The Genus *Codium* (Codiales, Chlorophyta) at Lord Howe Island (N.S.W.)

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Abstract

Jones, Rod, and Kraft, Gerald T. The genus *Codium* (Codiales, Chlorophyta) at Lord Howe Island (N.S.W.). *Brunonia* 7: 253–76 (1984). Five species of *Codium* have been found on the world's southernmost coral reef at Lord Howe Island, New South Wales (31°33'S.,159°03'E.). The genus forms, along with the brown algal order Dictyotales, a dominant marine algal group on the island. One species, the South African *C. extricatum* Silva, is a new record for the Australian region. *Codium platyclados* is newly described based on Lord Howe, Great Barrier Reef and Philippine collections. *Codium bulbopilum* Setchell and *C. spongiosum* Harvey have previously been recorded from the island and are major cover species in shallow lagoon waters. *Codium arabicum* is reported from the island and adjacent Australian mainland for the first time at what appear to be the species' southernmost limits of distribution. Anatomical variability and taxonomic relationships of the species are considered, and the geographical and local distributions discussed.

Introduction

The genus *Codium*, with about 80 species (Silva 1962), is distributed pantropically and into cold temperate waters of both hemispheres. Endemism among the species is high (Silva 1962), particularly in South Africa (Silva 1959), Australia (Silva and Womersley 1956), and the eastern Pacific (Silva 1962), as a result of the active speciation apparently taking place over much of the area of distribution of the genus (Silva 1962). The taxonomy of *Codium* is complicated by the high degree of anatomical and habit variability within and between species populations (Silva 1951), and requires that a wide range of specimens from as many habitats as possible be sampled by those engaged in regional floristic surveys. Such has been our goal at Lord Howe Island.

Codium is a bizarre marine genus which can adopt a suite of forms ranging from flattened crusts through solid or hollow spheres to erect dichotomous to orbicular fronds. Exemplifying the ultimate in complexity of the green-algal 'siphonous' line, its plant bodies each consist of a single giant cell (or are 'acellular' by some interpretations) containing a myriad of chloroplasts and nuclei but not partitioned by cross-walls into the cellular units typical of most macroscopic plants. Constructed somewhat like a mushroom, the *Codium* thallus consist of a central core of interwoven primary and secondary medullary filaments surrounded by a continuous surface layer of balloon-like structures called 'utricles' in which the photosynthetic pigments are largely aggregated and on which gametangia and hairs may be borne. The origin and sympodial development of primary and secondary utricles are illustrated and described in a number of publications by Silva (e.g. 1979), the leading taxonomist and biogeographer of the genus.

Lord Howe Island is uniquely situated at the southern limit of coral reef formation in a transition region between tropical and warm-temperate waters (Allender and Kraft 1983). Its volcanic origin and no prior connection to major land masses have made it an isolated habitat in which endemic terrestrial vegetation, invertebrates and animals have flourished (Paramanov 1963). Unlike most coral reefs, where herbivores generally maintain a low biomass of macroscopic algae, the reefs at Lord Howe are lush with extensive growths of both intertidal and subtidal marine plants. A limited number of algal groups tends to dominate the reef flats, lagoon floors and deep-water foreshore reefs, the main one being the brown algal order Dictyotales, whose members have recently been monographed (Allender and Kraft 1983). Second in importance, especially in depths of less than 2–3 m, is *Codium*, the next group to be monographed as the result of the second author's survey of the island's marine algae.

Methods

Voucher herbarium specimens studied are on file at the University of Melbourne Herbarium (MELU), with duplicates distributed to various herbaria (MEL, UC, ADU).

Material was stored in 4% formalin-seawater in opaque drums until curated. Dried material of old collections was soaked in a 1% solution of detergent (Teepol) for 24–72 h. Resoaking was hardest for prostrate species, which required a combination of slow boiling in 1 M NaOH or KOH for 1 h followed by soaking in 1% Teepol for at least 48 h.

At least three slide mounts in seawater were made of each specimen examined and the dimensions of 20 randomly selected utricles measured. Further observations of gametangial dimensions and position, number of gametangia per utricle, utricle apex morphology, hair and hair-scar position and number, medullary plug position and medullary filament diameter were also made when possible. Drawings were made on a Zeiss Winkel camera-lucida.

The Study Site

Lord Howe Island (31°33'S.,159°03'E.) lies 630 km due east of Port Macquarie in northern New South Wales. The island is roughly crescent shaped, 11 km long and averaging 1 6 km wide. Fringing reefs extend for two-thirds the length of the west coast and are cut by five passages that lead to a sandy floored lagoon of an average depth of 3 m. The reef outer slope rises rapidly in most places from a sandy floor at depths of 15–22 m to the reef flat above, which varies in width from 50 to 200 m (Veron and Done 1979). The upper reef slope is crossed by undercut channels and bordered by an irregular network of actively growing coral heads, or bommies. The north-eastern coast consists of sandy beaches, rocky headlands, and an extensive shallow calcarenite reef flat at Neds Beach, while the north and south coasts are composed of steep cliff faces. The collecting sites for *Codium* mentioned in this report are described by Allender and Kraft (1983).

Taxonomic Results

Key to the Species of Codium at Lord Howe Island

1.	Thallus prostrate or encrusting, attached continuously over most of undersurface
1.	Thallus erect or decumbent, attached basally or at numerous limited points
	2. Thallus tightly adhering, conspicuously flattened; utricles from upper surface of thallus less
	than 1000 µm long C. arabicum
	2. Thallus laxly to tightly adhering, subspherical or occurring in irregularly rounded aggregations;
	utricles greater than 1500 µm long C. spongiosum
3.	Branches of thallus terete throughout or, if flattened, then not predominantly so at
	dichotomies
3.	Branches distally compressed or terete, but distinctly flattened at the dichotomies
	4. Thallus wholly erect, with single basal attachment C. extricatum
	4. Thallus decumbent, imbricate; many points of anastomosis between overlapping branches; many
	points of attachment to substratum C. bulbopilum

1. Codium arabicum Kuetzing 1856: 35, pl. 100, fig. 2.

C. lucasii Setchell ex Lucas 1935: 202 (pro parte)

Thallus applanate, dorsiventral, to 20 cm broad, hard, flat and tightly adherent to substratum and developing orbicular excrescences (Figs 1A, 1B) when young, becoming more convoluted and spongy with age (Fig. 1C). Medullary filaments 15-33 μ m in diam., usually one arising from the base of each utricle as a relatively stout outgrowth, so that utricle and filament integrade (Figs 2A, 2D, 2F); 'blind' utricles (utricles budding directly

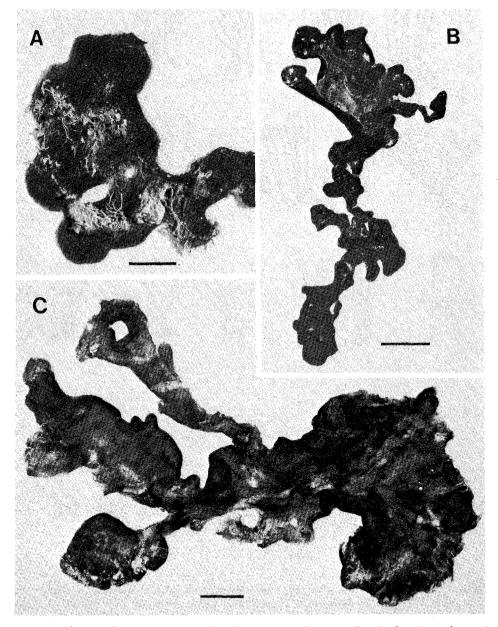


Fig. 1. Codium arabicum Kuetzing, habits of pressed specimens. A. Detail of under surface and marginal lobes of intertidal plant from Neds Beach, L.H.I., in December (MELU, K9420). Scale = 1 cm. B. Leathery-textured thallus from roof of undercuts at Far Rocks, L.H.I., in May (MELU, K9767). Scale = 2 cm. C. The largest specimen collected, from Comets Hole, L.H.I., in December (MELU, K9687). Scale = 2 cm.

