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A dichotomous species of *Codium* (Bryopsidales, Chlorophyta) is colonizing northern Chile

Una especie dicotómica de *Codium* (Bryopsidales, Chlorophyta) está colonizando el norte de Chile

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ABSTRACT

In late 2001 and early 2002, a dichotomous species of *Codium* appeared colonizing the low intertidal and shallow subtidal bottoms of Caldera Bay, northern Chile (27º03' S, 70º51' W). Due to the ecological and economic impact the species is having in Caldera Bay and its potential spread along the Chilean coastline, we studied the taxonomic identity of the species and examined its relationships with other dichotomous species of *Codium* reported for temperate Pacific South America. Morphological analyses suggest that the seaweeds from Caldera Bay belong to *Codium fragile* (Suringar) Hariot. Not only is there strong agreement in internal and external morphological characters, but among all the species reported for Peru and Chile, this is the only one exhibiting utricles with rounded, apiculate tip terminating in a mucron. This species has a broad geographic distribution in temperate waters. In Chile it was known only from the coasts of Valdivia to the Straits of Magellan (39º48' S, 73º26' W to 53º10' S, 73º49' W). This is the first record of *C. fragile* in northern Chile, and this study discusses several alternative hypotheses for the presence of the species into this area. The morphological characteristics of the material collected in Caldera partially agree with diagnostic characters known for *C. fragile* subspecies *tasmanicum* and *C. fragile* subspecies *tomentosoides*. However, the rapid population spread of the species in northern Chile, and recent molecular analysis support the identification of this form as the invasive *C. fragile* subspecies *tomentosoides*.

Key words: *Codium*, introduced species, Chlorophyta, seaweed, northern Chile.

RESUMEN

A fines de 2001 y principio de 2002 apareció en el norte de Chile una especie del género *Codium,* de morfología dicotómica, colonizando los niveles intermareales y submareales de la Bahía de Caldera (27º03' S, 70º51' O). Debido al impacto ecológico y económico que ha provocado esta especie en la Bahía de Caldera y a su dispersión potencial a lo largo de la costa de Chile, estudiamos la identidad taxonómica de la especie, examinando su relación con las especies de *Codium* de hábito erecto descritas para la costa temperada del Pacífico Sudamericano. El análisis morfológico sugiere que el alga encontrada en la Bahía de Caldera corresponde a la especie *Codium fragile* (Suringar) Hariot. Tanto los caracteres morfológicos internos como externos del alga son concordantes con la descripción de la especie, incluyendo utrículos de ápices redondeados apiculados terminados en un mucron puntiagudo. Esta especie posee una amplia distribución geográfica en aguas temperadas. En Chile, es conocida solo para las costas entre Valdivia y Magallanes (39º48' S, 73º26' O a 53º10' S, 73º49' O). Este es el primer registro de *C. fragile* en el norte de Chile y además este estudio discute diversas hipótesis alternativas de introducción de la especie en el área. Las características morfológicas de los materiales colectados en Caldera concuerdan parcialmente con los caracteres diagnósticos conocidos para *C. fragile* subespecies *tasmanicum* y *C. fragile* subespecies *tomentosoides*. Sin embargo, la expansión poblacional rápida que la especie está mostrando en el norte de Chile junto con análisis moleculares recientes apoyan la identificación de estas poblaciones como pertenecientes a la subespecie *tomentosoides*.

Palabras clave: *Codium*, especies introducidas, Chlorophyta, algas, norte de Chile.

INTRODUCTION

Codium Stackhouse (Bryopsidales, Codiaceae) is one of the most common and widespread seaweed genera in the world (Silva 1951). There are about 100 described species, growing on rocky or sandy habitats in tropical and temperate waters (Goff et al. 1992, Silva 1992). External morphology includes individuals that have either a crustose, cushion-like form that covers the substratum ("the prostrate species") or that attach to the substratum at a single point, with the rest of the plant being erect and with cylindrical dichotomously branched axes ("the dichotomous species"). Both morphological types are composed of a tightly woven mass of coenocytic medullary filaments surrounded by a cortex of utricles. The utricles, which are the swollen cortical tips of the filaments, typically have colourless spine-like, rounded or pointed cell wall projections and cell thickenings, frequently used as taxonomic characters (Silva 1955, Burrows 1991).

A total of 14 species of *Codium* have been described for temperate Pacific South America (see Ramirez & Santelices 1991 for listing). Of these, eight species are dichotomous and six are prostrate. Not a single dichotomous species has been reported from northern or central Chile (Arica to Concepción; 18º29' S, 70º19' W to 36º47' S, 73º14' W). The dichotomous *C. contractum, C. tomentosum* and *C. fragile* have been described for southern Chile (Concepción to the Straits of Magellan), while *C. fernandezianum, C. pocokiae* and *C. unilaterale* have been registered for the Chilean oceanic islands only (Isla de Pascua, Juan Fernández y Desventuradas). On the other hand, *C. peruvianum* and *C. foveolatum* have been ascribed to the Peruvian coast only (Paita, Piura and Lima, and Piura respectively).

