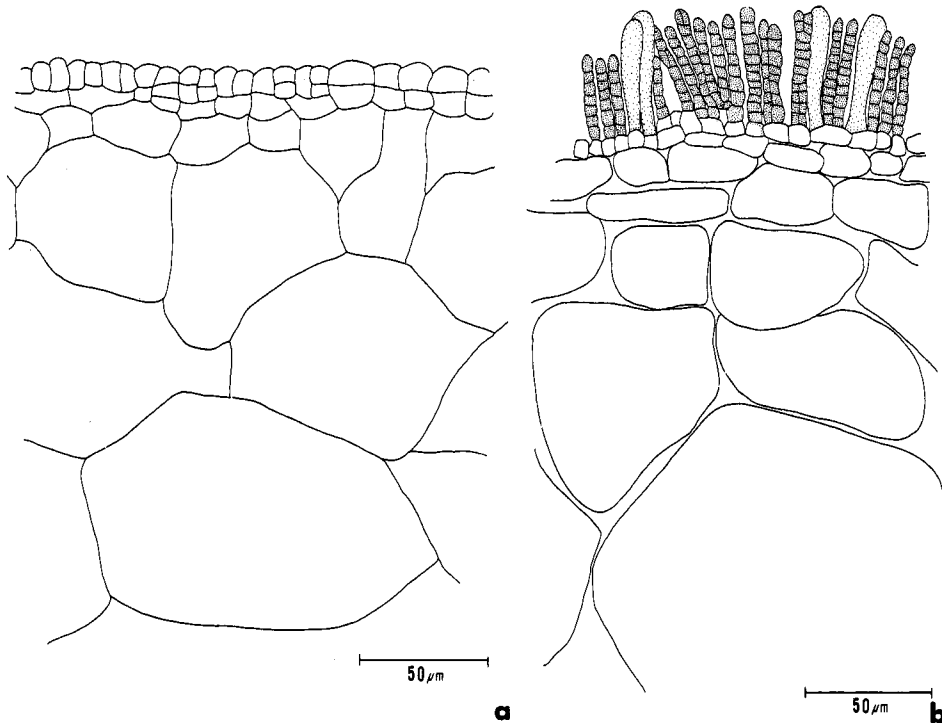


FIGURE 2.—Transsections of *Colpomenia sinuosa*: a, a sterile thallus from Playa Estación, Puerto Peñasco, (JN-4952); b, fertile plant showing the uniseriate plurilocular organs and unicellular paraphyses, also from Playa Estación (Wynne-3733).



FIGURE 3.—Open expanded-sheet form of *Colpomenia sinuosa* from 13–16 meter depth, off Isla la Ventana, Bahía de Los Angeles (JN-2995).

species of *Colpomenia* (*C. sinuosa* (Roth) Derbès et Solier 1856 and *C. peregrina* (Sauvageau) Hamel 1937) occurring on the west coast of North America, which had been confused in the literature (Setchell and Gardner, 1925; Smith, 1944). They had previously been recognized as distinct in Europe by Sauvageau (1927). Apparently it is only in the southern California region that the ranges of these two species overlap; *C. peregrina* occurs from Amchitka Island in the Aleutians to La Jolla, California, while *C. sinuosa* ranges southward from Point Conception including the Channel Islands (Blackler, 1964).

According to Sauvageau (1927) and Blackler (1964, 1967), *C. sinuosa* is characterized by fairly

firm, thick, often deeply folded thalli. With pressing, these are yellowish-brown in color. Discrete punctate sori of plurilocular organs are covered with a cuticle. On the other hand, *C. peregrina* is characterized by relatively thinner, smooth thalli, greenish in color upon pressing, with broad, confluent fertile zones,* lacking a cuticle, with plurilocular organs often composed of two rows of locules, and paraphyses shorter than the plurilocular

*Nonconfluent sori were reported in *C. peregrina* in Norway (Lund, 1949), whereas Clayton (1975) has presented statistical evidence that the shape of the sori and presence or absence of a cuticle over the plurilocular organs are the only criteria for effectively distinguishing Australian populations of these two species.

organs. Sauvageau (1927) reported that the thalli of *C. sinuosa* are 420–560 μm thick and the plurilocular organs are 40 (–50) μm high, while thalli of *C. peregrina* are 140–280 μm thick and plurilocular organs are about 20 μm high. The Gulf of California material agrees in large measure with the combination of traits of *C. sinuosa*, except that the plurilocular organs (Figure 2b) are both uniseriate and biseriata (or intermediate). Material illustrated by Okamura in Japan (1936, fig. 123) and Chamberlain for Gough Island in the South Atlantic (1965) showed a similar situation in *C. sinuosa*.

Colpomenia sinuosa f. *lacunosa* was described by Taylor (1947) from Paita, Peru. Subsequent treatment by Dawson et al. (1964) placed this taxon into synonymy with *C. sinuosa*. Since the present paper records *C. tuberculata* from Peru, we considered it desirable to examine the type material of *C. sinuosa* f. *lacunosa*. We have inspected the holotype (US) and concur with the conclusion of Dawson et al. (1964) that it should be placed with *C. sinuosa*. The thickness of the wall is in the range of *C. sinuosa* rather than *C. tuberculata*.

Open expanded blades (Figure 3) that appear to be a form of *C. sinuosa* were recently collected during subtidal surveys. Apparently a deep water form, they were found growing attached at 13–16 m depths. These sheets were smooth, fairly thin, and measured up to 25 cm broad. Our specimens lacked the "minute, spine-like projections" described by Setchell and Gardner (1924:726; 1925:541) for their *C. sinuosa* f. *expanissima*. Their form was found floating in Bahía de San Francisquito, whereas the recent collections were attached and subtidal. Dawson regarded the former taxon as a form of *C. sinuosa* f. *tuberculata*, which "achieved extensive development in a detached floating condition . . ." (1944:233). Unfortunately our open-sheet form is not fertile, and lacking this, it seems judicious to merely call attention to this new material. Thus far only known from the Gulf of California, for now we refer our specimens to *C. sinuosa*. The following collections are cited: Sonora: Ensenada de San Francisco, vicinity of Puerto San Carlos, 24 Mar 1949, Dawson 7231 (US). Baja California: Puerto Calamajue, 23 Mar 1973, JN-4607 (US), (leg. JN and KB); Punta La Gringa, Bahía de Los Angeles, 8 m, 28 Apr 1974, JN-6103b (US), (leg. JN); Isla la Ventana, Bahía de Los

Angeles, 13–16 m, 21 May 1972, JN-2995 (US, UC), (leg. JN and G. Boehlert); Bahía Salinas, Isla Carmen, 4–14 m, 20 Mar 1965, Dawson 6986 (US); Puerto Escondido, 4–8 m, 18 Mar 1949, Dawson 7144 (US). Las Islas de la Cintura: Isla San Esteban, 6.5–39 m, 26–27 Jan 1960, Dawson 21547 (US), (leg. Calif. Dept. Fish and Game).

2. *Colpomenia phaeodactyla*, new species

FIGURES 4, 5a,b, 11c

C. sinuosa f. *deformans* of Setchell and Gardner, 1924:726, pl. 19: figs. 61,62; 1925:542 [in part, with reference to the Gulf of California specimens only].—Dawson, 1944:233; 1966:11.—Wynne, 1972:137, fig. 1; 1973:141 [not *C. sinuosa* f. *deformans* Setchell and Gardner 1903:242].

Colpomenia bullosa of Norris 1972:6 [not *C. bullosa* (Saunders) Yamada 1948:6].