from parent utricles without rapidly forming a basal rhizoid) present in varying numbers (Fig. 2C, 2G). Primary utricles formed by enlargement of branches of a sympodial system; secondary utricles arising as buds from lower part of existing utricles, forming large clusters (Figs 2A-2D, 2F-2L), cut off from parent utricles at points of origin by plugs (Figs 2J-2L). Utricles variable in size on any given thallus (Figs 2J-2L), those from centre (35-)55-70(-110) μ m in diam., (320-)365-680(-820) μ m in length, cylindrical to clavate,

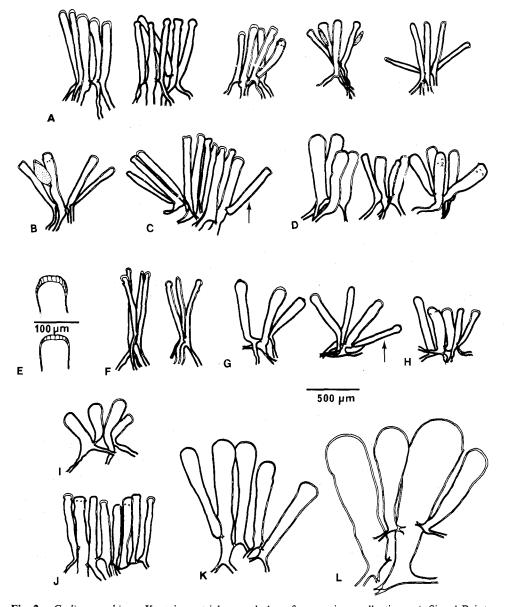


Fig. 2. Codium arabicum Kuetzing, utricle morphology from various collections. A. Signal Point, L.H.I., May 1977 (MELU, K10011). B. Sylphs Hole, L.H.I., December 1978 (MELU, K10380). C. Comets Hole, L.H.I., December 1978 (MELU, K9687). Arrow points to blind utricle. D. Lord Howe I., June 1933 (UC 507232). E. Signal Point, L.H.I., May 1977 (MELU, K10011), examples of alveolation in utricle apices. F. Coffs Harbour, N.S.W., January 1981 (MELU, AM397). G. Port Allen, Kauai, Hawaii, September 1959 (MELU, MD24998). Arrow points to blind utricle. H. Yule Point, Qld, June 1966 (MELU3112). I. Hayman I., Qld, June 1973 (MELU, MNC361). J-L. Sylphs Hole, L.H.I., December 1978 (MELU, K10380), utricle morphologies from the upper surface (J), upper margin (K) and edge (L) of a thallus.

apices subtruncate or slightly rounded, usually slightly constricted below apex (Figs 2B-2D, 2J); utricular wall 1 0-1 5 μ m thick, occasionally thickened to 10 μ m and pitted at apices (Fig. 2E). Utricles from margin of thallus long and relatively stout, clavate to pyriform, 120-500 μ m in diam., 60-1400 μ m long, with rounded, unthickened apices (Figs 2K, 2L). Hairs and hair scars common on older utricles in a zone approx. 70-140 μ m below apices of the utricles (Figs 2D, 2J). Gametangia fusiform or ovate, tapering distally, 40-100 μ m diam., 150-300 μ m long and borne on short pedicel in a zone around middle of utricles; one gametangium per utricle (Figs 2A, 2B).

Type locality: 'Tor, Sinai Peninsula, Gulf of Suez, Egypt' (Silva 1952).

Distribution

Indian Ocean: Red Sea; Mascarene Islands; Sri Lanka; India. Pacific Ocean: Malaya; Philippine Islands; Marshall Islands; Fiji; Tonga; Samoa; Cook Islands; Society Islands; Marquesas Islands; Hawaiian Islands; Tahiti; New Caledonia; Eniwetok Atoll.

Habitat, Seasonality and Material Examined

52 specimens of *Codium arabicum* have been examined from Lord Howe, collected at each of the four sampling periods of the survey (January-March; May; September/October; December). This is a shallow water species ranging from just above the lowest tide levels to 4 m depths. It is particularly common encrusting the roofs and sides of undercut ledges at Far Rocks and Neds Beach, and the undersides of coral rubble at Sylphs and Comets Holes. The largest plants (Fig. 1C) are from the latter two sites in December.

Material examined includes collections from the following localities:

(1) Sylphs Hole. 0.25-0.75 m deep under overhanging coral debris on the shallow flat shoreward of the living coral bank (*Kraft & O'Brien*, 14.v.1977. MELU, K9989); (*Kraft & Ricker*, 2.xii.1978. MELU, K10380).

(2) Far Rocks and Signal Point. Just emergent at low tide, always just back under the edges of reef undercuts (*Kraft, O'Brien & Wetherbee*, 11.v.1977. MELU, K10011); 1 · 0-1 · 5 m deep on roofs and floors of reef undercuts (*Kraft & O'Brien*, 28.ix.1976. MELU, K9872); roofs and undercuts just back from the edges (*Kraft & Lewis*, 5.iii.1976. MELU, K9236); (*Kraft & O'Brien*, 13.v.1977. MELU, K9767).

(3) Neds Beach. 0.2 m above low tide level along sides of narrow channels on the other reef arm in heavy surge (*Kraft & Ricker*, 1.xii.1978. MELU, K9420).

(4) Comets Hole, 4 m deep on side of slightly undercut bommie (Kraft & Ricker, 11.xii.1978. MELU, K9687).

(5) Lord Howe Island (Lucas & Perrin, June 1933. UC 507232).

The Lord Howe collections were compared with the following extra-island material: (6) Arrawarra Heads, Coffs Harbour, N.S.W. Low intertidal on roof of undercut channel (*Millar*, 10.i.1981. MELU, AM397).

(7) Yule Point (16 km south of Port Douglas), Qld. (Ducker, 5.vi.1966. MELU 3112).

(8) Hayman Island, Great Barrier Reef, Qld. (Clayton, 28.vi.1973. MELU, MNC 361).

(9) Port Allen, Kaui, Hawaii. On corals between 10-25 m depths (*T. Matsui*, 12.ix.1959. MELU, MD19144P).

Remarks

Silva (1952) refers all adherent forms of *Codium* with small (under 1000 μ m long) and non-trabeculate utricles from tropical Pacific localities to *C. arabicum* and concludes that a complex series of 'microspecies or subspecies' (Silva 1962, p. 207) is involved which includes a wide range of utricle lengths and shapes. Pacific specimens appear to differ from those described from the Red Sea in that many have pitted (alveolate) (Fig. 2*E*) and generally shorter, squatter utricles (Silva 1952). Alveolation is a consistent feature of the utricle apices in Indonesian–Philippine forms (Silva 1952), but becomes sporadic in central and southern Pacific representatives. This is the case at Lord Howe, where alveolation is seen only occasionally. Silva (1952, 1960) concludes that presence or absence of alveolation alone cannot be regarded as a diagnostic character in *C. arabicum* or in its western Atlantic counterpart, *C. intertextum* Collins & Hervey.

Lord Howe Island members of the *Codium arabicum* complex vary little from central Pacific (Hawaiian) specimens. Both have short, squat utricles tending to become longer and thinner with age, and both exhibit blind utricles that bud off from mature utricles without forming rhizoidal filaments (Figs 2C, 2G). Utricles from the centre of the thallus are usually less than 100 μ m in diam., but become balloon-shaped and up to 500 μ m in diam. at the edges of lobes or along the undersides of the thallus (Fig. 2L). These larger utricles appear to be common to all adherent forms and are perhaps a response to localized regions of high water movement (Silva, personal communication).