In late 2001 and early 2002, a dichotomous species of *Codium* appeared colonizing the low intertidal and shallow subtidal bottoms of Caldera Bay in northern Chile (27º03' S, 70º51' W, E. Martínez personal communication). By the end of August of 2003 the species had already spread to Obispito, 45 km to the north of Caldera Bay, and to Huasco, 176 km to the south of Caldera Bay (Neill et al. 2003)[1]. Many of these bays in northern Chile are habitat to a highly endemic native fauna and flora (Santelices 1980, Meneses & Santelices 2000, Santelices & Meneses 2000), and in recent years, they have become cultivation grounds for economically important seaweeds (e.g., *Gracilaria*) and shellfish (e.g., Pacific oysters).

Due to the ecological and economic impact the species may have in Caldera Bay, and in the rest of the northern Chilean coastline, here we report the taxonomic identity of the species, and discuss its potential means of introduction in this area.

MATERIAL AND METHODS

The algal samples were collected by E. Martínez by SCUBA and skin diving at different depths (2-10 m) in Caldera Bay (27º03' S, 70º51' W) between January and April 2002. In total, 19 specimens were analyzed and have been deposited in the herbarium of the Sala de Sistemática, Pontificia Universidad Católica de Chile (SS/UC nºs 6911-1 to 6911-16 and 6913-1 to 6913-4). The length of erect axes and diameter and number of dichotomies were used to compare the external morphology of this species with that of other species reported for the region. Size, shape and apical structure of utricles were used as internal taxonomic characters. Utricles were stained with aniline blue and micrographs were taken using a Nikon Labophot microscope.

RESULTS

Taxonomic identity at the species level

Eleven of the 19 specimens examined exhibited gametangia, suggesting 57.9 % fertility in the studied sample. All 19 specimens had similar external (Table 1, Fig. 1), and internal (Table 1, Figs. 2 and 3) characters.

Externally, the plants have several cylindrical, robust fronds, up to 40 cm long, which arise from a broad, spongy, basal disk (Fig. 1). Branches are blackish green, and dichotomous for up to six orders. The cylindrical or terete branches are 5 ± 2 mm in diameter at the base, 4 ± 0.5 mm in diameter at the middle portions and 2.4 ± 0.3 mm in diameter at the tips. The utricles are cylindrical to clavate, frequently with constriction at approximately around the middle of the utricle (see arrows in Fig. 2). The utricles measure 910 ± 150 m long and 316 ± 76 µm in diameter. The wall of the utricle is 160 ± 2.6 µm thick,

[1] NEILL P, O ALCALDE & J CORREA (2003) Presencia de la especie invasora *Codium fragile* (Chlorophyta) en el norte de Chile: efectos potenciales sobre cultivos de *Gracilaria chilensis* (Rhodophyta). Abstracts of the XLVI Reunión Anual de la Sociedad de Biología de Chile, XVI Reunión Anual de la Sociedad de Ecología de Chile, Puyehue, Chile: R-56.

TABLE 1

External and internal morphological characters used to segregate the species of *Codium* considered in this study. The species included are the eight dichotomous taxa known for the coasts of Perú and Chile

Caracteres morfológicos externos e internos utilizados para diferenciar las especies de *Codium* consideradas en este estudio. Estas especies incluyen los ocho taxa dicotómicos conocidos para las costas de Perú y Chile

	Unidentified species from Caldera bay	*C. fragile* (Suringar) Hariot	*C. contractum* Kjellman	*C. fernandezianum* Setchell	*C. foveolatum* Howe	*C. peruvianum* (Howe) Setchell	*C. pocockiae* Silva	*C. tomentosum* Stackhouse	*C. unilaterale* Setchell & Gardner
Thallus length (cm)	Up to 40	Up to 40	Up to 12	Up to 100	Up to 10	Up to 10	Up to 10	Up to 90	Up to 30
Diam at base of branches (cm)	0.2 - 0.8	0.3 - 1	No information	0.5 - 1	0.3 - 0.7	No information	0.3 - 0.7	0.3 - 0.5	0.2
Diam at tip of branches (cm)	0.2 - 0.3	0.2-0.4	No information	No information	No information	No information	No information	0.1 - 0.2	0.5
Branching pattern	Dichotomous up to 6 orders	Dichotomous up to 9 orders	Regularly dichotomous, flat and broad.	Dichotomous, with unequal growth	Subpalmate, 2-5 times, rather irregularly dichotomous	Dichotomous	Divaricately dichotomous	Dichotomous up to 9 orders	Dichotomous to subdistichous, with unequal growth of one of the primary branches
Holdfast	Broad, spongy	Broad, spongy	No information	Broad, spongy	No information	No information	Broad, spongy	Broad, spongy	Broad, spongy
Utricle									
Shape	Cylindrical-clavate	Clavate	Clavate	Clavate	Cylindrical-clavate, slightly enlarged and abruptly contracted	Clavate	Clavate	Cylindrical or slightly clavate	Cylindrical to clavate
Length (µm)	500 - 1200	600 - 1500	No information	800 - 1250	800 - 1150	500 - 1000	500 - 1250	420 - 1050	1250
Diam (µm)	180 - 450	150 - 630	No information	50 - 500	200 - 500	70 - 240	65 - 300	65 - 275	65 - 350
Tip	Rounded-apiculate, terminating in a sharp mucron	Acuminate, terminating in a mucron	Not acuminate	Rounded	Rounded with cuticle foveolate or rugulose	Rounded	Rounded	Rounded or tending to be pointed	Slightly conical to smoothly rounded

