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The marine species of *Cladophora* (Chlorophyta) from the South African East Coast

by

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With 16 figures and 5 tables

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Abstract: Twelve species of the genus *Cladophora* occur along the South African East Coast. Detailed descriptions and illustrations are presented. Four species are recorded for the first time in South Africa: *C. catenata*, *C. vagabunda*, *C. horii* and *C. dotyana*; the last two are also new records for the Indian Ocean. A comparison of the South African *C. rugulosa* specimens with specimens of *C. prolifera* from South Africa and other regions have shown that these species are not synonymous as previously considered, leading to the resurrection of *C. rugulosa* which is probably a South African endemic.

Key words: *Cladophora*, *C. catenata*, *C. dotyana*, *C. horii*, *C. prolifera*, *C. rugulosa*, *C. vagabunda*, South Africa, KwaZulu-Natal.

Introduction

Cladophora Kützing is one of the largest green-algal genera and has a worldwide distribution. Within the class Cladophorophyceae the genus *Cladophora* is characterized by its simple thallus architecture: branched, uniseriate filaments of multinucleate cells. Eleven different architectural types (sections) are distinguished in the genus (van den Hoek 1963, 1982; van den Hoek & Chihara 2000). Recent studies based on morphological and molecular data have proven that *Cladophora* is polyphyletic (van den Hoek 1982; Bakker et al. 1994; Hanyuda et al. 2002). The available molecular data are not sufficient yet to confirm (or reject) van den Hoek's morphological sections. A phylogeny of the Cladophorophyceae based on 18S rRNA (Bakker et al. 1994) suggests two lineages in the class: one containing predominantly tropical species including siphonocladean taxa and some *Cladophora* species, the other one containing mostly warm- to cold-temperate species of *Cladophora*. The addition of several

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species by Hanyuda et al. (2002) revealed a basal lineage within the class, containing a mixture of marine and freshwater species of *Cladophora* and other genera. The revisions of van den Hoek (1963, 1982), van den Hoek & Womersley (1984) and van den Hoek & Chihara (2000) are usually considered to represent the best taxonomic treatments of the genus *Cladophora*. Stegenga et al. (1997: 102-112, pls 20-23) studied the *Cladophora* species along the South African West Coast. Other papers dealing with the genus in South Africa are Levring (1938), Papenfuss (1940a, 1940b, 1943), Simons (1960, 1969, 1977), Seagrief (1967, 1980, 1988), and some of the earlier publications such as Chamisso (1821), C. Agardh (1824), Suhr (1834, 1840), Kützing (1849) and Martens (1868). Table 1 gives an overview of the *Cladophora* species recorded along the South and East Coast of South Africa (from Cape Agulhas to the Mozambican border) together with morphological characters, ecology and references to more detailed descriptions and illustrations. This paper deals with the marine *Cladophora* species along the South African East Coast, with the emphasis on the flora of KwaZulu-Natal (KZN).

Material and methods

Specimens examined were collected along the South African east coast on several occasions between November 1995 and February 2001. The collecting sites were located between Haga-Haga Mouth (north of East London) and Kosi Bay (northern KwaZulu-Natal) (Fig. 1). Specimens were processed as herbarium specimens in the field and preserved in 5% formalin in seawater. Voucher specimens are deposited in GENT and BOL. Herbarium abbreviations follow Holmgren et al. (1990).

Fig. 1. The South African East Coast, showing the sampling sites.

Table 1. *Cladophora* species recorded along the Indian Ocean coast of South Africa: type locality, morphological characters, ecology and references to more detailed descriptions and illustrations. Cell dimensions [from South African specimens measured and/or in literature if data was available; otherwise from other sources (see references)]: a = apical cell diameter (µm), m = main axis diameter (µm), b = basal cell diameter (µm), l/w = length-width ratio of the cells. Geographical distribution: uncertain records have been omitted, SA = distribution in South Africa, W = world distribution.