The Lord Howe collections are the southernmost records of *Codium arabicum*, which has not previously been reported at latitudes higher than the Tropic of Capricorn (Silva 1962, figure 5). The species seems to be confined to intertidal and shallow subtidal habitats on the island, but can occur considerably deeper at lower latitudes (e.g. Hawaii [MELU, MD19144]).

Codium arabicum is closely related to C. lucasii Setchell (ex Lucas 1935) from southern Australia. There are tendencies toward internal size differences between the two species, however, as C. arabicum has utricles that are shorter and squatter than C. lucasii, the latter also tending toward asymmetrical rather than uniformly contoured utricle apices (Silva and Womersley 1956). Blind utricles do not occur in C. lucasii, as every secondary utricle rapidly initiates a basal rhizoid (personal observation). It would appear that C. *lucasii* is a species extending up the eastern Australian mainland coast from Victoria to southern Queensland (Silva 1962; personal observation), whereas C. arabicum ranges from central N.S.W. northward and tends to occur in offshore regions such as Lord Howe Is., the Great Barrier Reef, and the Pacific islands, Because blind utricles are not common in material of C. arabicum from Lord Howe and the adjacent New South Wales coast region (Coffs Harbour), it is very difficult to separate northern populations of C. lucasii from the southern ones of C. arabicum, which suggests that the two species may overlap in range and intergrade in New South Wales and southern Queensland. Until a greater range of specimens from these areas is examined, we provisionally consider C. lucasii to be a cool to warm-temperate species, whereas C. arabicum is typically an inhabitant of tropical, coral reef waters.

The Codium lucasii record of Lucas (1935) from Lord Howe was previously questioned by Silva and Womersley (1956, p. 266); Lucas' specimens, as well as the material of our survey from Lord Howe, are very similar to members of the C. arabicum complex as described from Hawaii by Silva (1952) and New Caledonia by Valet (1968) and should no longer be identified with C. lucasii.

Codium spongiosum Harvey 1855: 565. Bailey 1913: 82. Lucas 1934: 350; 1935: 202. May 1951: 92.

Thallus pulvinate or applanate, spongy, to 14 cm diam., loosely adherent to substratum. Medullary filaments 30-80 μ m diam. Utricles in large clusters, cylindrical to clavate, often capitate, (165-)275-400(-620) μ m in diam., (1850-)2800-3300(-5000) μ m in length, apices subtruncate or rounded; utricular wall 2-3 μ m thick, slightly thickened (to 15 μ m) and with inwardly facing rounded protruberances (introrsely umbonate) at apices. Hairs and hair scars common in a zone 130-400 μ m below utricle apex. Gametangia lanceovoid or ampulliform, 50-175 μ m in diam., 215-360 μ m long, several per utricle, each borne on short pedicel in a zone 360-660 μ m below apex of utricle.

Lectotype: W. H. Harvey, Algae Australicae Exsiccatae no. 577 (TCD) (Silva and Womersley 1956).

Type locality: King Georges Sound, Western Australia.

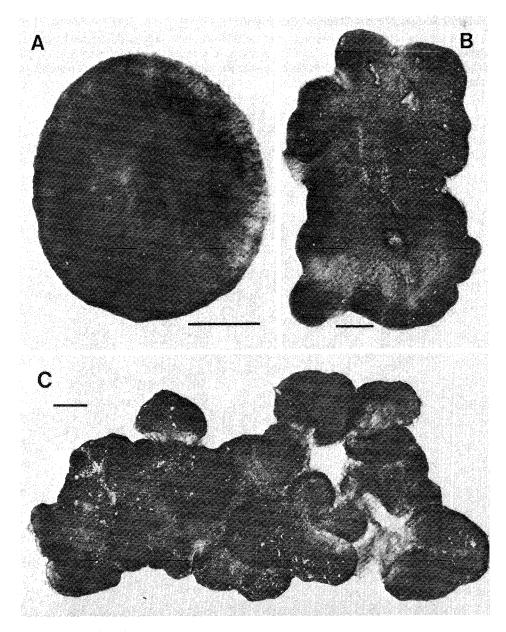


Fig. 3. Codium spongiosum Harvey, habits of pressed specimens. A. Spherical form typical in deeper water (-23 m) at Phillip Rock, L.H.I., in January (MELU, K10394). Scale = 1 cm. B. Two fused individuals from the shallow subtidal (1-3 m) at Neds Beach, L.H.I., in March (MELU, K9131). Scale = 1 cm. C. Consolidation of several individuals to form a dominant element of the algal cover in shallow subtidal depths (0.5-1.0 m) at Far Rocks, L.H.I., in March (MELU, K9298). Scale = 1 cm.

Distribution

Indian Ocean: South Africa; Mauritius; Madagascar; Western Australia. Pacific Ocean: southern coast of Australia; Tasmania; eastern Australia to Green I., Qld; Lord Howe I.; Fiji; New Caledonia; Hawaii. Atlantic Ocean: Brazil (Silva 1960).

Habitat, Seasonality and Material Examined

This species is locally very abundant at Lord Howe, especially in the Signal Point area, and can cover broad expanses of shallow reef flat. It is present in largest numbers at 1-2 m depths, but extends to over 20 m deep beyond the reef passes. 45 specimens from all the sample periods have been examined.

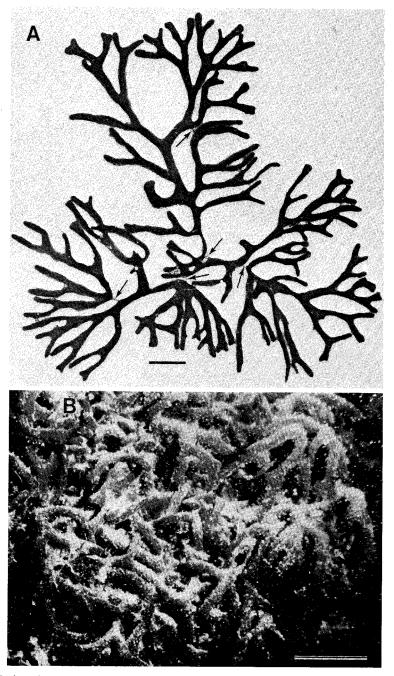


Fig. 4. Codium bulbopilum Setchell. A. Habit of dried specimen from South Lagoon, L.H.I., in March (MELU, K9162). Arrows indicate anastomoses between branches. Scale = 1 cm. B. Underwater habit of an imbricating clump of fronds at Far Rocks, L.H.I., in March (MELU, K9244). Axes are characteristically arching downward and plant mass is typically covered in silt. Scale = 1 cm.

(1) Phillip Rock. Isolated individuals on the reef flat at 23 m depth (*Kraft & Gabrielson*, 30.i.1982. MELU, K10394).

(2) Sylphs Hole. Scattered individuals at 1-2 m depth on coral rubble in sand flats (*Kraft & O'Brien*, 14.v.1977. MELU, K9994).

(3) Far Rocks and Signal Point. 0.0-1.5 m deep, large consolidated masses covering many square centimetres, the dominant cover organism in the area (*Kraft & Lewis*, 4.iii.1976. MELU, K9298). Intertidal, at +0.5-1.0 m levels during lowest yearly daytime tides, plants much desiccated and senescent (*Kraft & Ricker*, 4.xii.1978. MELU, K10532).

(4) Neds Beach, 8–9 m deep, scattered individuals on the open reef flat (*Kraft & Ricker*, 10.xii.1978. MELU, K9629); 1–3 m deep along the main channel (*Kraft & Lewis*, 5.iii.1976. MELU, K9131).

(5) Erskotts Passage. 7-10 m deep in the main channel (*Kraft & O'Brien*, 30.ix.1976. MELU, K9954).

The following extra-island tropical Australian material was also examined:

(6) Wistari Reef, Great Barrier Reef, Qld. On the reef flat at the low tide mark (*Wetherbee*, 19.xi.1979. MELU, K15400).

