Validation of the names of two new species of *Codium* (Chlorophyta, Bryopsidales) from Isla Guadalupe and Rocas Alijos, Pacific Mexico and the southern California Channel Islands, with some remarks on insular endemism

**Abstract:** The names *Codium schmiederi* and *Codium dawsonii* are validated by the provision of designated types. The species to which the invalidly published name *C. schmiederi* applies is known only from Isla Guadalupe and Rocas Alijos, Baja California, Mexico. The history of phycological exploration of these two remote localities is detailed. The species to which the invalidly published name *C. dawsonii* applies is found in those two localities as well as on coastal islands of Baja California and southern California. It is seldom found on the mainland. *Codium hubbsii*, originally described from Islas San Benito, has a distribution similar to that of *C. dawsonii*, but occurs more often on the mainland. The distributions of these three species constitute a pattern of insular endemism.

**Keywords:** California Channel Islands; *Codium dawsonii*; *Codium hubbsii*; *Codium schmiederi*; Isla Guadalupe; Rocas Alijos.

Introduction

Phycological exploration of Isla Guadalupe and Rocas Alijos, Pacific Mexico, has revealed striking similarities between the two marine floras, including the presence at both of these remote sites of two new species of *Codium*. Descriptions of the sites and the history of their phycological exploration follow.

Isla Guadalupe

Isla Guadalupe (28.8833° N, 118.3000° W) is a volcanic oceanic island 260 km west of the peninsula of Baja California. It is about 37 km long and 12 km wide, with a maximum height of 1295 m. An excellent account of the island, including its daunting physical features and history of exploration (and exploitation) is provided in detail by Moran (1996). The first naturalist to introduce to science the flora of this remote and inhospitable island was Edward Palmer (1831–1911), a professional collector with a special interest in plants. According to his biographer (McVaugh 1956), Palmer was eager to collect the plants before they were destroyed by goats, which had been put on the island for commercial purposes. After he visited the island in 1875 (February 1–May 16), his collections were arranged systematically and distributed by the Gray Herbarium at Harvard under the supervision of Sereno Watson, its curator and chief supporter of Palmer’s venture. Eleven sets were distributed, including one to Daniel C. Eaton of Yale University. Although the list of Palmer’s Guadalupe collections published by Watson (1876) is devoid of algae, Farlow (1877) stated that several interesting forms of marine algae had been collected, but he provided no details. Three of these have entered scientific literature, as follows.
Material of a *Sargassum* collected by Palmer was distributed under the name *Sargassum piluliferum* (Turner) C. Agardh as no. 102 in Exsiccatae Americae Borealis (Farlow et al. 1878). In his monograph of *Sargassum*, Grunow (1915) recognized this material as representative of an undescribed species, which he named *Sargassum palmeri*. During the hiatus of communication in World War I, Setchell and Gardner (in Gardner 1917) independently came to the same conclusion, proposing the name *Sargassum dissecifolium*, which they later (Setchell and Gardner 1925) abandoned in favor of *S. palmeri*.

Material of a *Codium* collected by Palmer remained undetermined in various herbaria. A duplicate of this *Codium* in the Daniel Cady Eaton Herbarium at Yale was sent to Setchell by F.S. Collins (UC 207177). Setchell and Gardner (1920) referred it to *Codium latum* Suringar, a foliose species originally described from Japan. Later, Setchell annotated the sheet “= C. Palmeri” Setchell sp. nov. May 1925”. Setchell and Gardner (1930) reconsidered Palmer’s collection of *Codium*, writing:

“We feel inclined to separate the Guadalupe plant and dedicate it to its collector, but in view of the uncertainty as to the situation among the Japanese species, we retain our previous disposition of it...” The name *Codium palmeri* was published by Dawson (1945). Silva (1962) treated the taxon as a subspecies of *C. latum*, a treatment maintained by Pedroche (1998) and Pedroche et al. (2002, 2005).

A single specimen of a *Microdictyon* collected by Palmer was observed in the Farlow Herbarium by Collins (1909, p. 366), who identified it as *Microdictyon agardhi-anum* Decaisne. In his monographic study of *Microdictyon*, Setchell (1925, pp. 104, 106; 1929, p. 535, figs. 57–61) recognized this specimen as representative of an undescribed species, which he named *Microdictyon palmeri*.