Species Type locality (T)	habit	cell dimensions (µm)	branching system	other characters	ecology	Reference(s)	Geographical distribution
C. aculeata (Suhr) De Toni, 1889: 353, *nom. illeg.* T: Algoa Bay (near Port Elizabeth), South coast of South Africa	rigid erect, fastigiate filaments	unknown	fastigiate, verticillate		unknown	De Toni (1889: 353)	SA: South coast (Barton 1893: 56)
C. afra Kützing, 1849: 411 T: mouth of Knysna River South Coast, South Africa	free erect, flaccid filaments	a: 20-30 b: 70-90	spreading, pseudodichotomous	filaments often curved	unknown	Kützing (1849: 411; 1854: 11, pl. 53: fig. I); De Toni (1889: 304)	SA: South coast (Barton 1893: 55)
C. albida (Nees) Kützing, 1843: 267 T: England	small (5 cm high) and spongy when exposed to wave action; large (50 cm) and erect in sheltered conditions.	a: 10-50, l/w 1-20 m: 20-80, l/w 1.5-8	dense, straight to refract, acropetally to irregular; growth mainly intercalary; 1-3 branches per cell		intertidal, wide ecological amplitude	van den Hoek (1963: 94-96, pl. 20-24 (p.p.); 1982: 100-105, figs 133-137, 144); van den Hoek & Womersley (1984: 206-208, figs 66C, 68A-D)	SA: South Coast (Bolton & Stegenga 1990: 236) W: world-wide in temperate zones of northern and southern hemispheres (van den Hoek & Chihara 2000: 129)
C. capensis (C. Agardh) De Toni, 1889: 354. T: Cape of Good Hope, West coast of South Africa	free erect filaments, 30-50 cm tall	a: 65-80, l/w 3-4 m: to 250, l/w 1.5-4	irregular, acute angled; growth mainly intercalary; 1-4 branches per cell	apical cells tapered	lower intertidal and below, epilithic	Seagrief (1988: 40, fig. 5:2); Stegenga et al. (1997: 103, pl. 20: 1)	SA: West coast (Stegenga et al. 1997: 103), South coast (Seagrief 1988: 40)
C. catenata (Linnaeus) Kützing 1843: 271 T: Bahamas	compact stiff cushions, composed of curved and intertwined branch systems	a: 300-360, l/w 7-25 m: 240-470, l/w 2-12	curved and intertwined, irregular; growth both apical and intercalary	very conspicuous long apical cells; filaments stiff and often curved; apical ends of decumbent axes often with terminal haptera	lower intertidal, surf-exposed rocky substrata	van den Hoek (1982: 59-64, figs 41-68); this paper	SA: East Coast (this paper) W: tropical W-Atlantic and Pacific Oceans (van den Hoek 1982: 58; van den Hoek & Chihara 2000: 45)
C. catenifera Kützing T: Cape of Good Hope, West coast of South Africa	*Cladophora catenifera* was proposed as a synonym of *C. pellucida* by van den Hoek (1982: 178). Barton (1896: 193) proposed the conspecificity with *C. radiosa*.						This species has been recorded from the South African West, South and East? coast (Delf & Michell, 1921: 93).
C. coelothrix Kützing, 1843: 272 T: Golfo di Genova, Italy	spherical tufts or compact moss-like or loose-lying mats	a: 57-75, l/w 5-15 m: 57-120, l/w 2.5-12	dense, irregular; 1 (-2-3) branches per cell; frequent intercalary cell division	many cells give off one rhizoid at their basal pole	intertidal to deep subtidal (-40 m) preferring shaded areas	van den Hoek (1963: 40-43, pl. 5-8 (p.p.); 1982: 47-52, figs 11-29); van den Hoek & Womersley (1984: 190-192, figs 60C, 61C,D); this paper	SA: East Coast (Bolton & Stegenga 1987: 168; this paper) W: world-wide in tropical to warm-temperate seas (van den Hoek & Chihara 2000: 37)