(7) Heron I., Great Barrier Reef, Qld. Between 5 and 12 m depths at Blue Pools (*Kraft & O'Brien*, 31.v.1977. MELU, K15512).

Remarks

Codium spongiosum is widely distributed in temperate to tropical waters and appears to be centred on the Indo-Pacific region (Silva 1960, 1962). At Lord Howe it is usually found as rounded, ball-shaped individuals (Fig. 3A) on open reef flats in deeper water (6-28 m depths), but can become aggregated (Fig. 3B) into large spongy mats (Fig. 3C) that cover considerable substratum in the shallow (<3 m) lagoon. Plants are vulnerable to surge and appear to be easily dislodged, for the species is the commonest element of drift on the island.

Internally, the large utricles (to 5 mm in length, 600 μ m in diam.) are characteristic (Fig. 5A). Medullary filaments grade evenly into the utricles (Fig. 5A), as opposed to being markedly constricted as in the superficially similar C. mamillosum Harvey (Silva and Womersley 1956) and C. ritteri Setchell & Gardner (1903). Gametangia in C. spongiosum are borne high on the utricles and are characteristically ampulliform (Silva and Womersley 1956). Hairs are always borne below the apex of the utricles, often in an area of slight constriction which gives the utricles a capitate appearance (Fig. 5A).

The morphology of *Codium spongiosum* appears to be quite uniform throughout its range, and southern Australian collections closely match tropical representatives.

3. Codium bulbopilum Setchell 1924: 173. Lucas 1935: 204.

Thalli terete, imbricating; axes arching downwards (Fig. 4B), attached at intervals to the substratum and anastomosing (Fig. 4A) by rhizoidal filaments. Plants dark green, turgid when living, irregularly dichotomous, frequently branched. Axes 2-4 mm in diam., to 11 cm in length. Medullary filaments 20-42 μ m in diam., one to several arising from the base of each utricle (Figs 5B, 5F), with a plug formed close to point of departure (Figs 5B-5F). Utricles obovoid, cylindrical to subcylindrical, (240-)500-820(-950) μ m long, (50-)120-170(-310) μ m wide, apices rounded, utricular wall thin (1-2 μ m), not obviously thickened at apex. Hairs occasional in zone towards apex of utricles (Figs 5D-5F). Gametangia cylindrical, pyriform or ellipsoidal (Fig. 5B), 220-320 μ m long, 60-100 μ m wide, borne on a short pedicel in a zone around the middle of the utricles, one per utricle.

Type locality: Aua, Western Samoa.

Distribution

Samoa; Tahiti; New Caledonia; Fiji; Lord Howe I.

Habitat, Seasonality and Material Studied

Codium bulbopilum is confined to sheltered, shallow lagoon habitats on the western side of Lord Howe, where it forms very distinctive hummocks of overlapping and downwardly curving terete branches (Fig. 4B). It seems to have a high tolerance for sand

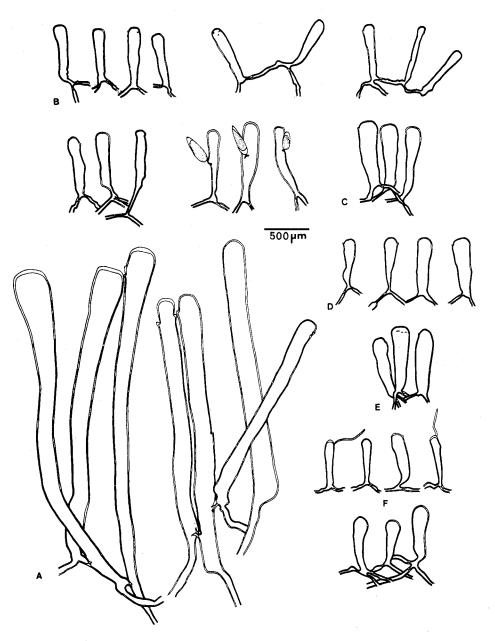


Fig. 5. A, Codium spongiosum Harvey. Utricles from Neds Beach, L.H.I., specimen of December, 1978 (MELU, K9629).

B-F. Codium bulbopilum Setchell, utricles from various specimens. *B.* Sylphs Hole, L.H.I., May 1977 (MELU, K10002). *C-E.* Utricles taken from the top (C), middle (D) and lower third (E) of a dried thallus from Lord Howe I., June 1933 (UC 507228). *F.* Lord Howe I., June 1933 (UC 507231), labelled *Codium cuneatum* by A. H. S. Lucas.

deposition and is often nearly covered with silt on the concrete blocks and coral debris at Sylphs Hole. Records have come from all seasons, but are fewest for the September/ October sample period. 41 specimens from the island have been examined from the following localities:

(1) Sylphs Hole. 1 0 m deep on coral shards shoreward of the living coral bank (*Kraft & O'Brien*, 14.v.1977. MELU, K10002). On concrete blocks at 3 m depth in the boat anchorage (*Kraft & Ricker*, 2.xii.1978. MELU, K10375).

(2) Far Rocks and Signal Point. 0 5–1 5 m depth, in scattered hummocks on calcareous substrata (*Kraft & Lewis*, 28.ii,1976, MELU, K9244).

(3) Comets Hole. 2 · 0-2 · 5 m deep on coral shards (*Kraft & Ricker*, 11.xii.1978. MELU, K9686).

(4) South Lagoon. 1-3 m deep on coral rubble (*Kraft & Lewis*, 2.iii.1976. MELU, K9162).

(5) Lord Howe I. (Lucas & Perrin, June 1933. UC507228; UC507231 [labelled C. cuneatum by Lucas]).

The following extra-island material was also examined:

(6) Suva, Fiji. 3 · 5 m deep on coral rubble behind the main reef (*Chidgey*, 26.ix.1981. MELU22815).

Remarks

Codium bulbopilum is easily distinguished by its terete, dichotomous branches (Fig. 4A) and its tendency to form imbricating hummocks (Fig. 4B). Rhizoidal connections are made at irregular intervals to itself (Fig. 4.4) and the substratum. It is closely related to the Pacific C. geppii Schmidt, the Hawaiian C. edule Silva, the South African C. prostratum Levring and the Tahitian C. taitense Setchell, but is distinguished from these species, particularly C. geppii, primarily on the basis of its larger utricles (Setchell 1926). Codium geppii, for example, has a utricle range of 200-300 µm compared to 500-700 µm in C. bulbopilum. Apparently Codium geppii does not form the prominent hummocks of C. bulbopilum as a general rule, a character said by Silva (1960) to be more the tendency of C. prostratum. Silva (1960) studied Codium repens P. L. & H. M. Crouan in Vickers from the Caribbean Sea, and found it the tropical Atlantic counterpart of the Pacific region C. geppii, which is widespread and in some regions the only *Codium* species to be represented (e.g. Womersley and Bailey 1970). Codium repens forms a continuous anatomical spectrum as the length of its utricles increases with the thickness of the branches (Silva 1960). Thus pyriform to obovoid utricles in slender branches appear subcylindrical to clavate in thicker branches because their widths change relatively little in proportion to their lengths. Such a spectrum has also been seen in our C. bulbopilum material from Lord Howe and further relates the species to the C. repens/C. geppii complex. The close relationship between C. geppii and C. bulbopilum was previously suggested by Setchell (in Lucas 1935, p. 204). In a letter to Lucas dated 11 January 1934, Setchell wrote 'I am practically on the point of uniting [C. bulbopilum] to C. geppii'. Silva (1960) preferred to treat the great variability within Codium geppii as elements of a species complex rather than representatives of discrete species, and considered the repent *Codiums* as a whole to represent 'several species or complexes of microspecies' (Silva 1962). In such a context Codium bulbopilum might be regarded as a fairly distinctive microspecies of the C. geppii complex.