Following Palmer’s lead, several naturalists and botanists visited Isla Guadalupe; significant collections of algae were first obtained in 1925, by Herbert L. Mason on the California Academy of Sciences Expedition to the Revillagigedo Islands. En route to the Revillagigedo Archipelago, the expedition spent 4 days at Isla Guadalupe (April 19–22, 1925), enabling Mason to collect a sufficient variety of seaweeds to supply Setchell and Gardner (1930) with type specimens of 24 new species and varieties. Mason’s collections also included representatives of *Codium fragile* (Suringar) Hariot, a species originally described from Japan but widespread in cold temperate waters everywhere, and *Codium simulans* Setchell et Gardner, originally described from the Gulf of California. Collections of algae were made on Isla Guadalupe by John Thomas Howell on the Templeton Crocker Expedition of the California Academy of Sciences in 1932 (the “Zaca Expedition” in reference to the name of the yacht), but only novelties were published (Setchell and Gardner 1937).

The Great Depression and World War II stopped further exploration. At the end of the war, several minor expeditions were mounted by the San Diego Natural History Museum and the Scripps Institution of Oceanography. Carl Hubbs, the eminent ichthyologist at Scripps, began sending seaweeds that had been collected incidentally to E. Yale Dawson, then at the Allan Hancock Foundation at the University of Southern California in Los Angeles. Dawson, himself, was able to visit the island in 1948, returning with several collections of *Codium*, which he sent to P.C. Silva.

Silva soon had an opportunity to see the Isla Guadalupe *Codium in situ*. He served as phycologist on a series of expeditions on board the RV *Orca*, sponsored by the Joseph W. Sefton Foundation of San Diego. One such trip, in January 1950, had as its goal the exploration of the Mexican Pacific coastal islands from Isla Los Corridos to Islas San Benito and, thence, to Isla Guadalupe. The terrain of the latter island is so rugged and the cliffs so daunting that only a few sites are suitable for intertidal collecting, and these are most readily accessible by jumping from a small boat. Silva landed on a narrow platform with deep tide pools at West Anchorage. He discovered that he was in a *Codium* garden, with six species at his fingertips. Back on board the *Orca*, he examined the anatomy of the *Codium* collections and found that there were two obviously undescribed species in addition to *C. palmeri*, *C. fragile*, *C. simulans*, and an adherent form soon to be described as *Codium hubbsii* Dawson (1950). The two undescribed species were tentatively named *Codium dawsonii* and *Codium seftonii*.

By comparing the list of Palmer’s collections of siphonophytes with the contemporaneously known distribution of these species, Moran (1996, p. 45) inferred that Palmer did not reach the south end of the island, which is the location of Melpomene Cove, an excellent collecting site. Rather, he probably got as far south as West Anchorage so that it is likely that Silva was standing on the same platform where Palmer collected *C. palmeri*.

The collections made by Dawson and Silva were put aside, while other regional monographs were being prepared. They were eventually entrusted to Pedroche, whose doctoral thesis on the *Codium* of Pacific Mexico was published in 1998 (Pedroche 1998). In 2000, Pedroche served as phycologist on a binational expedition to Isla Guadalupe sponsored by the San Diego Natural History Museum. Pedroche’s thesis was published as a monograph co-authored by Silva and Chacana (Pedroche et al. 2002).
Rocas Alijos

Rocas Alijos (24.9586° N, 115.7497° W) are the remnants of an ancient volcanic island lying about 550 km southeast of Isla Guadalupe and 320 km west of the Baja California peninsula at a latitude of 25° N. There are three main emergent pinnacles, the tallest of which is 34.5 m high. The first scientific expedition to Rocas Alijos was sponsored by the California Academy of Sciences (Hanna 1926). En route from Isla Guadalupe to Isla Clarión, the U.S. mine sweeper Ortolan lay at Rocas Alijos the morning of April 24, 1925. Dynamiting for fish resulted in a few seaweeds, but their fate is unknown. Dawson (1957) summarized subsequent algal exploration of Rocas Alijos, pointing out that the first comprehensive collections were made by Conrad Limbaugh, who SCUBA dived during an expedition sponsored by the Scripps Institution of Oceanography. Among Limbaugh’s collections was a specimen of Codium hubbsii (misidentified by Dawson as Codium setchellii).

In 1990, the Cordell Expeditions, a nonprofit organization founded by Robert W. Schmieder and based in Walnut Creek, California, mounted a full-scale operation with a scientific crew of 30. Robert A. Rasmussen (Humboldt State University, Arcata, California) was responsible for collecting or supervising the collections of marine algae. A second Cordell Expedition visited Rocas Alijos in November 1993, with 12 scientists. An account of these collections is given by Silva et al. (1996), who concluded that the marine flora may be considered an impoverished selection of the flora of Isla Guadalupe. Two previously undescribed species of Codium, Codium dawsonii and Codium schmiederi, were found to occur at both localities, in addition to C. hubbsii. While C. dawsonii and C. schmiederi have been cited (Silva et al. 1996, Pedroche 1998, Pedroche et al. 2002, 2005), their names have not yet been validly published. The purpose of the present account is to validate these names and to discuss the phytogeographic relationships of Codium as represented at Isla Guadalupe, Rocas Alijos, and coastal islands of California and Baja California, Mexico.