Table 1. continued

C. contexta Levring, 1938: 8-9, figs 4A,B, pl. I: fig. 2 T: Port Nolloth, West coast of South Africa	dark green cushions, a few cm high, composed of densely interwoven branch system	a: 70-100, l/w 1-3 m: up to 150, l/w 1-3	irregular, main axes often with numerous short ramuli in long secund series, 1 (-2) branches per cell, apical systems more polystichously branched; growth mainly intercalary	apical cells tapering to acute; many cells of the main axes give off rhizoids	sandy substrata	Stegenga et al. (1997: 105, pl. 21: 1-3)	SA: West coast (Stegenga et al. 1997: 105); East Coast (Farrell et al. 1993: 149). The East Coast record could not be verified since the voucher specimens are lost (Critchley pers. comm.).
C. flagelliformis (Suhr) Kützing, 1849: 388 T: Cape of Good Hope, West coast of South Africa	erect thallus, up to 30 cm tall, forming dense tufts	a: 50-80, l/w 0.5-8 m: 60-150 (-205), l/w: 1-5	1-4 laterals per cell; distal parts of the laterals unbranched and flagelliform	fertile cells developing in long unbranched apical sections	epilithic in lower intertidal and rock pools	Stegenga et al. (1997: 109, pl. 20: 2, colour plate 26); this paper	SA: West coast (Stegenga et al. 1997: 109); East Coast (Farrell et al. 1993: 149 as *C. virgata*) W: Tristan da Cunha (Baardseth 1941: 11) doubtful record
C. hospita (Mertens ex Chamisso) Kützing, 1843: 271 T: Cape of Good Hope, West coast of South Africa	According to Papenfuss (1940: 5-6) this species is conspecific with *C. mirabilis* (C. Agardh) Rabenhorst in Hohenacker. *C. mirabilis* however has only been recorded along the South African West coast while *C. hospita* has been recorded in the (sub)antartic regions and South Africa. See Stegenga et al. (1997: 110, plate 22:1) for a description and illustration of the species.						SA: West and South coast (Barton 1893: 55) W: St. Paul Island (Reichardt 1871); Antarctic and subantartic (Papenfuss 1964)
C. hutchinsiae (Dillwyn) Kützing, 1845: 210 T: Bantry Bay, Ireland	plants up to 35 cm long, coarse texture	a: 90-195, l/w: 1-4 m: 240-400, l/w: 1-3.5	pseudodichotomously branching main axes, set with branches of different lengths; terminal branch systems irregular to slightly acropetal, growth mainly intercalary; 1-2(-3) laterals per node.		intertidal to subtidal (-20 m)	van den Hoek (1963: 60-66, pl. 12-14 (p.p.)); Burrows (1991: 157-158, fig. 46); Schneider & Searles (1991: 65)	SA: South coast (Seagrief, 1988: 40) W: NW-Atlantic (Schneider & Searles, 1991); NE-Atlantic, Mediterranean (van den Hoek 1963: 61); NE-Pacific (Scagel et al. 1989)
C. lehmanniana (Lindenberg) Kützing, 1843: 268. T: Helgoland, Germany	fastigiate tufts	a: (22-) 90-160, l/w 2-10 m: (90-) 140-330, l/w 2-10	pseudodichotomously branching main axes which end in often falcate, acropetally organized branch-systems.		intertidal and subtidal in shaded habitats	van den Hoek (1963: 122-128, pl. 29-30 (p.p.)) van den Hoek & Womersley (1984: 198-200, figs 64B, 65C,D) Burrows (1991: 160-161, fig. 47); Huisman (2000: 235, +fig.)	SA: South coast (Barton 1893: 55) as *C. spinulosa* and *C. nuda* (misapplied names *fide* Papenfuss notes). W: warm-temperate Atlantic and Mediterranean coasts of Europe (van den Hoek 1963: 125); S-Australia (van den Hoek & Womersley 1984: 198); tropical Indian Ocean (Silva et al. 1996: 776).
C. liebetruthii Grunow in Piccone, 1884: 53. T: Gran Canaria and Ionian Sea	dark green, compact matted tufts or entangled, reticulate masses.	a: 60-80; l/w 2-5 m: 70-95; l/w 1.5-4	irregular wide angled ramification without distinct main axes; intercalary growth resulting in typical long, unbranched stretches of filaments; 1-3 branches per cell	apical cells often terminating in short rhizoids	intertidal to deep subtidal, epilithic	van den Hoek (1963: 59, Pl. 12, figs 128, 129; 1982: 69-72, figs 84-95); Kraft (2000: 564, fig. 22); this paper	SA: East Coast (this paper) W: tropical to warm-temperate Atlantic ocean (van den Hoek 1982: 70); tropical Pacific Ocean (Kraft 2000: 566); Indian Ocean (Raghukumar 1986: 290)