4. Codium extricatum Silva 1959: 145.

Codium indicum Setchell in Lucas 1935: 205, nom. nud. (pro parte).

Thallus erect to 17 cm in height, regularly dichotomous to 11 orders (Figs 6A, 6B) or slightly pseudomonopodial (Fig. 6C), dark green to olive green, slightly flattened and to 4 mm diam. in lower parts, often wholly terete and 2-3 mm diam. Medullary filaments $35-52 \ \mu m$ in diam., one to several arising from base of each utricle and most separated by a plug close to point of juncture (Figs 7A, 7D). Utricles pyriform, clavate to subcylindrical (Fig. 7), (320-)600-800(-1100) \ \mu m long, (80-)150-250(-460) \ \mu m wide, apices rounded,

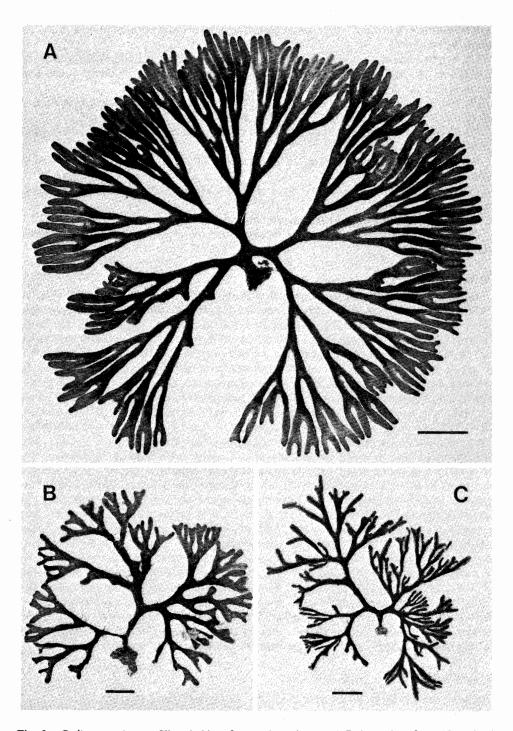


Fig. 6. Codium extricatum Silva, habits of pressed specimens. A. Robust plant from 15 m depth at Old Gulch, L.H.I., in January (MELU, K10501). Scale = 2 cm. Axes are terete and of mostly uniform length and width. B. Small thallus from 18 m depth at South Passage, L.H.I., in January (MELU, K10477). Scale = 1 cm. C. Plant from 21–28 m depth at Phillip Rock, L.H.I., in January (MELU, K10396). Axes are terete but of very uneven lengths. Scale = 2 cm.

truncate to subtruncate; utricular wall $1 \cdot 0 - 2 \cdot 5(-3 \cdot 5) \mu m$ thick, moderately thickened (to 22 μ m) at apices. Hairs or hair scars common apically on utricles (Figs 7A, 7C). Gametangia ellipsoidal, pyriform, 260-420 μ m long, 70-160 μ m wide, borne on short pedicel in a zone around the middle of the utricles, 1-3(-4) per utricle (Figs 7B, 7C).

Type locality: Mouth of Qolora River, Cape Province, South Africa.

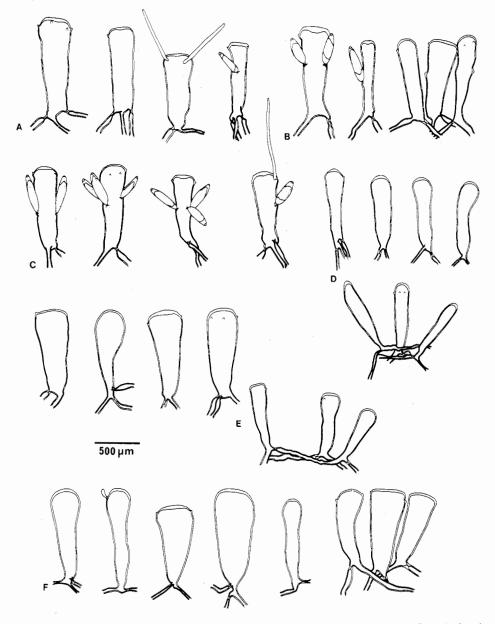


Fig. 7. Codium extricatum Silva, utricle morphology from various collections. A-C. Neds Beach, L.H.I., December 1978 (MELU, K9628). Utricles from the top (A), middle (B) and lower (C) third of the thallus showing hairs, hair scars and position of sporangia. D. Lord Howe I., February 1937 (UC 564512). E. Cape Cleveland, Qld, March 1980 (JCT 4976). F. Wistari Reef, Capricorn Group, Qld, November 1976 (MELU24220).

Distribution

From Cape Province to Natal, South Africa; Lord Howe I.

Habitat, Seasonality and Material Examined

At Lord Howe this species becomes more prominent with increasing depth, the records from shallower water being few and of somewhat aberrant plants while those from 9 m or more are comparatively numerous and more like their South African counterparts. 20 specimens have been examined, all from the December-March summer period and ranging from just subtidal to depths of 28 m. Specimens have come from the following areas:

(1) Old Gulch. Scattered individuals at 15 m depth on vertical walls at the mouth of the gulch (*Kraft & Huisman*, 29.i.1982. MELU, K10501); (*Kraft & Ricker*, 9.xii.1978. MELU, K9529).

(2) Phillip Rock. Scattered individuals on the sloping limestone flats between 21 and 28 m depths (*Kraft & Gabrielson*, 30.i.1982. MELU, K10396).

(3) Neds Beach. 9 m deep on the reef flat adjacent to sand flats (*Kraft & Ricker*, 10.xii.1978. MELU, K9627, K9628).

(4) South Passage. Isolated individuals on the reef face between 15 and 20 m depths (*Kraft & Huisman*, 31.i.1982. MELU, K10477).

(5) Lord Howe Island (Captain & Mrs J. D. McComish, Feb. 1937. UC 564512).

The Lord Howe collections were compared with the following extra-island material:

(6) NNW. of Cape Cleveland (19 deg., 02 min. S.; 146 deg., 58 min. E.), Qld. Trawled from 22-23 m depths (*Price*, 15.iii.1980. JCT 4976).

(7) Wistari Reef, Great Barrier Reef, Qld. (D. Fisk, 14.xi, 1976. MELU 24220).

Remarks

Silva (1959) erected *Codium extricatum* for a suite of highly variable dichotomous specimens with tendencies toward flattening of the lower axes. Utricles in the Lord Howe collections are similar to South African representatives in shape and dimensions. Like the South African assemblage, plants from Lord Howe are dark green, repeatedly dichotomously branched, and generally terete but tending towards slight flattening at the bases. Although South African material has not been examined in this survey, the strong similarity between it and the Lord Howe collections has been verified by Professor Silva.

With the present report, C. extricatum joins the relatively few Codium species reported from two widely separated land masses (Silva 1962) and shares with C. lucasii, C. spongiosum and C. duthieae an Australian/South African distribution.

5. Codium platyclados R. Jones & Kraft, sp. nov.

Codium cuneatum auct. non Setchell & Gardner (1924): Lucas 1935: 205.

Codium decorticatum auct. non (Woodward) Howe (1911): Lucas 1936: 56 (pro parte). Codium indicum Setchell in Lucas 1935: 205, nom. nud. (pro parte).

Thallus erectus, ad 18 cm altus, ex ramis quoad numerum variabilibus formatus in haptero discoideo ortis; rami complanati ad manifeste flabellati, ad 3 cm diametro, irregulariter dichotomi, cervicornes et cuneati. Fila medullosa 23-50 μ m diametro, singula vel aliquot per utriculum, ex base utriculi orta, obstructione proxime ad basim. Utriculi vel clavati vel pyriformes vel cylindrici, magnitudinem valde variabiles, (55-)110-215(-430) μ m diametro, (430-)655-1050(-1400) μ m longitudine, apices rotundati ad sub-truncati; paries utriculi 2-3 μ m crassitudine, ad apicem incrassatus ad 32 μ m. Trichotomata vel cicatrices trichomatum vulgares, semper autem prope apices utriculorum. Gametangia ellipsoidea, partibus distalibus angustatis, 60-90 μ m diametro, 240-410 μ m longitudine, in dedio utriculo, singula, aliquando bina.