Thalli e fasciculis saccorum cavorum longorum, qui plerumque ab 8 ad 15 cm long. (raro usque ad 25 cm long.) atque ab 0.8 ad 1.5 cm lat. (raro usque ad 5.5 cm lat.) variant, constantes, e basi adhaerente colponemioidea, c. 1–2 diam., enascentes; sacci ad basim attenuati, cavi, autem, per longitudinem suam, a 6 ad 12 e uno basi enascentes, interdum, autem, paucior vel numerosior (25–30); saccus vegetativus 70–88 (–110) μm crassus et compositus ex unico strato corticeo cellularum cuboidearum minorum, atque ex unico strato subcorticeo cellularum paululorum maiorum, atque e zona interiore 2–3 cellulis crassis, cellularum maiorum sine colore; sacci textura tenues delicatique, cum emersi omnino flaccidi; organa plurilocularia 28–30 μm longa, uni- atque biseriata, soros densos amplos super saccos erectos efficientia; paraphyses raras, quasi eadem altitudine ac organa plurilocularia, interdum, autem, breviores altioresve; penicilli pilorum sine colore rari; thalli aureo-brunnei, fusciore cum fertiles; chloroplastum unicum in cellulis omnibus corticeis; sporangia unilocularia ignota.

DESCRIPTION.—Thalli (Figure 4) consisting of clusters of long, hollow sacs, typically ranging between 8 and 15 cm in length (rarely up to 25 cm in length) and 0.8–1.5 cm in width (rarely up to 5.5 cm in width), arising from an adherent colpomenioid base of about 1–2 cm in diameter; sacs tapered toward the base yet hollow throughout their length, with (1–) 6–12 (–30) sacs arising from

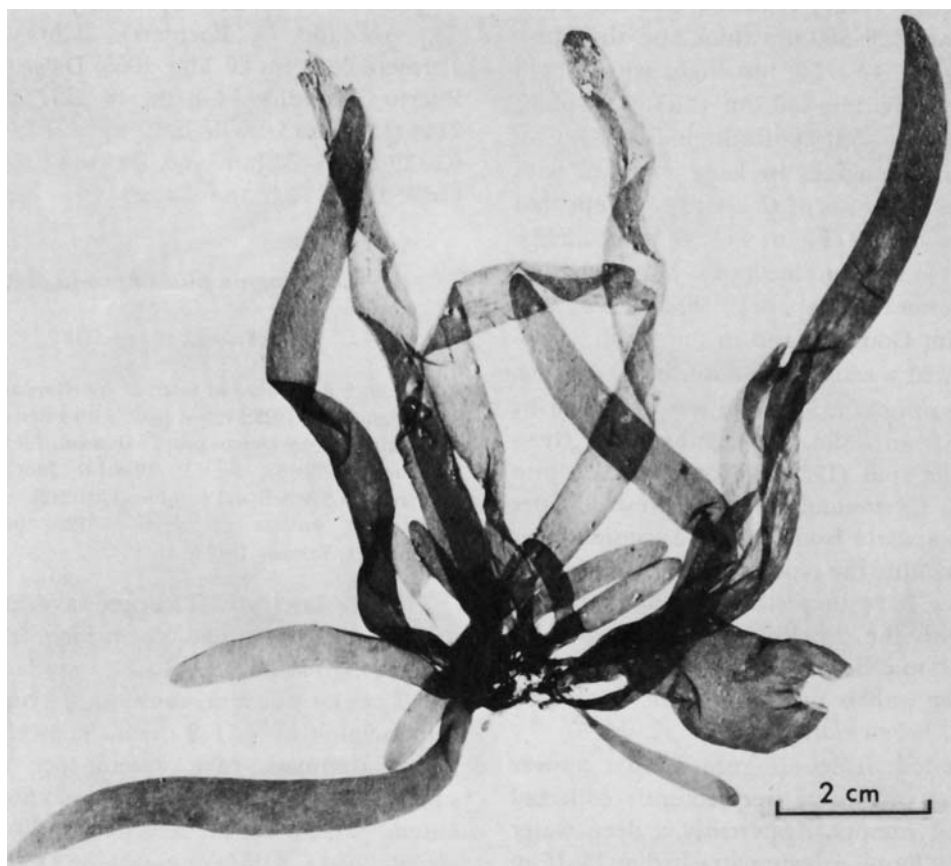


FIGURE 4.—Holotype of *Colpomenia phaeodactyla*, Playa Estación, in front of Laboratorio de Biología Marina, Puerto Peñasco, Sonora (JN-3629).

a single base; vegetative sac 70–88 (–110) μm thick and composed (Figure 5a) of a single cortical layer of smaller cuboidal cells, a single subcortical layer of slightly larger cells, and an inner zone 2–3 cells thick of larger colorless cells; sacs are thin and delicate in texture, completely flaccid when emersed; plurilocular organs (Figure 5b) 28–38 μm long, uni- and biseriolate, forming dense, extensive sori over the erect sacs; paraphyses of rare occurrence, approximately same height as plurilocular organs but at times shorter or taller; tufts of colorless hairs of rare occurrence; color of thalli golden brown, darker when fertile; cortical cells each with one chloroplast; unilocular sporangia unknown.

TYPE-LOCALITY.—Playa Estación, Puerto Peñasco, Sonora, Gulf of California, Mexico.

HOLOTYPE.—J. Norris 3629 (US), 22 Jan 1973, Playa Estación, Puerto Peñasco, Sonora, Mexico; isotype (MICH).

GULF OF CALIFORNIA DISTRIBUTION.—Growing on rocks, middle to low littoral and occasionally upper littoral, in Gulf of California from Puerto Peñasco south to Isla Partida.

GULF OF CALIFORNIA SEASONALITY.—December–May.

DISTRIBUTION.—Northern Gulf of California, and Pacific Baja California, Mexico; Pacific Coast of Costa Rica; southern and central Japan.

SPECIMENS EXAMINED.—*Pacific Coast of Baja California.* Punta Thurloe, San Bartolome, intertidal, Mar 1934, Taylor 34–611 (MICH, US); 3 Apr 1955, Dawson–13320 (US). Bahía Tortuga, Sulphur Is., intertidal, 12 Feb 1954, Dawson–12269 (US). *Gulf of California.* Sonora: Punta Pelicano, vicinity of Puerto Peñasco, littoral granite rocks, 17 Mar 1973, JN–3813 (TEX); 3 Mar 73, (US), (leg. M. and D. Littler); 19 Apr 1973, JN–3968 (MEXU); 9 Mar 1974, JN–4980 (US), (leg. JN and KB). Punta Pelicano, SE side, 17 Mar 1974, JN–5048 (TEX, US, MEXU), (leg. JN, KB, and D. Moore); 8 Apr 1966, Dawson 27389 (US); Playa Arenosa, Feb 1965,