C. prolifera (Roth) Kützing, 1843: 271. T: "in mare Corsicam"	thalli dark green, forming dense, coarse, stiff tufts of densely branched fasciculate filaments.	a: 90-130, l/w 2.5-5.5 b: up to 200, l/w 7-10	acropetally organized branch-systems, growth only by division of apical cells; 1-3 branches per cell; small angle of ramification.	basal cells elongated and club-shaped, often with basal annular constrictions; old cells give off a rhizoid with annular constrictions, which grows down to the substratum	shallow intertidal, epilithic	*see text*	SA: South (?) and East Coast (this paper) W: widely distributed in the tropical to warm-temperate seas (van den Hoek & Chihara 2000: 54)
C. radiosa (Suhr) De Toni, 1889: 354 T: Algoa Bay, (near Port Elizabeth), South coast of South Africa	thallus dark green, bushy, erect, up to 50 cm high	a: 150-200, l/w 4-8 m: up to 600, l/w 25-70	acropetally organized branch-systems, growth mainly apical cell division; 1-2 laterals per node.	*C. radiosa* resembles *C. prolifera* but lacks annular constrictions in the basal cells	intertidal or subtidal, epilithic	Stegenga et al. (1997: 110-111, pl. 22: 2-3, colour plate 25)	SA: West Coast (Stegenga et al. 1997: 110); South coast (Simons, 1977: 17); East Coast (Farrell et al. 1993: 149) W: SE-Atlantic: Gough Island (Chamberlain, 1965). The SA East Coast record could not be verified since the voucher specimens are lost (Critchley pers. comm.).
C. rugulosa G. Martens, 1868: 112 T: Durban, East Coast of South Africa	thalli dark green, forming dense, coarse, stiff tufts of densely branched fasciculate filaments.	a: 105-285, l/w 2-8 b: 230-550, l/w 5-50	acropetally organized terminal branch systems, growth by apical cell division; up to 5 laterals per node.	basal cells club-shaped, with distinct annular constrictions. The basal poles of the old cells with distinct protuberances that attach to the parent cell below.	shallow intertidal and infralittoral fringe, epilithic	*see text*	SA: South and East Coast (see text)
C. horii, van den Hoek & Chihara, 2000: 67 T: Okinawa, Sesoko Isl., Japan	dense, erect, dark green tufts, up to 5 cm high	a: 60-90, l/w 1.4-5.5 b: up to 160, l/w 3-4	Branching more or less acropetally organized, small angle of ramification. 1-2 lateral per node.	The habit of this species has some likeness to small specimens of *C. prolifera*.	intertidal rockpools or shallow subtidal, epilithic or epiphytic	van den Hoek & Chihara (2000 : 67-68, fig. 28)	SA: East Coast (this paper) W: Japan (type locality)
C. sericea (Hudson) Kützing, 1843: 264. T: Isle of Sheppey, Kent, England	light to grass green, densely tufted plants up to 20 cm high	a: 15-70, l/w 3-16 m: 50-170, l/w 2-10	terminal branch systems acropetal to irregular; main axis pseudodichotomously branched; growth mainly by intercalary cell division.	apical cells tapering with an obuse tip	common in intertidal rockpools, able to penetrate in water with low salinity	van den Hoek (1963: 77-79, pl. 17-21 (p.p.); 1982: 93, 95-100) van den Hoek & Womersley (1984: 210, figs 69A, 70A,B)	SA: South coast (Bolton & Stegenga 1990: 236) W: temperate N-Atlantic ocean, Mediterranean, N-Pacific, (van den Hoek 1982: 96); South Australia (van den Hoek & Womersley 1984: 210)
C. socialis Kützing, 1849: 416 T: Tahiti	spongy or compact moss-like mats, or individual plants interwoven among other algae	a: 25-50; l/w 10-40 m: 35-55; l/w 3-20	branching dense, irregular; intercalary cell divisions frequent, 1-2 branches per cell	Many cells give off rhizoids at their basal poles. Differs from *C. coelothrix* by smaller cell diam.	intertidal, epilithic or epiphytic, in exposed (forming compact spongy pompons) or sheltered (forming loose lying mats) conditions	van den Hoek (1963: 43, 46, 47, pls 8, 9 (p.p.); 1982: 52-57, figs 30-40)	SA: East Coast (Bolton & Stegenga 1987: 168; this paper) W: world-wide in tropical to warm-temperate seas (van den Hoek & Chihara 2000: 42)

Results

Section Repentes Kützing

1. **Cladophora coelothrix** Kützing, 1843: 272 Fig. 2

Type locality: Golfo di Genova, Italy (leg. Meneghini, L 937/278/392).

References: Børgesen (1939: 72-73, fig. 15); Sartoni (1992: 300, fig. 5B); van den Hoek (1963: 40-43, pl. 5, figs 55-67, pl. 6, figs 68-71, pl. 7, figs 72-77, pl. 8, fig. 78; 1982: 47-52, figs 11-29); van den Hoek & Chihara (2000: 36-40, fig. 14).

Description:

Thallus dark green, forming cushion-like mats, composed of interwoven, densely branched filaments; loosely attached to the substratum by unbranched or branched, uni- or multicellular rhizoids developing from the basal poles of the short cells of the basal, stolon-like filaments. Basal filaments giving rise to the upright branch systems. Growth mainly by division of conspicuous apical cells, and by intercalary cell division lower down; cells becoming barely longer and broader in basipetal direction. Upright filaments either unbranched and composed of 3-5 cells, or branched with a branch-system up to the 2nd order and a feebly acropetal organisation. Maximum of one lateral per cell; newly formed laterals often without cross-walls at their base; in older laterals cross-walls steeply inclined to the parent cell; angle of ramification 20°-50°; ultimate filaments and apical cells often curved. Apical cells cylindrical with rounded tip, 57-75 µm in diam., l/w ratio 5-15; cells of ultimate filaments cylindrical, 57-93 µm in diam., l/w ratio 8-12; basal, prostrate cells cylindrical, 75-120 µm in diam.; l/w ratio 2.5-5. Cell walls ca. 1-3 µm thick in apical cells and ultimate filaments, up to 15 µm thick in basal cells.