Typus: Neds Beach, Lord Howe I. 9 m on low limestone platform seaward of outer reef arm (*G. Kraft & R. Ricker*, 10.xii.1978; MELU, holotype K9626*a*, isotypes K9626).

Thallus erect, to 18 cm high, consisting of a variable number of axes arising from a discoid holdfast (Figs 8A-8C); branches compressed to markedly flattened (Fig. 9A), particularly at axils (Figs 10A, 10B), sometimes distally terete, to 3 cm diam., irregularly dichotomous (Figs 8A, 9C, 10A, 11A-11C), pseudomonopodial (Figs 8B, 8C), cervicorn

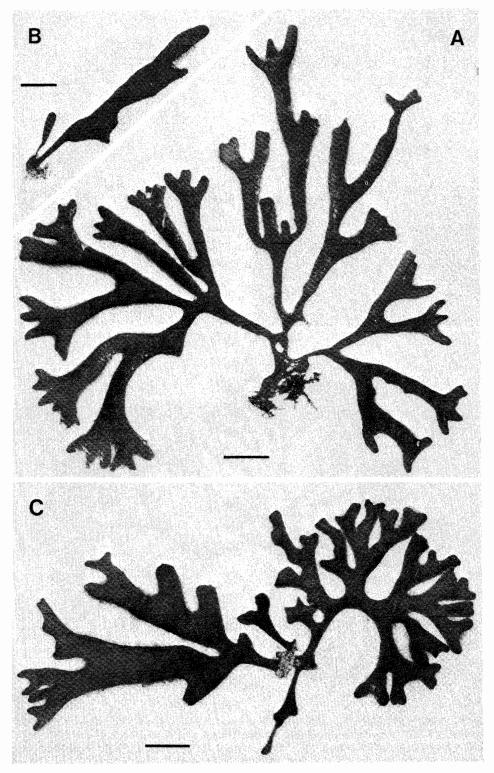


Fig. 8. Codium platyclados R. Jones & Kraft, sp. nov., habits of pressed specimens. A. The holotype specimen from 9 m depth at Neds Beach, L.H.I., (MELU, K9626a). Scale = 2 cm. B. A small, pseudomonopodial specimen from 18 m depth at North Point, L.H.I., between Kim's Lookout and Malabar, in December 1978 (MELU, K9594). Scale = 1 cm. C. An isotype specimen from Neds Beach, L.H.I., showing prominent hairs and varying degrees of regular dichotomies and branch widths on two adjacent specimens (MELU, K9626b). Scale = 2 cm.

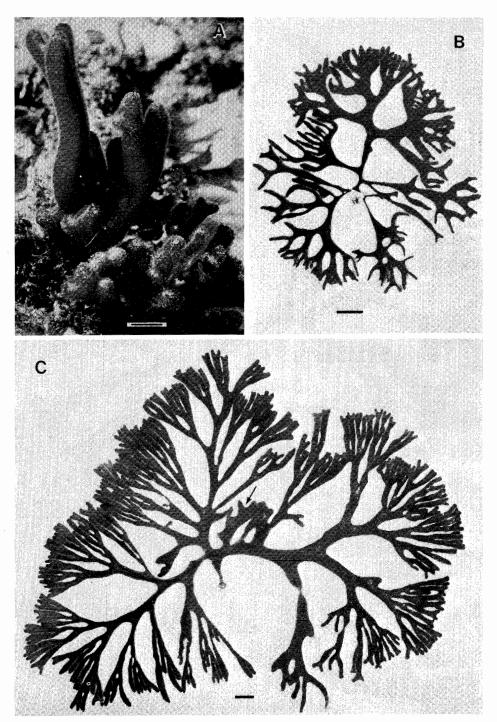


Fig. 9. Codium platyclados R. Jones & Kraft, sp. nov. A. Living plants in the shallow subtidal at Far Rocks, L.H.I., showing the broad and compressed axes typical of the species (MELU, K9875). Scale = 1 cm. B. Dried plant from the shallow subtidal at Far Rocks, L.H.I., in December, 1978, showing unusually pronounced cervicorn branching (MELU22827). Scale = 1 cm. C. Habit of one of the largest specimens, collected from -1.5 m at Far Rocks, L.H.I., in March, 1976 (MELU, K9232). One of the branches (arrow) has the pseudomonopodial branching of one of the deep water collections (Fig. 8B). Scale = 1 cm.

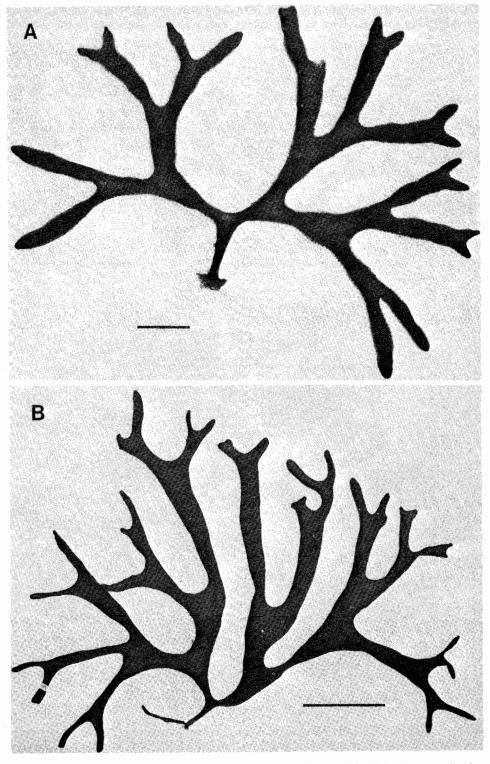
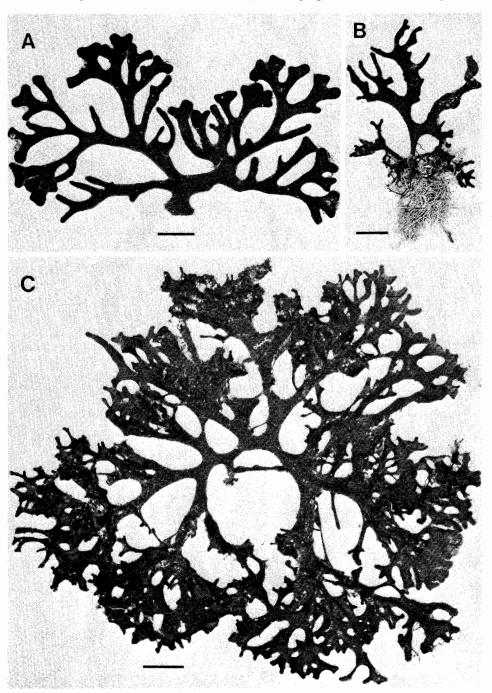


Fig. 10. Codium platyclados R. Jones & Kraft, sp. nov. A. Dried habit of the deepest collection, from 21–28 m depths at Phillip Rock, L.H.I., in January 1981 (MELU, K10395). Scale = 2 cm. B. Specimen of C. platyclados from San Bernardino I., Sorsogon Province, Luzon, Philippines (MELU, K934). Scale = 5 cm.