TABLE 1
(continuation)

	Unidentified species from Caldera bay	*C. fragile* (Suringar) Hariot	*C. contractum* Kjellman	*C. fernandezianum* Setchell	*C. foveolatum* Howe	*C. peruvianum* (Howe) Setchell	*C. pocockiae* Silva	*C. tomentosum* Stackhouse	*C. unilaterale* Setchell & Gardner
Wall thickness (µm)	10 - 20	2 – 3	No information	15 – 30	6 – 13	3 – 40	1.5 - 32	44	16
Hairs	Two (1 specimen)	Long hyaline, variable in frequency	numerous	One to two	No information	No information	Two or more	Common, numerous	Commonly arise from the upper half
Medullary filaments diam (µm)	85 - 250	26 - 112	No information	No information	No information	No information	22 - 39	20 - 50	No information
Gametangia									
Shape	Ovoid or fusiform	Ovoid or fusiform	No information	Eleipsoidal	Unknown	Ovoid to fusiform	Ellipsoidal	Ovoid, oblong or fusiform	Ellipsoidal
Nº per utricle	One	One to three	Numerous	One or two	Unknown	Two or three	One to three	One to four	No information
Length (µm)	200 - 425	220 - 450	No information	315	Unknown	200 – 350	225 - 350	165 - 340	300
Diameter (µm)	120 - 240	75 - 170	No information	75 – 90	Unknown	60 - 110	35 – 80	50 – 110	75
Insertion (distance below apex of utricle)	One-half the length of the utricle	One-half the length of the utricle	No information	One-half to two-thirds the length	Unknown	No information	One-half to two-thirds the length of the utricle	One-half to two-thirds the length of the utricle	Supra medium
References		1-7, 9, 12-14	2, 6	6	4, 11	4, 11	10	3, 8	6, 12

(1) Ardissone (1888), (2) Svedelius (1900), (3) Howe (1911), (4) Howe (1914), (5) Hylmö (1919), (6) Setchell (1937), (7) Silva (1951), (8) Silva (1955), (9) Silva & Womersley (1956), (10) Silva (1959), (11) Dawson et al. (1964), (12) Meneses & Hoffmann (1994), (13) Trowbridge (1998), (14) Hubbard & Garbary (2002)