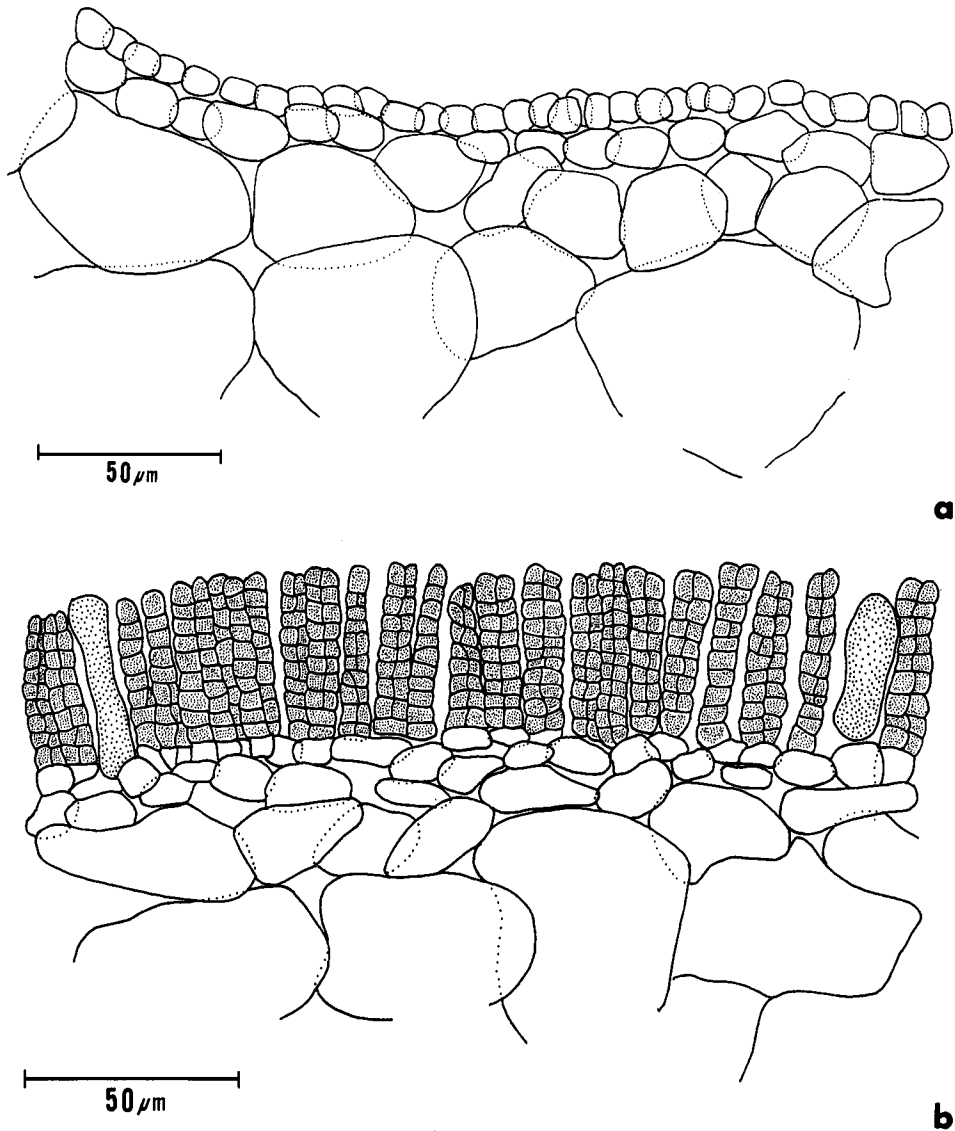


FIGURE 5.—Transsections of *Colpomenia phaeodactyla* from Punta Pelicano, Puerto Peñasco (JN-4980): *a*, the vegetative sac of a sterile thallus; *b*, uniseriate and biseriolate plurilocular organs and unicellular paraphyses of a fertile thallus.

Dawson 27557 (ARIZ, US); Playa Hermosa, Puerto Peñasco, littoral rock platform, 2 Feb 1973, JN-3700 (US); 19 Jan 1973, JN-4061 (UC); Playa Estación, Puerto Peñasco, mid-littoral rock platform and tide pools, Feb 1968, (leg. R. Hoshaw), (TEX); 25 Dec 1972, Wynne 3732 (TEX, MICH, UC, US); 22 Jan 1973, JN-3629 (US); 3 Feb 1973, JN-3727 (MICH); 4 Feb 1973, JN-3748 (MICH); 4 Mar 1973, JN-3784 (ARIZ); 18 Jan 1974, JN-4759 (UC, US), (leg. JN and KB); 5 Feb 1974, JN-4950 (MICH, UC, US), (leg. JN and KB); 24 Mar 1974, JN-5100 (US), (leg. JN and KB). Playa Estación,

Puerto Peñasco, on NASA buoy anchored offshore, 22 Mar 1973, JN-3834 (US). Cabo Tepoca, Puerto de Lobos, littoral rocks, 16 Mar 1973, JN-6020 (AHFH). Puerto de Lobos, littoral rocks, 17 Feb 1973, JN-6045 (MEXU), (leg. JN and M. Helvey). NW of Punta Robinson, vicinity of Puerto Libertad, rock outcropping, 17 Feb 1973, JN-5937 (MICH). Bahía Kino, 2 Jan 1973, Wynne 3857 (MICH, TEX). Baja California: Campo El Heurfanito, 20 miles S of Puertecitos, 2 Jan 1972, (US), (leg. M. and D. Littler). Punta Bufeo, N of Arroyo San Luis, 25 Feb 1975, (US), (leg. M. and D. Littler).

Punta Willard, Bahía San Luis Gonzaga, Jan 1940, Dawson 308 (MICH). N side of Puerto Calamajue, 28 Mar 1973, JN-4620 (MICH) and JN-4707 (UC), (leg. JN and KB). Punta La Gringa, Bahía de Los Angeles, 2.4-6.1 m depth, 22 May 1972, JN-3071 (UC), and on littoral rocks, 28 Apr 1974, JN-5431 (MICH, UC, US), (leg. JN and KB). Islas de la Cintura: Isla Mejía, Puerto Refugio, Isla Angel de la Guarda, littoral rocks, 23 Apr 1974, JN-5840 (GMS), (leg. JN and KB). NW of rock window on shore, Puerto Refugio, Isla Angel de la Guarda, littoral rocks, 21 Apr 1974, JN-5345 (ARIZ), (leg. JN and KB). Puerto Refugio, Isla Angel de la Guarda, littoral rocks, 20 Apr 1974, JN-5422 (US), (leg. KB). NE shore of Puerto Refugio, Isla Angel de la Guarda, littoral rocks, 23 Apr 1974, JN-5735 (AHFH) and JN-5769 (MICH, US), (leg. JN and KB). Isla Turner, off Isla Tiburón, Jan 1940, Dawson 96 (MICH). Isla San Esteban, Feb 1940, Dawson 435 (MICH). SE end of Isla San Esteban, littoral to 3 m depth, 25 Apr 1974, JN-5537 (MICH, UC, US) and JN-5726 (US). *Costa Rica*. Port Parker, Salinas Bay, Mar 1939, Taylor 39-76 (MICH). *Japan*. Nabeta, Shimoda, Shizuoka, Feb 1974, (MICH, TEX), (leg. M. Chihara).

REMARKS.—It was earlier pointed out by Wynne (1972) that specimens identified as *Colpomenia sinuosa* f. *deformans* (sensu Setchell and Gardner, 1924; Dawson, 1944, 1966) from the Gulf of California are quite distinct from those of the Pacific Coast of North America (Setchell and Gardner, 1903, 1925). The correct name for the Pacific Coast *C. sinuosa* f. *deformans* Setchell and Gardner (1903) is *Colpomenia bullosa* (Saunders) Yamada (1948) (Smith, 1969). Evidence supporting the recognition of *C. phaeodactyla* as a separate species includes the delicate nature of the sacs and their clustered aspect from a common basal system. This is in contrast to the usually solitary condition and firmer texture of the balloon-like sacs of *C. bullosa*.

An examination of Japanese works led us to believe that these two distinct entities were likewise passing under the name *C. bullosa* in Japan. Okamura (1936, fig. 124) presented the genuine *C. bullosa*, whereas the specimen presented in Chihara's account (1970, pl. 19: fig. 3) resembles *C. phaeodactyla*. An examination of samples of the latter kindly provided by Dr. M. Chihara confirmed this belief. Furthermore, Chihara (pers. comm.) has informed us that while *C. bullosa* occurs in northern Japan, including Hokkaido, Sanriku, and the Kurile Islands, where the Oyashio Current is predominant, the new species, *C. phaeodactyla*, occurs in southern and central Japan. Thus, *C. phaeodactyla* would fall in the category of algal species whose distribu-

tions are known in both the Gulf of California and southern Japan (Dawson, 1960; Hommersand, 1972).

Colpomenia sinuosa f. *deformans* was recorded, with a query, by Taylor (1945) from Isla Isabela in the Galapagos Archipelago and has remained in the literature (Silva, 1966). However, this material has been examined (W. R. Taylor #142 (MICH, US)) and is not *C. phaeodactyla*. It appears to be eroded specimens of *C. sinuosa*. Our new species, *C. phaeodactyla*, would resemble *C. mollis* Taylor (1945) from Colombia in the delicate nature of the wall, but the latter species is irregularly divided with branch endings truncate and bearing "spine-like projections" (Taylor, 1945:85).