Ecology: intertidal to subtidal (to 20 m deep).

Specimens examined: Adlams Reef, Sodwana Bay: KZN 321 (9/08/1999); Mabibi: KZN 2186 (13/02/2001).

Geographic distribution: *C. coelothrix* is widely distributed in the tropical to warm-temperate seas (van den Hoek & Chihara 2000: 37). Along the East African coast it has been recorded for Somalia (Sartoni 1992), Mozambique (Coppejans et al. 2002) and South Africa (Transkei) (Bolton & Stegenga 1987: 168).

Note: The possible absence of cross-walls at the base of newly formed laterals is a result of the delay in their formation, a phenomenon also occuring in *C. socialis* and *C. catenata*. *C. coelothrix* may be confused with *Cladophoropsis sundanensis* Reinbold [recently recorded from South Africa (Leliaert et al. 2001)] due to similarities in growth form, presence of hapteroidal rhizoids, delayed cross-wall formation and comparable cell dimensions. *C. sundanensis* can be distinguished by its light green thallus and cells which occasionally divide by segregative cell-division.

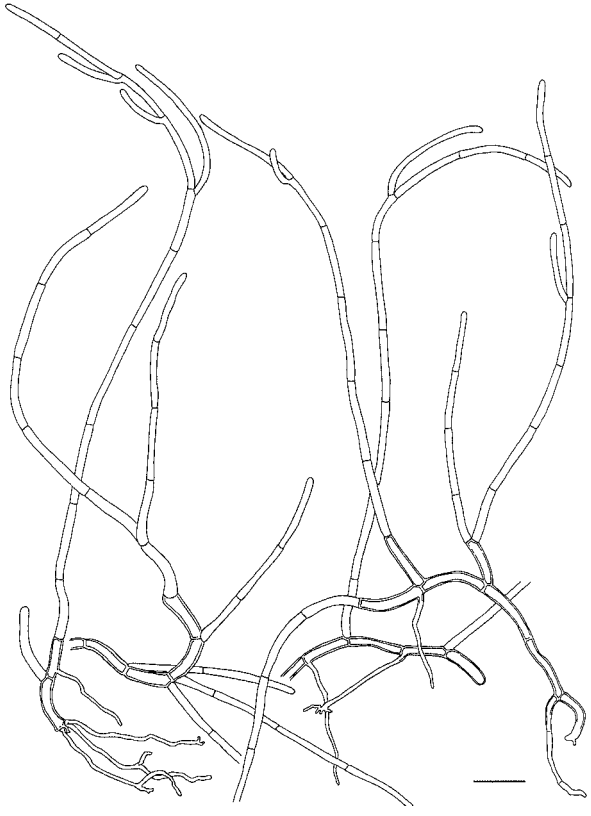


Fig. 2. *Cladophora coelothrix* (KZN 2186). Basal, stolon-like filaments giving rise to the upright branch systems. Scale bar = 500 µm.

2. **Cladophora socialis** Kützing, 1849: 416 Fig. 3

Type locality: Tahiti (L 937/253/440).

References: Børgesen [1940: 36-37, fig. 12 (as *C. patentiramea* (Montagne) Kützing forma *longiarticulata* Reinbold *in* Weber-van Bosse)]; Egerod (1974: 137-138, figs 17-21); Jaasund [1976: 9, fig. 17 (as *C. patentiramea* f. *longiarticulata*)]; Sartoni (1986: 361, 363, fig. 4A; 1992: 302-304, figs 6A,B); van den Hoek (1963: 43, 46-47, pl. 8, figs 79-85, pl. 9, figs 86-91; 1982: 52-57, figs 30-40); van den Hoek & Chihara (2000: 40-42, fig. 16).