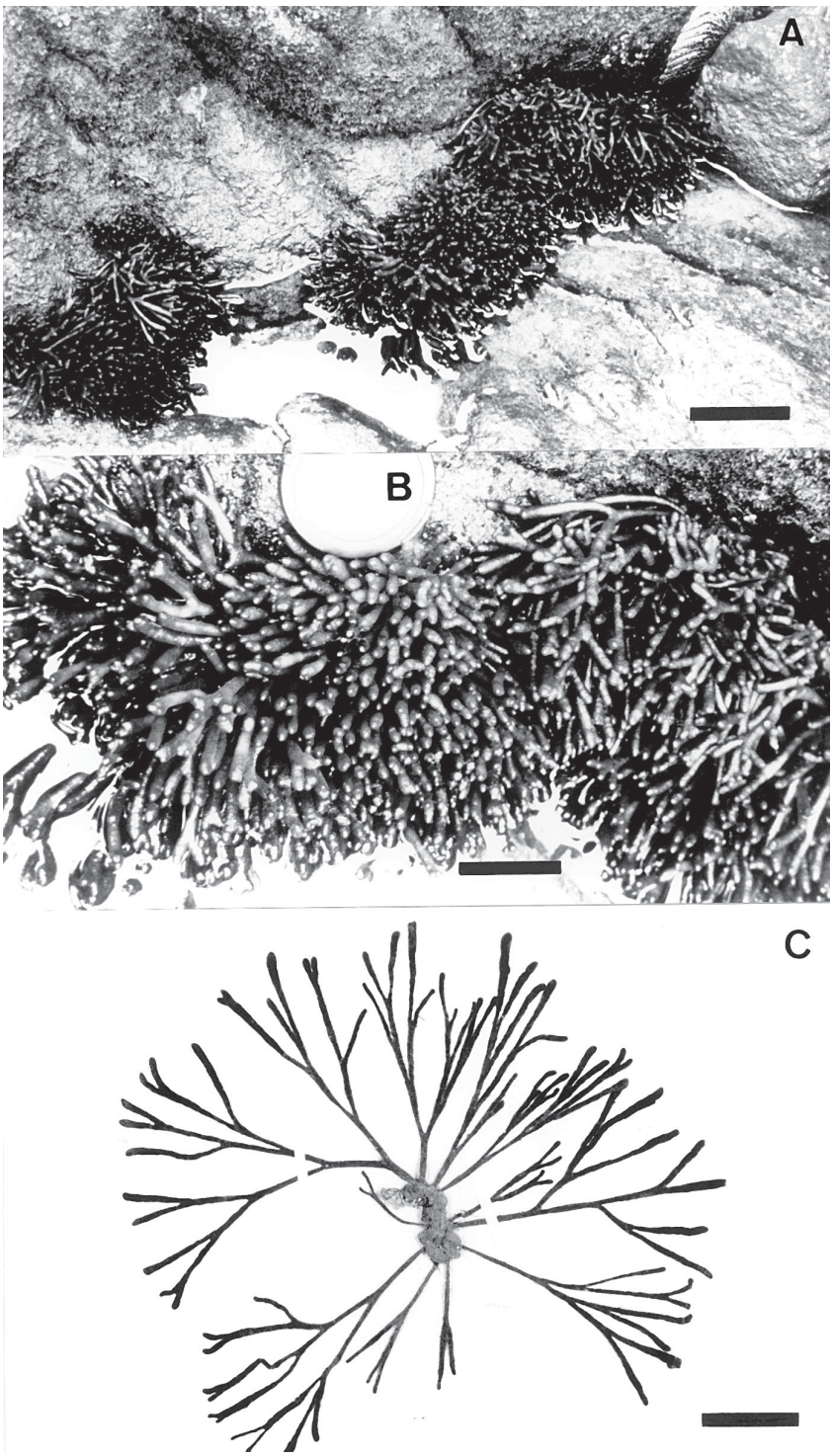

Fig. 1: Specimens of *Codium fragile* from Caldera Bay. (A) & (B) exhibit the thallus external morphology of the species growing on rocky, wave sheltered habitats. Scales = 8 and 4 cm, respectively. (C) Elongated herbarium specimen (SSUC Nº 6913) exhibiting the basal disk and the dichotomously branched erect axes. Scale = 4 cm.

Especímenes de *Codium fragile* recolectados en la Bahía de Caldera. (A) y (B) muestran la morfología externa del talo de la especie creciendo sobre sustrato rocoso en ambientes protegidos del oleaje. Escala = 8 y 4 cm, respectivamente. (C) Ejemplar de herbario (SSUC Nº 6913) mostrando el disco basal y los ejes erectos con ramificaciones dicotómicas. Escala = 4 cm.