3. *Colpomenia tuberculata* Saunders

FIGURES 6, 7a,b 11b

Colpomenia tuberculata Saunders, 1898:164, pl. 32: figs. 1-3. *Colpomenia sinuosa* f. *tuberculata* Setchell and Gardner, 1903:242; 1924:725; 1925:541.—Dawson, 1944:233; 1949:234, 242; 1959:19; 1966:11,—Norris, 1972:6.

DESCRIPTION.—Thalli (Figure 6) sessile, hollow, rigid, crisp, hemispherical to irregularly shaped, flattened expanses, covered with blunt tubercles 1-10 mm high and 1-10 mm across; surface coriaceous, deeply convoluted, and folded; 0.6-1.5 mm thick; cortex (Figure 7a) of 4-5 cuboidal cells, inner layer of 4-8 increasingly larger colorless cells; plurilocular organs (Figure 7b) 16-23 μ m long, uni- and biseriolate, 5-7 locules high, occurring in extensive soral regions over entire thallus; paraphyses present, slightly shorter than plurilocular organs; hairs arising in tufts from deep invaginations (Figure 9), especially in soral areas; color olive brown; unilocular sporangia unknown.

TYPE-LOCALITY.—Near San Pedro, California.

HOLOTYPE.—Unknown (see "Remarks").

GULF OF CALIFORNIA DISTRIBUTION.—Growing on rocks and occasionally epiphytic on other algae, mid-littoral to upper-littoral; Puerto Peñasco to San José del Cabo.

GULF OF CALIFORNIA SEASONALITY.—December-June.

DISTRIBUTION.—Southern California, U.S.A.; Pacific Baja California, Gulf of California, and Sinaloa, Mexico; and Peru.



FIGURE 6.—Habit of *Colpomenia tuberculata*, from Bahía Cholla, vicinity of Puerto Peñasco, Sonora (Dawson-27203).

SPECIMENS EXAMINED.—*California*. Los Angeles County: San Pedro, Feb 1932, (AHFH), (leg. Templeton). San Diego County: Pacific Beach, Nov 1900, (NY), (leg. Saunders). La Jolla, Nov 1900, (*Phycotheca Boreali-Americana* in AHFH and TEX), (leg. E. Snyder); Jul 1946, Dawson 2445-2446 (mixed with *C. sinuosa*) (AHFH). *Pacific Coast of Baja California*. N of Bahía de Todos Santos, Oct 1948, Dawson 5207 (AHFH). Bahía San Quintín, Nov 1949, Dawson 8720 (AHFH). Punta María, Apr 1946, Dawson 1542 (AHFH). Miller's Landing, Bahía Viscaíno, Apr 1951, Dawson 1366 (AHFH). Isla Piedras, Laguna Ojo de Liebre (Scammon's Lagoon), Apr 1946, Dawson 2521 (AHFH). Punta Mallarimo, Bahía Viscaíno, Apr 1951, Dawson 9902 (AHFH). Bahía Asunción, Apr 1950, Dawson 9162 (AHFH). Punta Abreojos, Apr 1950, Dawson 9479 (AHFH). Bahía Magdalena, Apr 1946, Dawson 7875 (AHFH). Punta Entrada, Isla Magdalena, May 1950, Dawson 9258 (MICH, AHFH). *Gulf of California*. Sonora: Bahía Cholla, Apr 1968, B. Gittins 4823 (MICH); Apr 1966, Dawson 27203 (ARIZ). Punta Pelicano, vicinity of Puerto Peñasco, littoral rocks, 17 Mar 1973, JN-3812 (ARIZ); 19 Apr 1973, JN-3967 (MEXU); 9 Mar 74, JN-4983 (US, MEXU). Punta Pelicano, SE, vicinity of Puerto Peñasco, 17 Mar 1974, JN-5027 (US), (leg. JN, KB, and D. Moore).

Playa Hermosa, Puerto Peñasco, littoral platform, 2 Feb 1973, JN-3701 (US); 3 Mar 1973, JN-4015 (MICH), (leg. JN and KB). Punta Peñasco, Feb 1940, Dawson 351 (AHFH); Mar 1942, Poindexter (AHFH). Playa Estación, Puerto Peñasco, littoral rock platform and tide pools, May 1965, Dawson 27522 (ARIZ); 3 Feb 1973, JN-3729 (MICH) and JN-3747 (ARIZ); 4 Mar 1973, JN-3785 (UC) and JN-3800 (US), (leg. JN and KB); 18 Mar 1973, JN-3855 (TEX); 20 May 1973, JN-4047 (US); 18 Jan 1974, JN-4761 (ARIZ); 9 Feb 1974, JN-4928 (US), (leg. JN and KB); 5 Feb 1974, JN-4951 (US), (leg. JN and KB); 6 Feb 1974, JN-4954 (TEX) and JN-4957 (US), (leg. JN and KB); Feb 1968, (TEX), (leg. R. Hoshaw); 24 Mar 74, JN-5073 (US, UC). Playa Estación, Puerto Peñasco, vicinity of transect line, 4 Jun 1974, JN-5626 (AHFH). Playa Arenosa, 26 Dec 1972, Wynne 3748 (MICH). Cabo Tepoca, vicinity of Puerto de Lobos, littoral rocks, 16 and 17 Feb 1973, JN-5950 (US), JN-5965 (GMS), and JN-5977 (AHFH), (leg. JN and M. Helvey); Feb 1940, Dawson 824 (AHFH); Feb 1940, Dawson 384 (AHFH). Punta Lobos, Puerto de Lobos, tide channel, sand covered rocks, 16 Feb 1973, JN-5989 (US), (leg. M. Helvey). NW side, Punta Robinson, Puerto Libertad, 19 Feb 73, JN-5927 (MICH, ARIZ). Puerto Libertad, Mar 1946, Dawson 693

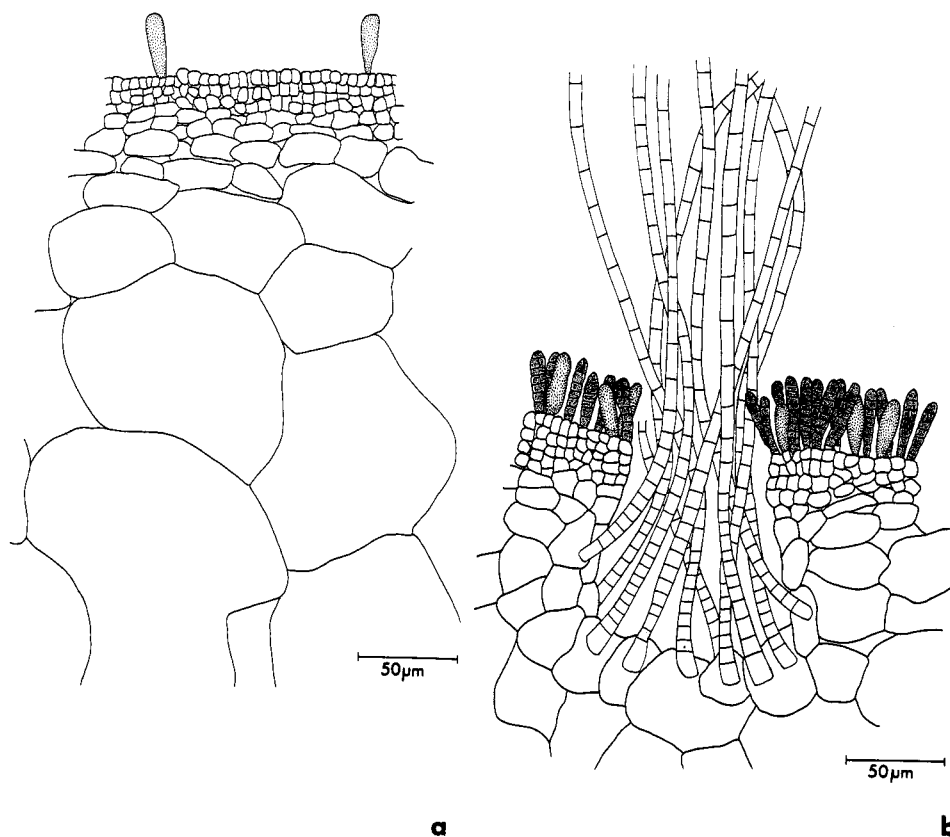


FIGURE 7.—Transverse sections of *Colpomenia tuberculata*, from Playa Estación, Puerto Peñasco, Sonora (JN-5073): *a*, sterile thallus with unicellular paraphyses; *b*, fertile thallus with plurilocular organs and unicellular paraphyses (note the long true hairs arising from a depression in the cortex).