(Fig. 9B), commonly cuneate (Fig. 10B). Medullary filaments 23-50 μ m in diam., one to several arising from the base of each utricle, with a plug formed close to the point of

Fig. 11. Codium platyclados R. Jones & Kraft, sp. nov., aberrant and non-typical forms. A. Apparently young thallus with flattening confined to the distal dichotomies; collected from Far Rocks, L.H.I., in October 1977 (MELU, K10183). Scale = 1 cm. B. Irregularly branched and flattened thallus from just subtidal depths on the reef flat at Neds Beach, L.H.I., in March 1976 (MELU, K9087). Scale = 1 cm. C. Specimen from Johnsons Beach, L.H.I. (MELU, K9379), in May, 1977, with crowded distal dichotomies similar in habit to the Hawaiian Codium reediae Silva. Scale = 1 cm.

departure (Figs 12, 13). Utricles clavate, pyriform or cylindrical, highly variable in size, $(55-)110-215(-430) \ \mu m$ diam., $(430-)655-1050(-1400) \ \mu m$ long, apices rounded to subtruncate; utricular walls 2-3 μm thick, moderately thickened (to 32 μm) at apices (Figs 12A, 12D, 12E, 13A-13C). Hairs or hair scars common, always in a zone high up

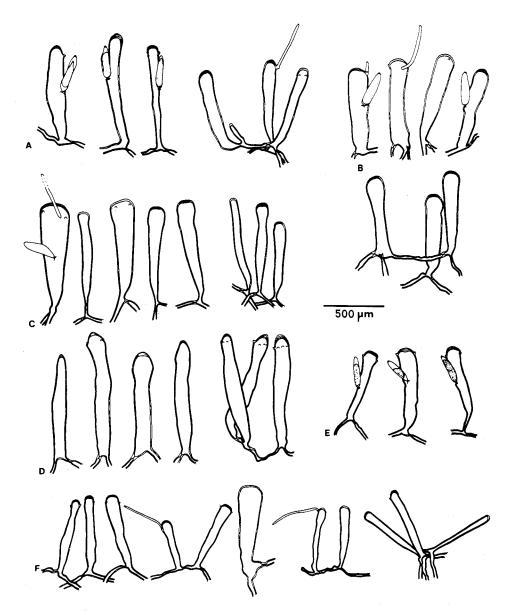


Fig. 12. Codium platyclados R. Jones & Kraft, sp. nov., utricle morphology from various collections. A. Sylphs Hole, L.H.I., December 1978 (MELU, K10382). B. Coffs Harbour, N.S.W., January 1981 (MELU22824). C. San Bernardino I., Luzon, Philippines, June 1968 (MELU, K934). D. Lord Howe I., June 1933 (UC507234). E. Middle Beach, L.H.I., December 1978 (MELU22822). F. Neds Beach, L.H.I., December 1978 (MELU, K9420).

towards the apex of the utricles (Figs 12A-12D, 13A). Gametangia ellipsoidal, tapering distally, 60-90 μ m in diam., 240-410 μ m long, borne on short pedicels in a zone around the middle of the utricles (Figs 12A-12C, 13A), one, occasionally two, per utricle.

Distribution

Lord Howe Island; Coffs Harbour, N.S.W.; Great Barrier Reef, Qld; Fiji; Philippine Islands.

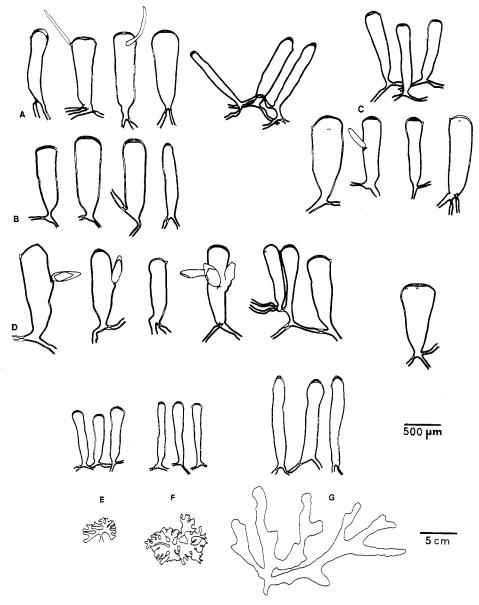


Fig. 13. Codium platyclados R. Jones & Kraft, sp. nov.

A-D, utricle morphology from various collections A, B. Neds Beach, L.H.I., December 1978 (MELU, K9626). Range of utricle forms from the holotype specimen. C. Split Solitary I., N.S.W., January 1981 (MELU24221). D. Saunders Beach, Townsville, Qld, November 1968 (JCT 1001). E-F. Plant habits drawn to the same scale showing corresponding lengthening of utricles with increase in plant size. E. Split Solitary I., N.S.W., January 1981 (MELU24221). F. Neds Beach, L.H.I., December 1978 (MELU, K9420). G. Lord Howe I., June 1933 (UC507234).

Habitat, Seasonality and Material Studied

Codium platyclados was present in most of the collecting sites and during all the seasons sampled. It ranges from just below the lowest tide marks to at least 28 m depths, but

reached its largest sizes in the shallow waters (<3 m) of the lagoon. Plants occurred as scattered individuals on open flats, in channels and gullies, and around the bases of undercut coral hummocks. 20 specimens have been examined from the following localities:

(1) Phillip Rock. In gullies on the sloping reef flat between 21 and 28 m depths (*Kraft & Gabrielson*, 30.i.1982. MELU, K10395).

(2) Neds Beach. 0.2 m deep on an iron rail of the boat ramp (*Kraft & O'Brien*, 12.v.1977. MELU, K9711); 3-8 m deep on coral outcrops (*Kraft & O'Brien*, 12.v.1977. MELU, K9723); barely subtidal on the southern reef flat (*Kraft & Lewis*, 1.iii.1976. MELU, K9087); 0.2 m deep in channels on the southern reef flat (*Kraft & Ricker*, 1.xii.1978. MELU, K9420).

(3) Sylphs Hole. 3-4 m depths on concrete blocks and coral shards at the boat anchorage (*Kraft & Ricker*, 2.xii.1978. MELU, K10382).

(4) Far Rocks and Signal Point. 1 0-1 5 m deep at bases of low calcarenite mounds on the reef flat (*Kraft & O'Brien*, 13.v.1977. MELU, K9765); (*Kraft & Lewis*, 5.iii.1976. MELU, K9232); (*Kraft & O'Brien*, 3.x.1976. MELU, K10183); (*Kraft & Ricker*, 1.xii.1978. MELU 22827).

(5) Middle Beach. 0.7 m deep in pool on the reef flat (*Ricker*, 10.xii.1978. MELU 22822).

(6) South Passage. 7-10 m deep along channel sides through the reef (*Kraft & O'Brien*, 1.x.1976. MELU, K10124); scattered individuals on coral shards at 22 m depth (*Huisman & Millar*, 31.i.1982. MELU, K10476).

(7) Johnsons Beach. At the low tide mark (*Evans*, 15.ix.1966. MELU 2874); $1 \cdot 0 - 2 \cdot 5$ m deep at bases of low coral mounds just offshore (*Kraft & O'Brien*, 21.v.1977. MELU, K9366); drift (*Kraft & O'Brien*, 20.v.1977. MELU, K9379).

(8) Lord Howe Island (Lucas & Perrin, June 1933. UC 507234 [identified as C. cuneatum S. & G. by W. A. Setchell]).

The following extra-island material was also examined:

(9) Coffs Harbour, N.S.W. 2-4 m deep on basalt on north side of North Muttonbird I. (*Millar & O'Brien*, 5.i.1981. MELU, AM804).

(10) Split Solitary I., N.S.W. 10-12 m deep (Millar & Chidgey, 4.i.1981. MELU 24221).

(11) Heron I., Great Barrier Reef, Qld. 8-10 m deep at Gorgonian Holes (F. Scott, 15.xi.1977. MELU, K15080).

(12) Saunders Beach, Townsville, Qld. Drift (I. Price, 8.xi.1968. JCT 1001).

(13) Suva, Fiji. 3-4 m deep behind the outer fringing reef (S. Chidgey, 26.ix.1981. MELU 22825).