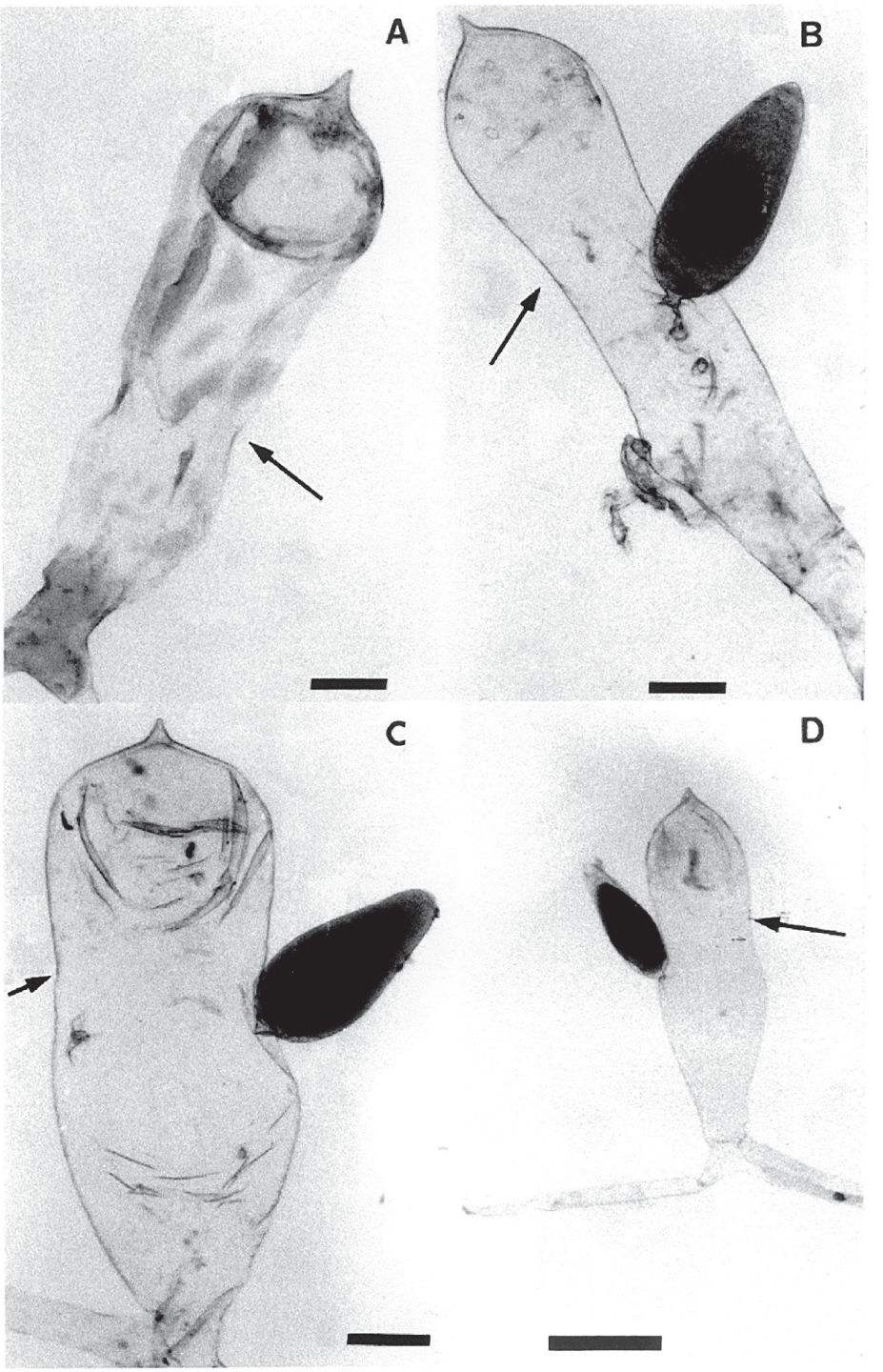

Fig. 2: Variability in the dimensions and shapes of utricles and gametangia. Arrows indicate the constriction at or slightly below the middle points of the utricles. All the utricles exhibit the pointed mucron. Scales in A, B and C are 100 µm. Scale in D is 200 µm.

Variabilidad en dimensiones y forma de utrículos y gametangios. Las flechas indican la constricción del utrículo en el punto medio o por debajo de este punto. Todos los utrículos muestran el mucron puntiagudo. La escala en A, B y C es de 100 µm. La escala en D es de 200 µm.

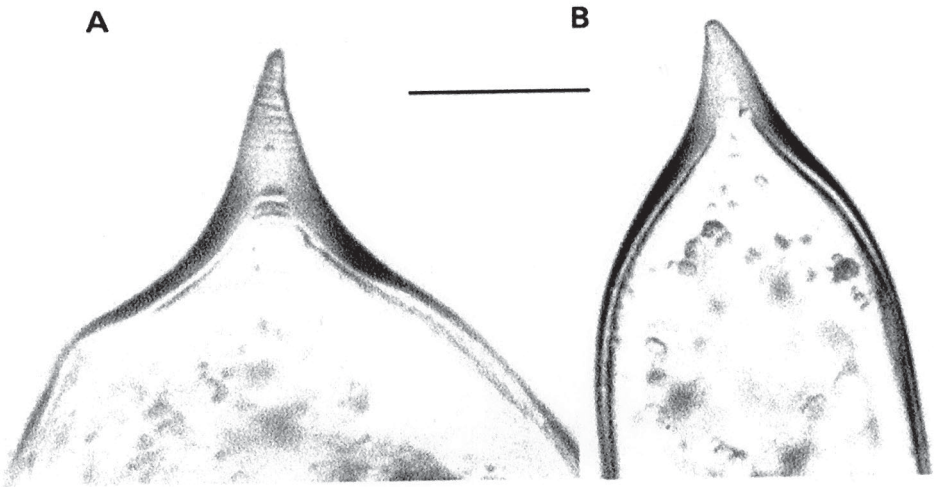

Fig. 3: Details of the mucron at the tip of the utricle in the materials from Caldera Bay (SSUC Nº 6913). Scale = 100 µm.