Description:

Thallus medium to dark green, forming 0.5-1 cm thick prostrate mats, composed of interwoven, densely branched filaments. Thallus loosely attached to the substratum by branched or unbranched, uni- or multicellular rhizoids arising from the basal

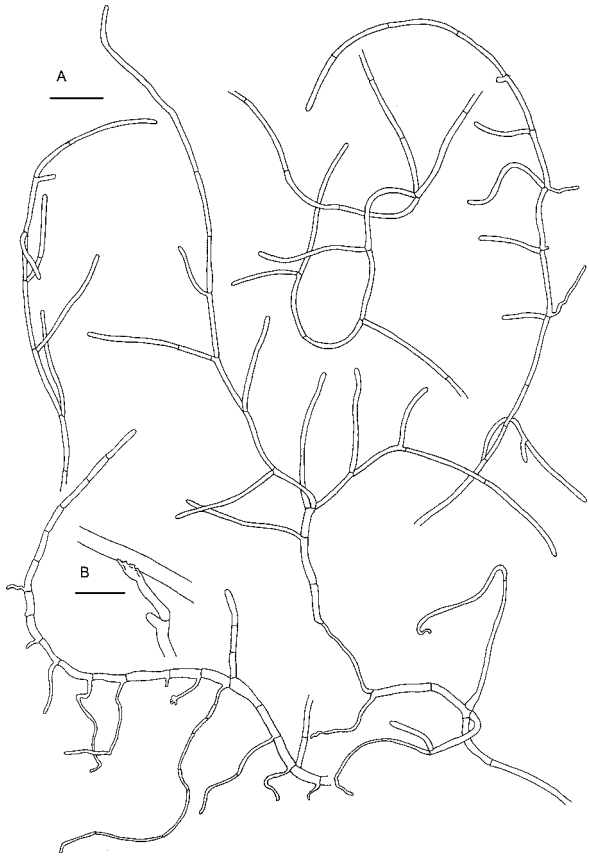


Fig. 3. *Cladophora socialis* (KZN 2185). A. Basal, stolon-like filaments giving rise to the upright branch systems. Scale bar = 500 µm; B. Attachment of filaments with one another by terminal hapteroidal holdfasts at the tips of the apical cells. Scale bar = 100 µm.

poles of the short cells of the stolon-like filaments. These basal filaments give rise to the upright, terminal branch-systems. Growth by division of apical cells, and by intercalary cell division lower down; cells in basipetal direction becoming barely longer and broader. Terminal branch-systems feebly acropetal to irregular, wide-angled (45°-90°), with occasional rhizoids from the basal poles of the cells. Laterals mostly one (rarely two) per cell. Newly formed laterals often without cross-walls at their base; in older laterals cross-walls steeply inclined to the parent cell. Filaments of basal and terminal branch-systems sometimes attached to one another by terminal hapteroidal holdfasts at the tips of the apical cells. Apical cells cylindrical with rounded tip, 25-50 µm in diam., l/w ratio 10-40; cells of terminal branches cylindrical, 35-55 µm in diam., l/w ratio 3-20; basal cells cylindrical, 60-120 µm in diam.; l/w ratio 3-5. Cell walls ca. 1 µm thick in apical cells, up to 8 µm in basal cells.

Ecology: intertidal sand covered rock, loosely attached to the substratum.

Specimens examined: Mabibi: KZN 2185 (13/02/2001); Rabbit Rock, Bhanga Nek: KZN 548 (13/08/1999).

Geographic distribution: *C. socialis* is widely distributed in tropical to warm-temperate regions of the Atlantic and Indo-Pacific Oceans, and has previously been collected in the Transkei (Bolton & Stegenga 1987: 168).

Note: *C. socialis* closely resembles *C. coelothrix* from which it only differs by its smaller cell diameter.

Section Aegagropila (Kützing) Hansgirg

3**. Cladophora catenata** (Linnaeus) Kützing, 1843: 271 Fig. 4

Conferva catenata Linnaeus 1753: 1166-1167

Type locality: Bahamas [van den Hoek (1963: 19, 123) has designated the material of *Conferva ramosa, geniculis longioribus cateniformibus* Dillenius, present in Dillenius's herbarium (OXF) as the type of *C. catenata*].

References: Littler & Littler (2000: 320, fig. on p. 321); Tseng (1983: 260, fig. 1 as *C. fuliginosa*); van den Hoek (1963: 123, note, pl. 55, fig. 722; 1969: 134-136, fig. 1; 1982: 59-60, figs 41-68); van den Hoek & Chihara (2000: 45-49, fig. 18).

Description:

Thallus dark green, forming compact cushions, 3-14 cm in diameter, up to 2 cm high, composed of entangled, stiff, often incurved axes. Growth by division of conspicuous apical cells and by intercalary cell division lower down; cells in basipetal direction becoming barely longer and broader. Branch system unilateral or irregular; maximum one lateral per cell; newly formed laterals often without cross-walls at their base; older branches inserted with a steeply inclined cross wall cutting it off from the parent cell. Angle of ramification 20°-70°. Some axes decumbent and attached to the substratum by terminal haptera on the apical, rhizoid-like cells (inversion of polarity). Apical cells cylindrical or gradually tapering, with rounded tip, often curved, 300-360 µm in diameter, l/w ratio 7-25, up to 8000 µm long; cells of the main axes cylindrical, 240-470 µm in diameter, l/w ratio 2-12. Decumbent axes composed of 4-8 cells, 150-300 µm in diameter; diameter gradually decreasing towards the distal ends. Cell walls 4-12 µm thick in apical cells, up to 40 µm in the main filaments.