Systematic treatment

Codium schmiederi P.C. Silva, F.F. Pedroche, M.E. Chacana (Figures 1 and 2)

Thallus prostrate, pulvinate, with erect or repent portions branched irregularly or subdichotomously (Figure 1). Branches cylindrical or compressed, 3–12 mm wide at interdichotomies, 20 mm broad at dichotomies, intertwining, anastomosing, attached to substrate here and there; pulvinate portion 3–5 mm thick, spongy, adhering loosely to the substrate. Thallus easy to dissect, mature utricles cylindrical, (900–) 1000–1300 (–1800) μm long, (89–) 110–190 (–390) μm in diameter. Utricles from adherent portion of thallus showing much reduced sympodial growth, resulting in groups of utricles, most with two septa, one for each medullary filament (Figure 2A). Utricles of the branched portion of the thallus showing less compact growth (Figure 2B). Apices truncate or slightly rounded with thin walls (no more than 2–4 μm in thickness). Hairs (or hair scars) common in zone 110–280 μm below apex. Medullary filaments 30–60 μm diameter. Gametangia fusiform or lanceolate, (150–) 210–300 (–350) μm long, (45–) 60–90 (–120) μm diameter, several per utricle borne on cylindrical pedicel 15–30 μm long in zone 330–540 μm below apex.

Holotype

Isla Guadalupe, Baja California, Mexico, on shore, 2.5 miles N of South Bluff, E.Y. Dawson 8518, 20.xii.1949 (UC 1718021). Isotype at US (USNM 230805) (Figure 1).

UC specimens and label information may be viewed by entering the collection number at: //ucjeps.cspace.berkeley.edu/ucjeps_project/public/publicsearch/.
Figure 2 Utricles of *Codium schmiederi* (UC 1718021). Scale bar=750 μm. (A) Utricles from prostrate portion. Utricles with much reduced sympodial growth, resulting in small groups in which interutricular filaments are eliminated. (B) Utricles from upright axes. Primary utricles produce additional utricles by emitting basally a filament that grows periclinally, enlarging to form a new utricle. A plug (arrows) is always formed at or very close to the point of origin of the filament.

**Specimens examined**

Isla Guadalupe: UC 1718024, AHFH 79209 in UC (UC 1831543), UC 1718018, UC 1718019, UC 1718020, AHFH 72024 in UC (UC 1831545). Rocas Alijos: UC 1946216, UC 1946217.

*Codium schmiederi* is dimorphic in habit, with a prostrate base from which upright or repent axes arise. The utricles are also dimorphic, differing in basal and upright portions (Figure 2A, B). This morphological and anatomical dimorphism is unique among known species of *Codium*.

In *Codium*, all primary utricles are formed by enlargement of deflected apices of sympodially growing filaments. In most species, the development of secondary utricles follows one of two paths. In erect dichotomously branched thalli, primary utricles produce additional utricles by emitting basally a filament that grows periclinally, enlarging terminally, and deflecting anticlinally to form a new utricle. A plug is always formed at or very close to the point of origin of the filament. (For examples, see Silva and Womersley 1956, figs. 8–16; Silva 1959, figs. 10–21.)

In *C. schmiederi*, by contrast, the adherent portion of the thallus, which initially resembles a thallus of *Codium hubbsii*, does not produce “families” of utricles typical of adherent species. Instead, small groups of utricles result from greatly reduced sympodial growth in which interutricular filaments are eliminated. Perversely, the intertwining branches produce small groups of utricles resembling families typical of adherent species.

The pattern of utricle formation described above as being typical of *Codium* has many exceptions, depending on the length of the interutricular filament. The pattern most closely similar to that of *C. schmiederi* is that of *Codium coralloides* (Kützing) P.C. Silva. In that species, however, the branches are rudimentary. In *Codium pelliculare* P.C. Silva (1959), in which the thallus is membraniform, secondary utricles bud off the lower or middle portion of an existing utricle, but most do not develop rhizoids. In *Codium pictatum* F.F. Pedroche et P.C. Silva (1996), which has an extremely thin adherent thallus with a tightly woven medulla, some interutricular filaments are so short that clusters of secondary utricles are formed. In some parts of the thallus, the distribution of secondary utricles, interutricular filaments, and plugs is chaotic (Pedroche and Silva 1996, figs. 3, 4).