Detalle de extremo apical del utrículo con el mucron en los especímenes de la Bahía de Caldera (SSUC Nº 6913). Escala = 100 µm.

the apex is rounded, apiculate, terminating in a sharp mucron of 108 ± 30 µm long (Fig. 3). The medullary filaments are 191 ± 40 µm in diameter. Hairs (two per utricle) were observed on only one of the 19 specimens studied. Gametangia (Fig. 2) are ovoid or fusiform, 313 ± 67 µm long, 160 ± 37 µm diameter, one per utricle, with each borne on a 90 ± 40 µm long protuberances or on pedicels produced near the middle part of the utricle (about 436 ± 96 mm below the apex). Generally the gametangium does not extend beyond the tips of the utricles.

The spongy body of *Codium* serves as a host to various epiphytes and endophytes. The specimens from Caldera harbored a particularly rich epiphytic flora, including species of *Ectocarpus, Ceramium, Ulva* and *Chaetomorpha*.

A comparison of the microscopic and macroscopic characteristics of the specimens from Caldera Bay with the diagnostic characteristics of the other eight species reported for temperate Pacific South America (Table 1) suggests that the Caldera specimens belong to the species *Codium fragile* (Suringar) Hariot. Not only is there strong agreement in internal and external morphological characters, in addition, *C. fragile* is the only species exhibiting rounded–apiculate tips terminating in a sharp mucron, as observed in the material from Caldera.

Subspecific identity in Codium fragile and geographic distribution

Although most of the species of *Codium* have narrow geographic ranges and exhibit little morphological variability (Silva 1951), *C. fragile* has an extended distribution and a bewildering spectrum of morphological types (Goff et al. 1992). Regarded as native from Japan, the species also has been found in Korea and China. In the eastern north Pacific, the species is known from Sitka, Alaska to Puerto San Bartolomé in Baja California, Mexico. In the South Pacific it has been collected in Australia, New Zealand and southern Chile (Valdivia, Osorno and Puerto Montt). In the Indian Ocean it is known from Natal (South Africa), Kerguelen Island and Australia. In the north Atlantic it has been found in Norway, Sweden, Denmark, The Netherlands, Scotland, Ireland and Atlantic Canada. In the south Atlantic it is known from southwest Africa, Cape Province (South Africa), and southern Argentina (Tierra del Fuego and the Falkland Islands) (Silva 1951, Trowbridge 1998, Hubbard & Garbary 2002).

Along with this widespread geographic distribution, *Codium fragile* exhibits much morphological variation, which has formally been recognized under the identity of seven subspecies. Gross morphological differences

among the subspecies of *C. fragile* are not always obvious, particularly in areas where several subspecies coexists (Trowbridge 1999). However, the most reliable subspecific characters are the size and shape of the utricle, dimensions of the mucron, number of fronds per thallus and branch width. Less reliable diagnostic characters include length and thickness of the thallus and the flatness of fronds below the dichotomies (Silva 1951, 1957, Silva & Womersley 1956, Trowbridge 1996, 1998, Hubbard & Garbary 2002). It should be noted, however, that no experimental study has yet evaluated whether the different morphologies represent independent subspecies, or patterns of phenotypic plasticity adapting to local environments (Trowbridge 1996, Hubbard & Garbary 2002).

Four of the seven subspecies of *Codium fragile* are considered non-invasive and exhibit restricted geographic distributions. Thus, *C. fragile capense* occurs on South African shores only; *C. fragile fragile* is found from Sitka, Alaska down to Baja California and the islands along that coast (Silva 1951). *C. fragile novae-zelandiae* is restricted to New Zealand, southeast Australian shores and southern Argentina; while *C. fragile tasmanicum* is found on southeast Australian shores (Trowbridge 1996).

The other three subspecies of *Codium fragile* are considered invasive. One of them, *C. fragile atlanticum*, is thought to have originated in Japan and been unintentionally introduced with shellfish in southwest Ireland in about 1808 (Silva 1955, Trowbridge & Todd 1999, Hubbard & Garbary 2002, Trowbridge 2002). Subsequent spreading, most likely through rafting or floating, expanded its range to now include Norway, the rest of The British Isles and eastern Canada (Silva 1955, 1957, Hubbard & Garbary 2002). *Codium fragile scandinavicum*, was introduced to Denmark in 1919, and thereafter spread throughout northern Europe. Now it is found in Sweden and Norway and other parts of Scandinavia as well as Vladivostok, Siberia, and Yokohama (Japan) (Silva 1957). *C. fragile tomentosoides* is more or less cosmopolitan throughout temperate waters. It was first detected in Holland, Europe around 1900, in Denmark in 1919, Sweden in 1933, England in 1939, Norway in 1946 and Scotland in 1953. The alga rapidly spread throughout the Mediterranean during World War II (Silva 1955, 1957, Trowbridge 1999 and references therein). *C. fragile tomentosoides* next appeared on northwest Atlantic shores in 1957 and is now distributed from North Carolina to Nova Scotia, Price Edward Island, and eastern Canada (Silva 1957, Carlton & Scanlon 1985, Garbary et al 1997, Garbary & Jess 2000, Hubbard & Garbary 2002). In the mid-1970's, *C. fragile tomentosoides* appeared in San Francisco, California, on the Pacific coast of the United States (Coleman 1996). The first appearance of *C. fragile tomentosoides* in the Southern Hemisphere was in Auckland harbor, New Zealand in 1973 (Trowbridge 1995, 1996, 1999). In 1995 the alga was first reported in Australia at Corner Inlet, Victoria, thereafter it has spread some 160 km to southwest Australia (Trowbridge 1999 and references therein).