(AHFH). Desemboque de San Ignacio, drift, 3 Apr 1974, JN-5139 (MEXU, TEX, UC, US), (leg. R. S. Felger, R. E. Schultes, and A. T. Weil). Isla Alcatraz, Bahía Kino, Feb 1946, Dawson 1059 (AHFH). Bahía Kino, 1 Jan 1973, Wynne 3843 (MICH) and 2 Jan 1973, Wynne 3858 (MICH). Bahía San Carlos, near Guaymas, 31 Dec 1972, Wynne 3813 (MICH, TEX, UC). Baja California: Playa Blanca, N of San Felipe, littoral rocks, 15 May 1972, JN-2961 (UC). Punta Estrella, S of San Felipe, 15 May 1972, JN-3311 (US), (leg. JN and G. Boehlert). Punta Willard, Bahía San Luis Gonzaga, littoral to 6.1 m depth, 20 May 1974, JN-5410 (MICH), (leg. JN and KB) and JN-5382 (US). Puerto Calamajue, N side, 23 Mar 1973, JN-4618 (MICH, US), (leg. JN and KB). Bahía de los Angeles, Apr 1946, Dawson 1308 (AHFH). Islas de los Gemelos, Bahía de los Angeles, 21 May 1972, JN-3012 (UC). La Mona, Bahía de los Angeles, littoral rocks, 20 May 1972, JN-2983 (ARIZ), (leg. JN and G. Boehlert). Bahía San Francisquito, 24 May 1972, JN-3219 (US) and JN-3272 (US). San Marcial Reef, S of Bahía Agua Verde, Mar 1937, Dawson (AHFH). San José del Cabo, Feb 1940, Dawson 636 (AHFH). Islas de la Cintura: Isla Mejía, Puerto Refugio,

littoral rocks, 23 Apr 1974, JN-5838 (AHFH), (leg. JN and KB). Puerto Refugio, Isla Angel de la Guarda, Jan 1940, Dawson 220 (AHFH). Puerto Refugio, littoral rocks, NE shore, Isla Angel de la Guarda, 23 Apr 1974, JN-5770 (MICH). Isla Estanque, Feb 1940, Dawson 422 (AHFH). Isla Partida, Feb 1946, Dawson 987 (AHFH). Isla Turner, off Isla Tiburón, Jan 1940, Dawson 90 (AHFH). Sinaloa: Mazatlan, Apr 1952, Dawson 10822 (AHFH). Peru. Telegraph Point, 13 Apr 1968, I. A. Abbott 4586 (GMS), (leg. D. P. Abbott).

REMARKS.—After careful scrutiny of “tuberculate” material from both the Gulf of California and elsewhere, we have concluded that Saunders’ *C. tuberculata* (1898) should be revived as a legitimate species, not merely a form of *C. sinuosa*, to which rank it had been relegated by Setchell and Gardner (1903, 1924, 1925) and Dawson (1944, 1966). We have been unsuccessful in locating the holotype of *C. tuberculata*. Although some collections made by Saunders are now housed in the herbaria of the

New York Botanical Garden, the University of California, Berkeley, and Farlow Herbarium, they did not include any specimen of *C. tuberculata* from San Pedro, California, the type-locality. It is possible that the specimen was deposited in the Herbarium of the California Academy of Sciences, San Francisco, California, and could have been lost in the 1906 San Francisco earthquake. In any case, the Gulf of California material is consistent with Saunders' description of this species in regard to thickness, averaging 0.6 to 0.9 mm. The average length of plurilocular organs measured slightly less than the figures given by Saunders, but the ranges overlap. Although Saunders recorded the plurilocular organs to be uniseriate, those observed in the Gulf of California specimens occasionally possessed biseriate portions as well.

Tuberculate forms of *C. sinuosa* have been variously reported in the literature (e.g., Dawson, 1954; Joly, 1957; Chamberlain, 1965), but what often seems to be represented are much divided, gnarled

forms of *C. sinuosa* rather than the distinctly tuberculate and crisp texture of *C. tuberculata*. Furthermore, it is likely that contorted forms of *C. peregrina* have been mistakenly recorded as *C. tuberculata* from Alaska (Dawson, 1961).

4. *Colpomenia ramosa* Taylor

FIGURE 8a,b

Colpomenia ramosa Taylor, 1945:84, pl. 6: fig. 2.—Dawson, 1949:228; 1951:52; 1952:431; 1954a:117; 1961:394.

Rosenvingea intricata of Dawson, 1944:233, pl. 52; fig. 1 [in part].

DESCRIPTION.—Thalli (Figure 8) forming adherent clumps to 4 cm broad, to 2 cm tall, crisp, with several areas of attachment, irregularly subdichotomously to polychotomously branched, the branches in congested, closely set vertically directed series from broader (to 8 mm) basal portions; the terminal divisions small, cylindrical, 1–2 mm across, 2–3 mm

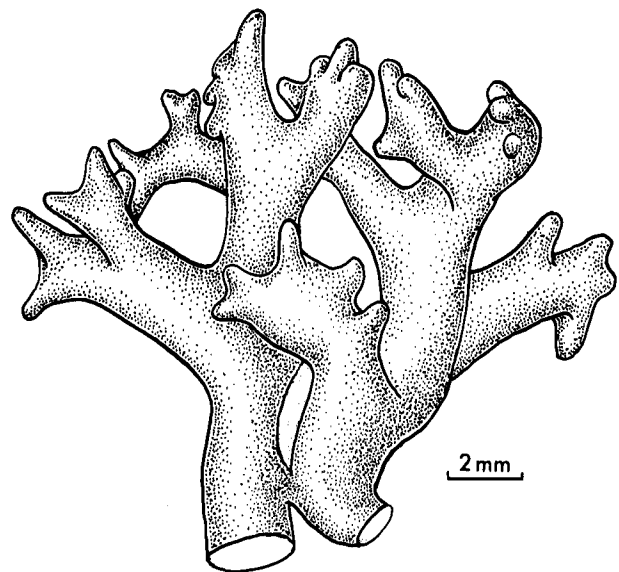


FIGURE 8.—*Colpomenia ramosa* from Puerto Calamajue, Baja California del Norte: a, portions from a clumped thallus (JN-4688); b, detail showing the cylindrical to slightly compressed nature of the branches (JN-4697).

long, with rounded ends; becoming hollow, the wall 200–400 μm thick (to 500 μm thick in type material), 6–8 cell layers thick; small-celled cortex progressing into larger cells inward; plurilocular sporangia in sori, uniseriate, 10–12 locules, 35–40 μm long.

A collection from Academy Bay, Santa Cruz Island, Dawson 26219 (US), now extends the known distribution southward to the Galapagos Archipelago. Previously it had been reported from Isla Cedros to Costa Rica (Dawson, 1954a; Dawson, 1961).

TYPE-LOCALITY.—Bahía Sur, Isla Cedros, Pacific Baja California, Mexico.

HOLOTYPE.—*W. R. Taylor* 34–651 (AHFH); isotypes (MICH, US).

GULF OF CALIFORNIA DISTRIBUTION.—Occasional, Bahía San Luis Gonzaga to Bahía Tepoca, northern Gulf; Isla Espíritu Santo, southern Gulf.

GULF OF CALIFORNIA SEASONALITY.—January–March.

DISTRIBUTION.—Pacific coast of Baja California, and Gulf of California, Mexico; Pacific coast of Costa Rica; and the Galapagos Islands.