Previous records: as *C. schmiederi* Silva ined. in Schmieder (1996: 235); as *C. schmiederi* Silva, Pedroche et Chacana ined. in Pedroche et al. (2002: 30, figs. 24–28), Pedroche et al. (2005: 76).

In 1952, after returning from an expedition to islands off the coast of Baja California on board the RV *Orca*, Silva undertook a study of the collections of *Codium* and intended to name this species *Codium seftonii* in honor of Joseph W. Sefton, Jr., a San Diego banker and owner of the ship. Prior to the publication of this species, however, Mr.
Sefton died. The intended honor was transferred to Robert W. Schmieder, the remarkably enterprising explorer who organized the expedition to Rocas Alijos.

Codium dawsonii P.C. Silva, F.F. Pedroche, M.E. Chacana et K.A. Miller (Figures 3 and 4)

Thallus erect, profusely branched to 10 orders, delicate (Figure 3). Branching usually dichotomous or subdichotomous, but often irregular, giving monopodial aspect to thallus. Branches cylindrical to compressed, especially at the dichotomies and apices, 4 (–5) mm diameter at base, 1.5–2 mm diameter distally, to 13 (–20) cm high. Thallus attached to substrate (rocks or shells) by discoid holdfast. Color olive green to grass green. Thallus dissecting out into individual utricles. Utricles claviform or campanulate, slightly constricted below the apex, (69–) 100–170 (–200) μm diameter, (370–) 400–500 (–580) μm long in upper portion of thallus, (40–) 60–90 (–110) μm diameter basally. Apices of utricles truncate or rounded, apical wall slightly thickened (to 13 μm thick). Hairs or hair scars borne in zone 45–100 μm below apex of utricle. Medullary filaments 20–30 μm diameter (Figure 4). Gametangia lanceolate or fusiform, (58–) 62–75 (–85) μm diameter, (140–) 160–190 (–210) μm long, borne singly on short pedicel in zone 200–300 μm below apex of utricle.

Holotype: Mosquito Cove, San Clemente Island, California, on shallow boulders and reefs with dense algal cover, 6–9 m depth, K.A. Miller SC V-012-88, 22.v.1988 (UC 1718035) (Figure 3).

Specimens examined (north to south)

Channel Islands, California
Santa Cruz Island: UC1612968, UC1574488, UC1574797, UC1574793, UC1996200. Anacapa Island: UC1996201. Santa Barbara Island: UC1574796, UC1718036, UC1996198, UC1996199, UC1996197. Santa Catalina Island: UC1574794, UC1819304, UC1985389, UC1883562, UC1819309, UC1985388, UC1985390; UC1985392, UC1985391, UC1883561, UC1996193. San Clemente Island: UC1574789, UC1717994, UC1996196, UC1996195.

Baja California, Mexico (insular)
Islas Los Coronados: UC1965988, UC1574387. Isla Guadalupe: UC1818855, UC1818854, UC1818857, UC1718031.

Baja California, Mexico (mainland)
Ten miles west of Punta Malarrimo, Bahía Viscaíno: UC1918822.

Previous records: as Codium dawsonii Silva ined. in Goff et al. (1992: 1280); Schmieder (1996: 235); as C. dawsonii Silva, Pedroche et Chacana ined. in Pedroche et al. (2002: 49, figs. 59, 60), Pedroche et al. (2005: 71).
Following a preliminary study of *C. dawsonii* from Isla Guadalupe, Silva (1951) published a monograph of the *Codium* of California, but failed to recognize the presence of *C. dawsonii* in the Channel Islands. Instead, he assigned a collection from Santa Cruz Island and one from Santa Catalina Island to *Codium cuneatum* Setchell et Gardner (1924) a species originally described from the Gulf of California that was merged with *Codium simulans* Setchell et Gardner (1924) by Pedroche (1998). Silva included in *C. cuneatum* a disparate array of specimens from southern California and northern Baja California.

In the 1980s, Kathy Ann Miller began making sublittoral surveys of the Channel Islands and discovered that *C. dawsonii* grows abundantly and luxuriantly in the southern Channel Islands at depths of 9–12 m. In an attempt to determine whether the Gulf species, *C. simulans* (≡ *C. cuneatum*), occurs in California, Miller provided material from the type specimens of all species described by Setchell and Gardner (1924) from the Gulf of California to Jeffrey R. Hughey. On the basis of comparison of nucleotide sequences obtained from these specimens, he concluded (pers. comm.) that *C. dawsonii* is distinct from all species of *Codium* described from the Gulf of California by Setchell and Gardner (1924).