The morphological characteristics of the material collected in Caldera Bay agree well with the diagnostic characters known for *C. fragile* subspecies *tasmanicum* and *C. fragile* subspecies *tomentosoides* (Table 2). Both subspecies are similar in many external and internal characters but differ in the presence of a constriction in the middle parts of the utricles and in the shape of the tip of the utricle. The material from Caldera Bay resembles *C. fragile tomentosoides,* having a constriction at or just below the middle parts of the utricles (Fig. 2). But they also resembles *C. fragile tasmanicum* because the utricle tips end in a sharp mucron (Fig. 3). The rapid population spread the species experiencing in northern Chile add support to the identification of this form as the invasive *C. fragile tomentosoides*, a conclusion additionally supported by application of molecular techniques to the materials from northern Chile (C. Maggs personal communication to Dr. J. Correa). It should be mentioned, however, that the Caldera materials exhibit some morphological variation with *C. fragile tomentosoides*. The Caldera materials generally lack hairs on the utricles which are described as common in *C. fragile tomentosoides*. Additional populations should be studied to achieve a more comprehensive view of the taxonomic importance of this morphological variation.

DISCUSSION AND CONCLUSIONS

Among the eight dichotomous species of *Codium* described for Pacific temperate waters, the materials found in Caldera Bay exhibit morphological characters typical of the species *Codium fragile.* This finding constitutes a new record for the species along the Chilean coast. At a subspecific perspective, the morphological characters used did not allow discrimination

TABLE 2

Qualitative and quantitative morphological characters used to distinguish the subspecies of *C. fragile*

Caracteres morfológicos cualitativos y cuantitativos utilizados para distinguir las subespecies de *C. fragile*

	C. fragile tasmanicum (J. Agardh) Silva	*C. fragile* Northern Chile	*C. fragile tomentosoides* (Van Goor) Silva	*C. fragile scandinavicum* Silva	*C. fragile atlanticum* (Cotton) Silva	*C. fragile capense* Silva	*C. fragile novae-zelandiae* (J. Agardh) Silva	*C. fragile fragile* Silva
Thallus length (cm)	10 - 30	Up to 40	90	Up to 30	Up to 50	10 - 30	10 - 30	Up to 40
Diam. at base of Branches (cm)	0.7 - 0.8	0.2 - 0.8	No information	0.2 - 0.4	10	0.5 - 0.8	0.7 - 0.8	0.3 - 0.8 (to 1.0)
Diam. at tip of Branches (cm)	0.3	0.2 - 0.3	No information	No information	0.24 - 0.4	0.3	0.3	No information
Branching pattern	Dichotomous	Dichotomous up to 6 orders	Dichotomous	Closely dichotomous up 7 orders; often with proliferous lateral branching superimposed	Dichotomous up 9 orders, dichotomies at times telescoped to give fastigiate appearence	Dichotomous	Dichotomous	Dichotomo-fastigiate
Holdfast	Broad, spongy	Broad, spongy	No information	No information	No information	Broad, spongy	Broad, spongy	Broad, spongy
Utricle								
Shape	Slender, cylindrical clavate	Cylindrical-clavate, frequently with broad constriction at or just below middle	Irregularly often cylindrical or more clavate, frequently with broad constriction at or just below middle	Irregularly cylindrical, or clavate, pyriform or quadrate	Irregularly cylindrical or clavate	clavate	Slender, cylindrical, clavate	Narrowly to broadly clavate
Length (µm)	700 - 1750	500 - 1200	550 - 1050	480 - 1200	780 - 1200	730 - 1100	710 - 1750	600 - 1500
Diam. (µm)	70 - 390	180 - 450	105 - 400	190 - 670	139 - 330	80 - 355	70 - 390	150 - 630
Long as broad	3 - 10	2 - 3	2.5 - 5.5	1.5 - 3	3 - 5	3 - 6	3 - 10	1 - 10
Tip	Pointed into sharp mucron	Rounded apiculate, terminating in a sharp mucron	Rounded apiculate	Rounded or truncate, often with broad blunt point	Slightly rounded, often terminating in blunt point or umbo	Mucron chambered, lamellate, sometimes with concentric striations	Rounded and bluntly mucronate apice	Acuminate terminating in a mucron
Apical wall (µm)	2	10 - 20	12	Thickened	12	1.5 - 2	2	2 - 3
Prolonging point (µm)	77	70 - 190	68	20	10 - 14	60	No information	120