SPECIMENS EXAMINED.—*Pacific Coast of Baja California.* Punta Santa Rosalía, 13 Apr 1946, Dawson 1422 (AHFH), Dawson 1514 (AHFH); 9 Oct 1946, Dawson 2760 (AHFH, US); 10 Oct 1946, Dawson 2898 (AHFH). Miller's Landing, Bahía Sebastian Vizcaino, 12 Apr 1946, Dawson 1365 (AHFH). Bahía Sur, Isla Cedros, 10 Mar 1934, *W. R. Taylor* 34–651 (WRT); 5 Mar 1949, Dawson 6550 (US); 19 Apr 1951, Dawson 9836 (AHFH). Punta Malarrimo, Bahía Sebastian Vizcaino, 16 Apr 1951, Dawson 10016 (AHFH). Punta San Eugenio, 1 Nov 1951, Dawson 10351 (AHFH). Bahía San Bartolome (Bahía Tortugas), 11 Feb 1954, Dawson 12267 (US). Bahía Asunción, 28 Apr 1950, Dawson 9163 (AHFH). Punta Abreojos, 30 Apr 1950, Dawson 9478 (AHFH, MICH, US). Punta Pequeña, Bahía San Juanito, 1 May 1950, Dawson 9218 (AHFH, MICH, US). Isla Santa Magdalena, 21 Aug 1946, Dawson 7876 (AHFH); 6 Apr 1955, Dawson 13406 (US). Punta Hughes, Isla Santa Magdalena, 4 May 1950, Dawson 9333 (AHFH). Isla Santa Margarita on Bahía Magdalena side, 9 Mar 1949, Dawson 6613 (US). Bahía Almejas, 7 mi NW of Cabo Tosco, Isla Santa Margarita, 24 Apr 1955, Dawson 13445 (US). *Gulf of California.* Sonora: Bahía Tepoca, 4 Feb 1940, Dawson 385 (AHFH); 19 Feb 1946, Dawson 825 (AHFH); 17 Feb 1973, 5 m depth, JN-6059, (US, UC). Baja California: Isla Willard, Bahía San Luis Gonzaga, 30 Jan 1940, Dawson 306 (AHFH). Puerto Calamajue, 7 m, 28 Mar 1973, JN-4688 (US), and 6 m, JN-4697, (MICH). Bahía San Gabriel, Isla Espíritu Santo, 14 Feb 1940, Dawson 606 (AHFH). *Pacific Coast of Costa Rica.* Port Parker, near Salinas Bay, 24, 25 Mar 1938, *W. R. Taylor*

39–76 (AHFH, US, WRT). *Galapagos Archipelago.* Academy Bay, Santa Cruz Island, 24 Jan 1964, Dawson 26219 (US).

REMARKS.—Up to the present *C. ramosa* Taylor was recorded from Pacific Baja California (Taylor, 1945; Dawson, 1961) and *Rosenvingea intricata* (J. Agardh) Boergesen was recorded from within the Gulf of California (Dawson, 1944). Yet both algae, although placed in two different genera of the same family, present very similar forms and emphasize the tenuous nature of the distinction between these two genera. After examining many specimens, we have concluded that differences do exist to distinguish two species and that although *C. ramosa* is more frequently encountered, there is evidence that *R. intricata* also occurs both in the Gulf of California and on the Pacific coast of Mexico. The specimen presented by Dawson (1944, pl. 52: fig. 1) as "*Rosenvingea intricata*" conforms to *Colpomenia ramosa*. One of his collections cited (Dawson 424) is identifiable as *R. intricata*; the others cited (Dawson 1944:234) are herein referred to *C. ramosa*. The four collections from the Gulf and Pacific Mexico we examined in this study and identified as *Rosenvingea intricata* (J. Agardh) Boergesen (1914:26) are the following: Gulf of California, Baja California: Punta Bufo, N of Arroyo San Luis, in drift, 25 Feb 1975, (US), (leg. M. and D. Littler); Lagoon, Isla Estanque (off S end of Isla Angel de la Guarda) 4 Feb 1940, Dawson 424 (AHFH); Punta Colorada, Bahía de la Paz, 20 May 1965, P-1711 (US), (leg. O. Holquin and J. Vazquez). Guerrero: Acapulco, inner bay, 3 Feb 1947, Dawson 3891 (AHFH, US).

Taylor (1945) described *C. ramosa* as forming a broad, crisp clump, with multiple attachments and with irregular subdichotomous to polychotomous branches. Occasionally this species has thalli resembling those of *R. intricata*. Thalli of the latter taxon are usually erect with loose branching and attached by a basal disk (Taylor, 1928, 1960; Boergesen, 1914; Earle, 1969), but specimens tending toward a subrepent habit also occur. One distinction is that specimens of *C. ramosa* are basically prostrate expanses, coarsely branched and often with short peglike branches, approaching more closely the adherent forms expressed in the genus *Colpomenia* (especially *C. tuberculata*) in contrast to the erect forms typical of *Rosenvingea*. Another difference is that the wall of *C. ramosa*

is much thicker than that of *R. intricata*. According to Taylor (1945), the wall of *C. ramosa* is 6–8 cell layers and about 400–500 μm thick, and the plurilocular organs are uniseriate. Our observations confirm the presence of uniseriate plurilocular organs, up to 12 locules in length, which are in fairly extensive sori.

Although the type material of *C. ramosa* and other collections from Pacific Baja have relatively thick walls, specimens from within the Gulf of California generally have thinner walls, often in the range of 200–300 μm . The wall of *R. intricata* is much less thick, however, being only 3–4 cell layers and less than 100 μm thick (Vickers and Shaw, 1908, as *Striaria attenuata*; Srinivasan, 1960, 1969). Srinivasan (1960) illustrated plurilocular organs in *R. intricata* as biseriate, and we have seen similar short, ovate biseriate plurilocular organs in *R. intricata* collected in Florida and Hawaii (Cape Haze Marine Laboratory, Sarasota, S. Earle 66–303 (US); Waikiki Beach, Honolulu, Oahu, O. Ravanko, 8 Jun 1967 (MICH)). Branching in *C. ramosa* is highly irregular, often with branches arising in groups (polychotomously) randomly over the surface, whereas in *R. intricata* branching is typically divaricate. The texture of *C. ramosa* ranges from crisp to stiff, while that of *R. intricata* is flaccid. Finally, the sori of *C. ramosa* are fairly extensive and visible to the naked eye, but those of *R. intricata* are discrete and small.

Discussion

The assemblage of *Colpomenia* species within the Gulf of California has stimulated us to re-examine the generic delimitations usually employed for the family Scytosiphonaceae. The species of *Colpomenia* discussed in this paper demonstrate that the criteria used in distinguishing *Colpomenia* from related genera, *Scytosiphon* C. Agardh (1811), *Iyengaria* Boergesen (1939), and *Rosenvingea* Boergesen (1914), are often blurred. For example, the cylindrical sacs of *C. phaeodactyla* taken individually could be mistaken for enlarged forms of *Scytosiphon lomentaria* (Lyngbye) Link. One might question the placement of this species in *Colpomenia*, which is regarded as having spherical or globose thalli in contrast to the tubular thalli of *Scytosiphon*.

We concur with Dawson (1944), who posed this

same question, concluding that *C. phaeodactyla* (as *C. sinuosa* f. *deformans* of Dawson) has a very different development from that of *Scytosiphon*. Ontogenetically, the sacs of the former arise as hollow evaginations that push outward from the colpomenioid prostrate basal system; they are hollow from their earliest formation and are hollow even at the juncture with the basal system which produces them. The tubes of *Scytosiphon*, on the other hand, develop as uniseriate filaments (Tatewaki, 1966; Wynne, 1969; Luning and Dring, 1973), that undergo a series of transverse and longitudinal divisions resulting in a hollow tube but remaining solid at the base. Thus, the initial form observed in these two genera is quite different. Wynne (1972) has shown in culturing *C. phaeodactyla* that the young germlings are spherical (conforming to its assignment to *Colpomenia*). From field studies we have also seen that the young stages of *C. phaeodactyla* consist of spreading colpomenioid systems from which erect tubes will be produced as evaginations.