*Codium dawsonii* can be distinguished from *Codium fragile* subsp. *californium* C. Maggs et J. Kelly by its lighter color, shorter internodes, and numerous orders of branching. The compressed dichotomies and apices are diagnostic.

### *Codium hubbsii* E.Y. Dawson


#### Holotype

Islas San Benito, Baja California: *Hubbs 46-205, 18.viii.1946* (AHFH 36930 in UC).

#### Specimens examined (from north to south)

**Channel Islands, California**


San Diego County: UC1953501, UC1953498, UC1953497.

**Baja California (insular)**


**Baja California (mainland)**


This species is one of several adherent forms distinguishable from one another by anatomical characters that may seem trivial to the nonspecialist. The differences are, in fact, sufficiently large to suggest that these species constitute a distinct phylogenetic group. On the Pacific coast of North America, the only adherent species other than *Codium hubbsii* is *Codium setchellii* Gardner (1919: 489, pl. 42: figs. 10, 11; type locality Pacific Grove, California), which is readily distinguished by the lack of hairs or hair scars and by the smooth, unornamented apical walls of the utricles. In contrast, utricles of *C. hubbsii* frequently bear hairs and have apical walls that are usually at least slightly alveolate.

On the mainland of California, *C. setchellii* usually grows on the sides of boulders partly buried in sand, in the lowest intertidal zone. The thallus forms a tightly adherent carpet that spreads out in all directions. The advent of SCUBA, however, has led to the discovery of a subtidal adherent *Codium* that is anatomically indistinguishable from the intertidal form. According to Dawson et al. (1960a,b), *C. hubbsii* and *C. setchellii* are common inhabitants of kelp beds in Baja California at depths of 9–23 m, where they have the same habit and habitat and are macroscopically indistinguishable.

Whereas *C. setchellii* survives cold water as far north as Sitka, Alaska, and thrives in upwelling areas in Baja California as far south as Punta Baja (Dawson 1953: 109), *C. hubbsii* requires a higher optimal temperature. It occurs as far north as the southern Channel Islands of California, proceeding southward through the Mexican coastal islands and thence along the coast of Baja California Sur as far as Punta Abreojos. At Isla Guadalupe, *C. hubbsii* grows both intertidally and subtidally (to depths of 25 m). The attribution of *C. setchellii* to Isla Guadalupe, Isla Asunción, and other localities south of Punta Baja by
Pedroche (1998) and Pedroche et al. (2002, 2005) is based on a misidentification of *C. hubbsii*.

**Discussion and conclusion**

Endemic marine algae are well known for the Juan Fernandez, Galapagos, and Hawaiian archipelagos, but they also exist among smaller islands, such as Isla Guadalupe and Rocas Alijos off the Pacific coast of Baja California. *Sargassum palmeri* Grunow, *Stephanocystis neglecta* (Setchell et Gardner) S. Draisma, E. Ballesteros, F. Rousseau, et T. Thibaut and *Liagora californica* Zeh, which are known only from Isla Guadalupe and the southern Channel Islands, are examples of island endemics in California and northern Baja California, Mexico.

*Codium schmiederi* is a narrow endemic, found only at Isla Guadalupe and Rocas Alijos. *Codium dawsonii* is a near island endemic that is common in the southern California Channel Islands but absent from the California mainland. It has been found at one site on the mainland of Baja California, Mexico (Bahía Viscaíno); it is very possible that further searches in southern Baja California or the Mexican mainland may discover more specimens of this species. *Codium hubbsii* also occurs at Isla Guadalupe and Rocas Alijos, as well as the Channel Islands of southern California. It, too, is absent from the southern California mainland but occurs on the mainland of Baja California southward to Bahía Asunción.

It is not possible to determine the factors that gave rise to the different degrees of endemism exhibited by these species of *Codium*. They may be the result of evolutionary history, a pattern of survival following changes to the mainland coast, evidence of differing dispersal capabilities – or a combination of these possibilities.

**Acknowledgments:** Collections in the California Channel Islands were possible due to the extraordinary generosity of the Tatman Foundation’s Channel Islands Research Program (John M. Engle, Jerry and Henri Chomeau, Chris Bungener), who sponsored and operated diving cruises in the R/V Cormorant for the last 35 years. We thank the Editor and reviewers for comments that improved this manuscript.

**References**


Setchell, W.A. and N.L. Gardner. 1924. Expedition of the California Academy of Sciences to the Gulf of California in