TABLE 2
(continuation)

	C. fragile tasmanicum (J. Agardh) Silva	*C. fragile* Northern Chile	*C. fragile tomentosoides* (Van Goor) Silva	*C. fragile scandinavicum* Silva	*C. fragile atlanticum* (Cotton) Silva	*C. fragile capense* Silva	*C. fragile novae-zelandiae* (J. Agardh) Silva	*C. fragile fragile* Silva
Hairs	Stout, gradually expanding upward, abundant densely tomentose with long hyaline hairs	Rare observed in one specimen only	Common 1 - 5	Common, one or three per utricle	Common, one or two per utricle	Stout, gradually expanding upward, 1-3 per utricle	No information	Abundant, densely tomentose with long hyaline hairs
Insertion of hairs (distance below apex of utricle, µm)	185 - 450	170	160 - 260	130 - 195	130 - 200	160 - 235	No information	No information
Medullary filaments diam. (µm)	26 - 46	85 - 250	26 - 68	34 - 68	28 - 64	26 - 46	26 - 46	26 - 112
Gametangia								
Shape	Lanceolate-ovoid narrowly ellipsoidal or cylindrica	Ovoid or fusiform	Ovoid, oblong or fusiform	Ampulliform, ovoid or oblong	Ovoid, oblong or fusiform	Lanceolate-ovoid, ellipsoidal or cylindrical	Lanceolate-ovoid, narrowly ellipsoidal or cylindrical	Ovate, fusiform or clavate
Nº per utricle	One to four	One	One or two	One to three	One or two	One to three	One to four	One to three
Insertion (distance below apex of utricle, µm)	460 - 850	300 - 700	In the middle of utricle	In the middle of utricle	In the middle of utricle	430 - 630	460 - 850	350 - 650
Length (µm)	260 - 450	200 - 425	260 - 330	185 - 395	260 - 400	275 - 460	260 - 450	220 - 450
Diameter (µm)	90 - 130	120 - 240	72 - 92	78 - 140	80 - 130	70 - 130	90 - 130	75 - 170
References	4	This study	2	2	2	3	4	1

(1) Silva (1951), (2) Silva (1957), (3) Silva (1959), (4) Silva & Womersley (1956)

between the subspecies *tomentosoides* and *tasmanicum*. It should be noted that some recent experimental evidence (Trowbridge 1996, Hubbard & Garbary 2002) suggests that subspecific differences in *C. fragile* could be attributed in part to environmental factors such as wave exposure, substrate stability and light availability. Future studies with a larger number of individuals and with additional techniques (e.g., molecular markers) may help to evaluate the validity of the Chilean *C. fragile* subspecies. The application of the molecular techniques (plastid microsatellites) adds support to the identification of this form as the invasive *C. fragile tomentosoides*.

One can only speculate about the mechanism by which *Codium fragile* might have arrived into Caldera Bay. A first possibility would be the transplantation of shellfish (e.g., Pacific oysters) or seaweed (e.g., *Gracilaria*) contaminated with *C. fragile* either from southern Chile or abroad (Japan). This mechanism has been used by several authors to explain the arrival of *C. fragile tomentosoides* on the shores of England and Scotland, the Mediterranean and Virginia, Maine, Massachusetts, Rhode Island and San Francisco in the United States (see review by Carlton & Scanlon 1985, Trowbridge 1999). Alternatively, *C. fragile* may have inadvertently been introduced via ballast waters or attached to the hull of a ship or pleasure craft. The Caldera harbor and nearby ports are home to a commercial fleet that transports Chilean fruit, fishmeal and minerals along the Chilean coast and to other countries. A similar mechanism has been used to explain the introduction of *C. fragile* on New Zealand shores, because the alga first appeared at the container terminal in the port of Auckland (Trowbridge 1999 and references therein).

As it has occurred in other latitudes, the size and abundance of this recent invader of bays and sheltered habitat in northern Chile will provide a good opportunity to experimentally test several biological hypotheses related to its origin, physiological plasticity and community effects. Molecular studies similar to those done with *Caulerpa taxifolia* (Vahl) C. Agardh and *Codium fragile* (Goff et al. 1992, Wiedenmann et al. 2001) should help to trace its geographic origin and genetic similarity at the intraspecific and interspecific levels. In addition, while in other parts of the world, the economic effects of the *C. fragile* invasions have mainly affected tourism and harbor activities, in northern Chile, it will probably impact more importantly the shellfish and seaweed farming industries.

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