The problem of distinguishing *Iyengaria* Boergesen (1939) from *Colpomenia* has been discussed earlier (Wynne, 1972). The only species of this genus, *I. stellata* (Boerg.) Boergesen was described as *Rosenvingea stellata* Boergesen (1928) and later transferred to *Colpomenia* (Boergesen, 1930). Boergesen's primary distinguishing trait in establishing *Iyengaria* (Boergesen, 1939) was the localization of growth to projections covering the thallus rather than the diffuse growth present in *C. sinuosa*. Although the surface of *C. tuberculata* is not covered with the densely clustered projections that occur in *I. stellata*, there would seem to be a difference in degree rather than in kind, and we would suggest that *Iyengaria* be merged with *Colpomenia* and that *C. stellata* (Boerg.) Boergesen (1930) be reinstated. Chamberlain (1965) also referred to the dubious nature of *Iyengaria*, but states that another apparent difference from *Colpomenia* is the absence of paraphyses among the plurilocular organs in *Iyengaria*. The latter character is of questionable value, and in other genera of the family, such as *Scytosiphon* (cf. Wynne, 1969), there is variation from one species to the next.

A third difficult distinction is that between the genera *Colpomenia* and *Rosenvingea*. The primary

characteristic for separating *Rosenvingea* from the remaining Scytosiphonaceae is its branching nature. Yet branching *Colpomenias* have been described as *C. ramosa*, *C. mollis* Taylor (1945), and *C. nainativensis* Durairatnam (1962). Difficulties arise in distinguishing taxa such as *C. ramosa* from *R. intricata* (J. Agardh) Boergesen and in distinguishing *C. nainativensis* from *R. nhatrangensis* Dawson (1954b). We will focus our attention on the former pair of species. *Rosenvingea* contains species with typically erect, tubular, branching thalli. Specimens of *R. intricata* are usually erect with loose branching and attached by a basal disk

(Taylor, 1928, 1960; Boergesen, 1914; Earle, 1969, figs. 111, 112), but sometimes specimens tending toward a subrepent condition occur. On the other hand, specimens of *C. ramosa* are basically prostrate expanses, coarsely branched, approaching more closely the adherent forms expressed in the genus *Colpomenia* (e.g., *C. tuberculata*) than the erect forms typical of *Rosenvingea*. Other differences might be cited to distinguish *C. ramosa* from *R. intricata*. The wall of *C. ramosa* is 6–8 cell layers about 400–500 μm thick, and, according to Taylor (1945), the plurilocular organs are uniseriate. The wall of *R. intricata* is much less thick, being only

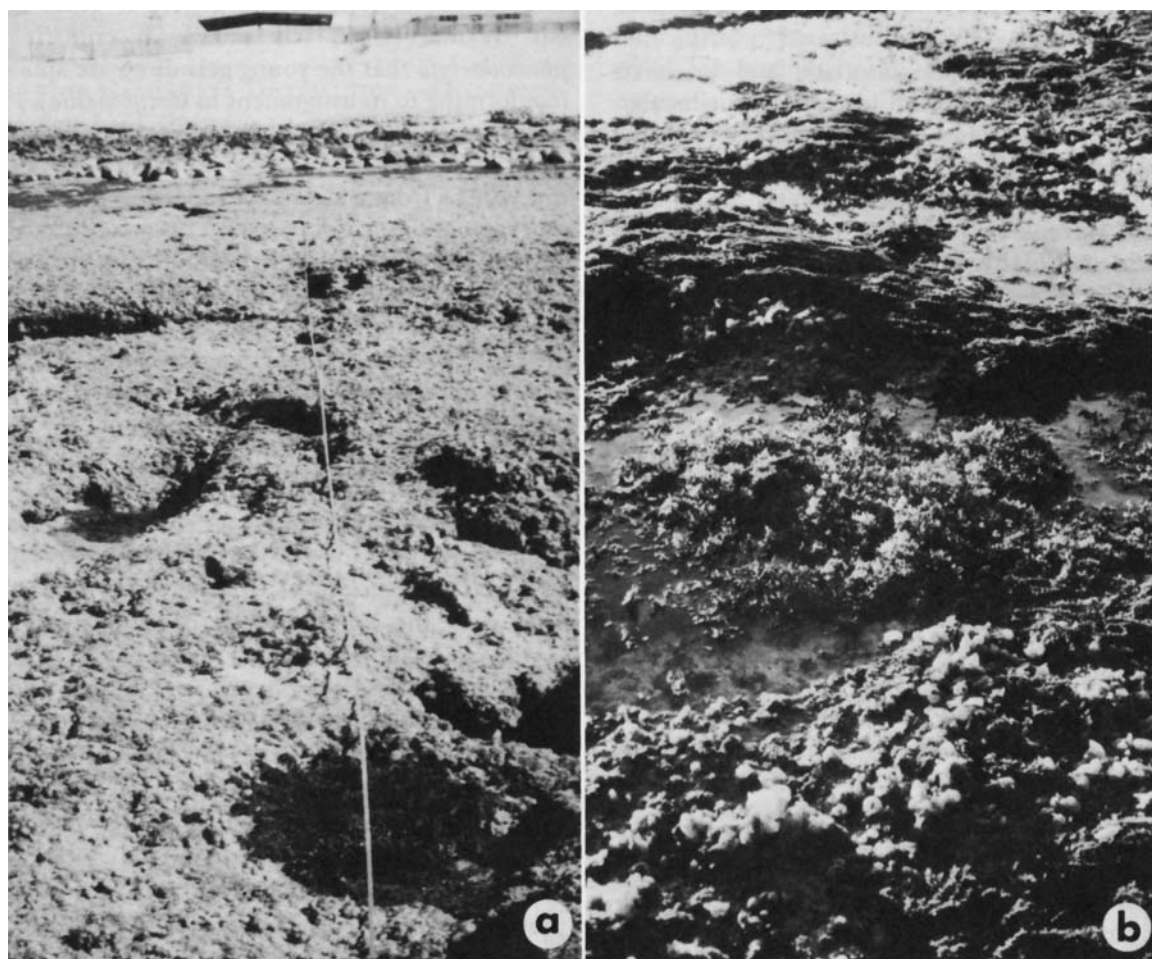


FIGURE 9.—Intertidal region of Playa Estación (in front of Laboratorio de Biología Marina), Puerto Peñasco: *a*, high to middle tidal levels in the spring dominated by *Colpomenia tuberculata* and *Laurencia paniculata*, with a few plants of *C. phaeodactyla* also present (April 1974) (note the transect line running between permanent markers); *b*, lowermost intertidal region, dominated at this season by *Colpomenia sinuosa* and *Sargassum herporhizum* (February 1974).

3–4 cell layers and less than 100 μm thick (Vickers and Shaw, 1908, pl. xxiv, as *Striaria attenuata*; Srinivasan, 1960). Srinivasan (1960) illustrated plurilocular organs to be biseriate. So in conclusion, we are of the opinion that forms of these two genera closely approach each other in their morphologies, but *Colpomenia* includes forms which range from spherical to saccate to prostrate expanses, while *Rosenvingea* includes freely branched, primarily erect forms.

Ecological Observations

Studies on the intertidal biotic community at Playa Estación, Puerto Peñasco, Sonora, (Figure 9a,b) have shown marked seasonal changes in algal species and their population sizes. Data from bi-monthly censuses, February to December 1974 (Norris, unpublished), were obtained from a 100 meter line transect placed perpendicular to the shoreline. Frequency, number of individuals, and percent cover were recorded on each census for seasonal comparisons. Seasonal differences in the population sizes of the three *Colpomenia* species present (*C. phaeodactyla*, *C. tuberculata*, and *C. sinuosa*) are summarized in Figure 10.