Ecology: Epilithic in intertidal pools and in the infralittoral fringe, forming dark green mats.

Specimens examined: Mabibi: KZN 398 (09/08/1999), KZN 454 (11/08/1999); Rabbit Rock, Bhanga Nek: KZN 547 (18/08/1999); Kosi Bay: KZN 767 (16/08/1999).

Geographic distribution: *C. catenata* possibly has a very disjunct distribution in tropical seas; it has been recorded (often as *C. fuliginosa* Kützing) in the Caribbean

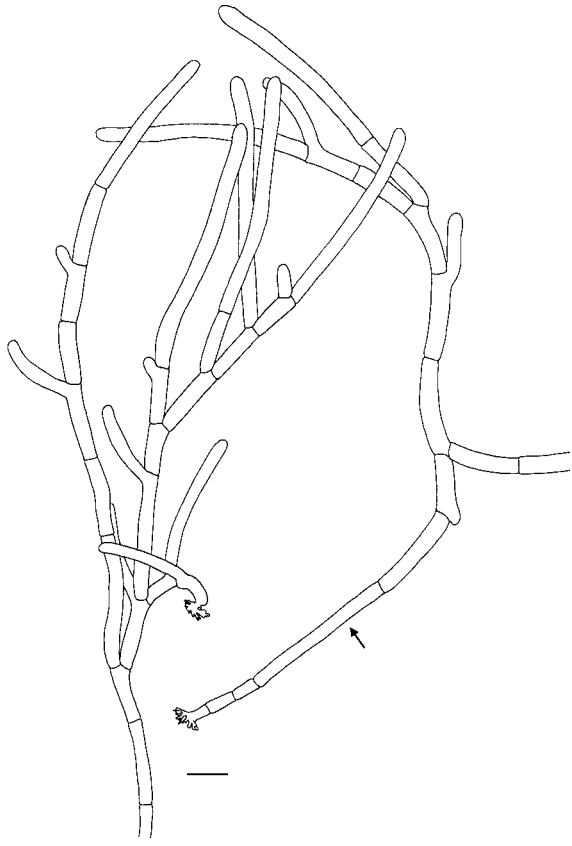


Fig. 4. *Cladophora catenata* (KZN 454). Branching filaments with decumbent filament with inversion of polarity (arrowhead). Scale bar = 1000 µm.

Sea (Littler & Littler 2000: 320), southern Japan and Taiwan (van den Hoek & Chihara 2000: 45), China (Tseng 1983: 260); Philippines (Silva et al. 1987: 97), the Caroline Islands and Queensland, Australia (Phillips 1997: 12). The Mediterranean records of *C. catenata* are possibly misidentifications of *C. lehmanniana* (Lindenberg) Kützing (van den Hoek 1963: 123, note). Recently we collected *C. catenata* in Mozambique, which was the first Indian Ocean record (Coppejans et al. 2002). This is the first record for South Africa.

Note: The dimensions and other morphological characters are in good agreement with the amended description of the species by van den Hoek (1982: 59-60, figs 41-68) and the drawings of Kützing (1854: 14, Tab. 65, fig. 1, as *C. fuliginosa* Kützing). For nomenclatural notes see van den Hoek (1963: 123; 1969: 134; 1982: 59). The species may be confused with some *Cladophoropsis* species, due to the similarities in growth form, the thick, stiff filaments, terminal haptera on the apical cells and the

delayed cross wall formation in young laterals. Distinction between *Cladophora* and *Cladophoropsis* is primarily based on the relative presence or absence of cross walls in laterals. This character, however, shows considerable variation within the genus *Cladophora* where cross wall formation may be postponed in some branches, but not as distinctly as in *Cladophoropsis*.

Section Boodleoides van den Hoek

4. **Cladophora liebetruthii** Grunow *in* Piccone, 1884: 53 Fig. 5

Type locality: Gran Canaria, Islas Canarias according to Silva et al. (1996: 777); isotype from Ionian Sea according to van den Hoek (1963: 59) (leg. Liebetruth, isotype in L 937/264/51).

References: van den Hoek (1963: 59, pl. 12, figs 128, 129; 1982: 69-72, figs 84-95).