(14) San Bernardino Island, Luzon, Philippines. 5 m deep on basaltic reef platform in strong surge (*Kraft*, 14.vi.1968. MELU, K934).

Remarks

Codium platyclados is extremely variable in form at Lord Howe, particularly in May when the greatest number of juvenile plants was collected. The largest specimens of the survey (Fig. 9C) were from shallow subtidal habitats at Far Rocks in March, when individuals were collected which dried to 18 cm in length and were 32 cm across the spread of the branches.

Codium platyclados belongs to the decorticatum group of species which includes a near southern Australian relative, C. duthieae Silva & Womersley (1956) and several other species (C. pocockiae Silva from South Africa, C. taylori Silva from the Caribbean Sea, C. cuneatum Setchell & Gardner from California, and C. reediae Silva from Hawaii) allied by their common tendency to form compressed axes, particularly at the dichotomies. Early records of C. platyclados from Queensland and New South Wales were referred to the Caribbean C. decorticatum and were recognized by Silva and Womersley (1956, p. 287) to apply to an undescribed species. Although C. platyclados closely resembles C. taylori and C. cuneatum in habit, we have followed Silva (1951, p. 102; personal communication) in considering Codium to be generally a genus of geographically limited species. The New World localities of C. cuneatum and C. taylorii show few algal affinities with Australia

(Silva 1962), and partly for this reason we have described the Lord Howe material as new. Codium cuneatum, which Setchell (in Lucas 1935) named Lucas' Lord Howe collections, has very similar utricle dimensions to C. platyclados, but its utricles reach much greater apical thicknesses [to 96 μ m (Silva 1951)] and commonly produce 'scalariform or chambered modifications' (Silva 1951) at the apices, which C. platyclados lacks. Codium duthieae tends to be a larger plant than C. platyclados overall, both in habit, utricle and gametangial dimensions, and medullary filament diameters. Where C. platyclados has 1(-2)gametangia per fertile utricle, C. duthieae can have as many as eight (Silva & Womersley 1956). Codium pocockiae is distinguished from C. platyclados by its asymmetrically thickened utricle apices (Silva 1959), whereas C. reediae differs mainly in the shorter length of its utricles and in the generally lesser stature of its plants. Certain forms of Lord Howe C. platyclados (Fig. 11C) closely resemble the habit of C. reediae in their narrow branch widths, numerous crowded distal dichotomies (Fig. 11C) and mostly terete lower crosssections, but suites of intergrading forms have convinced us that a single highly variable species is involved at Lord Howe. This extreme habit variation has not been documented in other Indo-Pacific and Australian members of the decorticatum group and has also influenced our decision to treat the Lord Howe species as distinct.

The Codium cuneatum records of Lucas (1935) consist of two sheets in the Lucas Herbarium (NSW) and at least one sheet in UC. Records of the same taxon from Bowen and Dunk Islands in Queensland were given as C. lineare C. Agardh and C. decorticatum (Woodward) Howe by Lucas (1931). Codium lineare is now considered to represent a later name for the Mediterranean species C. vermilare (Silva 1960), whereas Codium decorticatum is restricted by Silva and Womersley (1956, p. 287) to the Atlantic region.

Lucas (1935) ascribed *Codium indicum* Setchell, *nom. nud.*, to Lord Howe Island. This is a manuscript name first applied to a specimen sent to Setchell by Boergesen from western India. Although Silva and Nizamuddin have described the Boergesen material formally in manuscript (Silva, personal communication), Silva considers it to be distinct from Lucas' Lord Howe records of narrow, mostly terete forms which we consider on grounds of anatomy and time of year collected (mid-winter) to represent *C. platyclados* rather than *C. extricatum*.

Discussion

The species of *Codium* at Lord Howe Island are generally distinct and easily identified, with the exception of some individual specimens which could be either *C. platyclados* or *C. extricatum*. Plants of the latter tend to differ from the former mainly in overall terete habit and a tendency to form multiple gametangia per fertile utricle, and are unlikely to be confused when from their typical deep water habitats. Where habit ambiguities exist there is difficulty in separating the two species because of the relatively broad continuum of utricle lengths in both, which tend to increase with branch thickness. Certain shallow-water plants have been identified as *C. extricatum* only tentatively, and there is some question whether the species occurs regularly in shallow waters at all at Lord Howe, unlike its tidepool and surf-zone distribution in South Africa (Silva 1959). The phenomenon of increasing utricle lengths as a function of increasing branch thickness is also a feature of *C. bulbopilum*, which is, however, very distinct from other Lord Howe species by its procumbent, imbricating habit.

In the case of all the Lord Howe species save C. spongiosum, the problem of continuous variation in utricle dimensions leads to difficulties in separating each of our identified taxa from certain other species in which overlapping utricle dimensions have been reported. Thus C. bulbopilum intergrades with C. geppii, plants at the geppii end of the scale having utricles typically around 300 μ m in length whereas those at the bulbopilum end are 600 μ m or more in length. Between these extremes fall numerous specimens whose alignment with one end of the scale or the other would be rather arbitrary.

The same difficulty affects the distinction between *C. arabicum* and *C. lucasii* as these two entities seem to occur in eastern Australia. Two solutions suggest themselves for such difficulties, one being to lump all the overlapping forms into single large and widely

dispersed species, the other to consider clear-cut internal differences between specimens as representative of two distinct entities at opposite poles of a gradient and to treat ambiguous, intergrading forms as belonging to a species complex. We have chosen the latter approach as being less apt to gloss over large disjunctions in geographic distribution and in ignorance of the interbreeding potentials of widely separated populations.

The species of *Codium* at Lord Howe show some evident trends in both distribution and seasonality, with *Codium arabicum* and *C. bulbopilum* being confined, as far as we know, to shallow subtidal habitats. With few exceptions, *C. extricatum* is a species of deeper waters, the largest number and most typical forms coming from greater than 9 m. *Codium spongiosum* and *C. arabicum* are the only species to occur regularly in the intertidal, but *C. spongiosum* ranges subtidally to at least 28 m depths. *Codium platyclados* has a similar range, occurring from just below the low tide marks to the deepest areas sampled.

Within their vertical ranges, the species tend to occupy characteristic positions on the reef. *Codium arabicum* is typically an alga of the roofs of undercuts and the under surfaces of coral rubble. *Codium spongiosum* tends to line the margins of lee reef drop-offs and undercuts when growing in the lower eulittoral/upper sublittoral, but occupies open flats when permanently submerged. Plants from greater than 5–6 m depths tend to be isolated and subspherical, whereas those on shallow flats in the lagoon form large irregular aggregations covering extensive patches of reef.

Codium bulbopilum, with its distinctively imbricating, hummock formations, covers solid calcareous mounds, coral shards or concrete blocks on the lagoon side of the island. At Signal Point it is one of the dominant cover species in all but the September/October sample period, the hummocks expanding to diameters of over 30 cm and reaching 6–8 cm in thickness.

Codium platyclados is generally associated with the bases of low coral or calcarenite mounds in shallow waters and grows as scattered individuals on open flats and along gullies in deeper water. This pattern is followed by *C. extricatum*, which also occurs on vertical walls at the mouth of Old Gulch.

Codium arabicum, C. bulbopilum, C. platyclados and C. spongiosum were collected in all the sample periods, although numbers of both C. bulbopilum and C. platyclados appeared to be greatly reduced in the September/October collections. Plants of C. platyclados were largest in March and tended to either host large numbers of epiphytes and appear senescent or to be juvenile in May. Although present all year round, C. arabicum was largest in December, whereas May and September collections were of smaller plants with tougher consistency and smaller, more numerous marginal lobes.

Codium extricatum was collected only from the December, January and March sample periods, and was largest in the latter month. It is possible that it has the most limited growing season of any of the species, although its tendency to favour deeper habitats may have led to its being overlooked at other times.

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