SEASONALITY.—Plants of each species begin to appear in November. By December populations of *C. phaeodactyla* (Figure 11c) and *C. sinuosa* (Figure 11a) are larger than those of *C. tuberculata* (Figure 11b). In February the populations of the three species are similar in numbers of individuals and percent coverage. Combining the percent coverage figures for all three species shows that during February *Colpomenia* species covered 19% of the entire intertidal transect. With such a high coverage, it intuitively seems that biomass would also be high (not measured, since it would have disturbed the sample transect), and the species of *Colpomenia* would play an important ecological role from February to April (12.5% coverage). Populations of *C. phaeodactyla* and *C. sinuosa* dropped by April; in June they appeared absent. In contrast, *C. tuberculata* reached its peak in April, and during that month it was the most abundant organism present. No species of *Colpomenia* were observed on the study line in August or October.

DISTRIBUTION.—*Colpomenia phaeodactyla* is re-

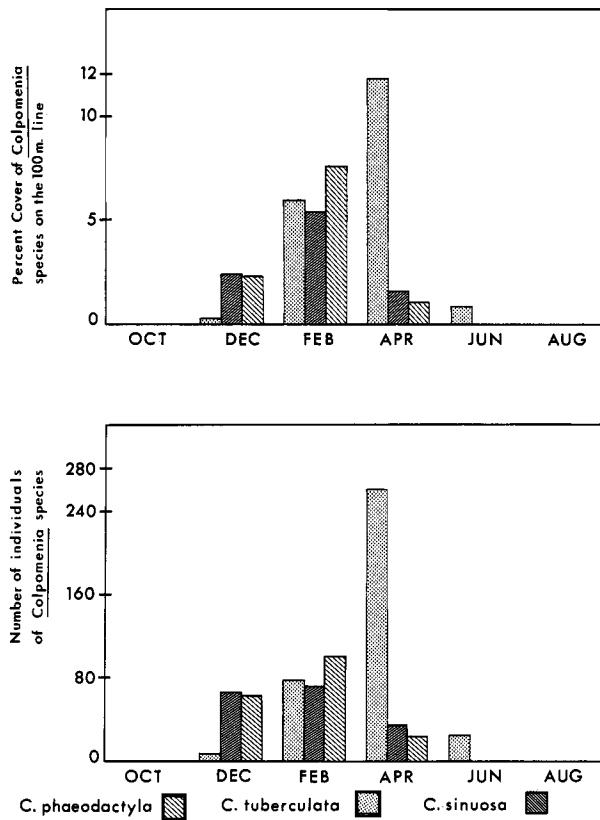


FIGURE 10.—Seasonal comparison of the numbers of individuals and coverage of the species of *Colpomenia* on the intertidal transect at Playa Estación, Puerto Peñasco during 1974.

stricted mostly to the middle and low intertidal range, growing on top of the platform (caliche capped coarse sandstone with shell materials) and occurring only occasionally in tide pools. *Colpomenia tuberculata* ranges throughout the intertidal zone from high to low tidal levels, growing on the platform, or epiphytic on other algae, particularly *Laurencia paniculata*. *Colpomenia sinuosa* is almost entirely found in the low tidal range (sometimes at higher levels, but then usually in tide pools) and extended into the shallow subtidal. While occasionally attached to rocks, it is mostly epiphytic on other algae including *Sargassum*.

PRODUCTIVITY.—Measurements for two species of *Colpomenia* growing sympatrically, reveal different rates of carbon fixation. *Colpomenia phaeodactyla* has a mean net rate (\pm one S.D.) of $2.58 \pm$

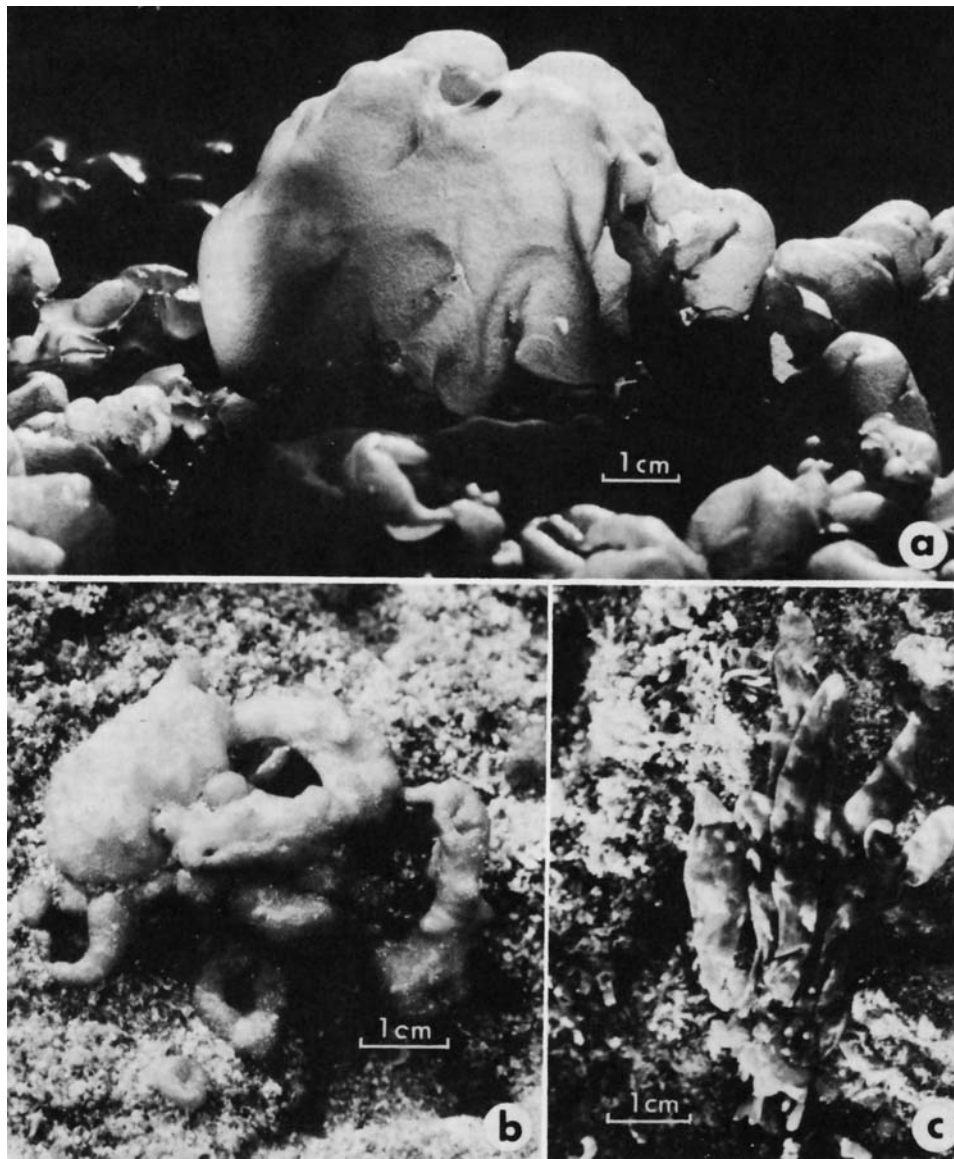


FIGURE 11.—Habitat photographs of *Colpomenia* species from Playa Estación, Puerto Peñasco (February 1974): a, *C. sinuosa*; b, *C. tuberculata*; c, *C. phaeodactyla*.

0.08 mg C fixed/gram dry weight/hour, and in contrast, *C. tuberculata* shows a mean rate of 1.10 ± 0.04 mg C fixed/gram dry weight/hour. These data were obtained by Dr. M. Littler (pers. comm.) during a high tide period using three light and two dark bottle replicates (each containing 3–5 thalli)

for each species at Punta Bufeo (just north of Punta Willard, Bahía San Luis Gonzaga), Baja California del Norte, 25 Feb 1975. Light varied between 1200–1700 $\mu\text{E}/\text{m}^2/\text{sec}$ (PAR) and 52,500–66,000 lux during the 10:30 am to 2:50 pm period of in situ incubation.

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