Description:

Thallus dark green, forming three-dimensional netlike cushions, composed of entangled, short-celled filaments. Thallus loosely attached to the substratum by rhizoids developing from the basal or apical poles of cells in the basal region but even in the distal parts of the thallus. Growth mainly by intercalary cell division, giving rise to unbranched filaments of up to 25 cells. Branching irregular, wide-angled (40°-80°); mostly one, sometimes two laterals per cell. Laterals at first laterally inserted at the apical pole of the parent cell; the basal cells of the laterals soon become fused, at their basal poles, with the adjacent cell of the axis. Apical cells often terminating in hapteroidal discs or rhizoid-like structures by means of which they attach to other filaments. Apical cells cylindrical with rounded tip, 60-80 µm in diameter, l/w ratio 2-5; cells of the main axes cylindrical, 70-95 µm in diameter, l/w ratio 1.5-4. Cell walls 2-5 µm thick in the apical cells, up to 8 µm in the branches.

Ecology: Collected on a single occasion, epilithic in intertidal rock pools.

Specimen examined: Palm Beach: KZN 802 (19/08/1999).

Geographic distribution: *C. liebetruthii* has a wide distribution in the tropical to warm-temperate Atlantic Ocean (van den Hoek 1963: 59, 1982: 70-72, map 6). In the Pacific Ocean the species has been recorded from the Philippines (Fortes & Trono 1980: 55, fig. 4), the Great Barrier Reef (Cribb 1984) and Lord Howe Island (Kraft 2000: 564, fig. 22). In the Indian Ocean *C. liebetruthii* has so far only been recorded from India and the Laccadive Islands (as *C. frascatii* Collins & Hervey) (Raghukumar 1986: 290, 293, figs 8-15; Silva et al. 1996). The species is listed in Seagrief's (1984: 17) catalogue but no reference for a South African record could be retrieved.

Note: *C. liebetruthii* is the type and was until recently the only species in the section Boodleoides. The section is characterized by irregularly branched short-celled filaments which anastomose with one another, forming two- or three-dimensional

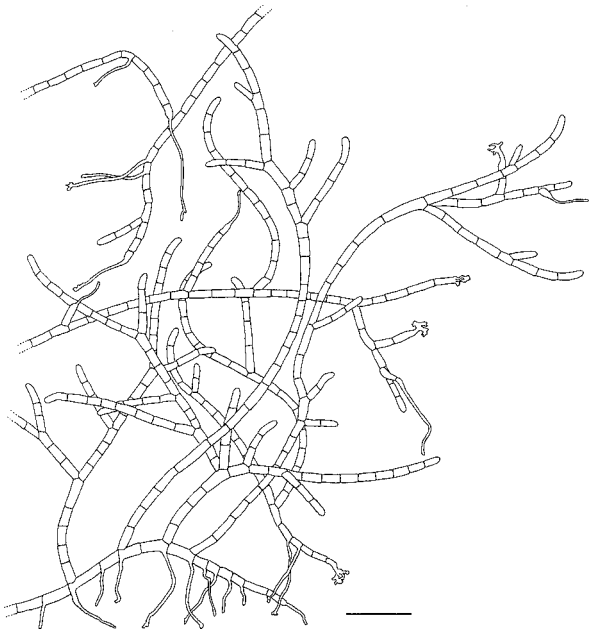


Fig. 5. *Cladophora liebetruthii* (KZN 802). Entangled, short-celled, branched filaments forming the netlike thallus. Scale bar = 500 µm.

netlike thalli, resembling *Microdictyon* or *Boodlea* species in habit. Recently two other species have been described in the section: *C. vandenhoekii* Norris & Olsen, a deep-water species from the Bahamas and *C. pachyliebetruthii* van den Hoek & Chihara, an intertidal species from Japan. Kraft (2000: 565) discusses the rather arbitrary nature of the separation of *Cladophora* section Boodleoides and the genus *Microdictyon*. van den Hoek (1982: 31-33, text figure 4) already formulated a hypothesis for the close relationship between both taxa. This hypothesis was confirmed by a phylogeny of the Cladophorophyceae (18S rRNA) showing that *C. liebetruthii* is indeed closely related with *Microdictyon*, but also clusters with *C. catenata*, *C. coelothrix*, *C. socialis* and *C. prolifera* (Bakker et al. 1994).

Section Rugulosae Sakai

5. **Cladophora prolifera** (Roth) Kützing, 1843: 271 Figs 6A-C, 7

Conferva prolifera Roth, 1797: 182-183, pl. III: fig. 2.

Type locality: "in mare Corsicam" [type lost; neotype designated by van den Hoek (1963: 208): leg. Hauck, locality: Miramare, Italy, L 937/264/23].

References: Isaac & Chamberlain (1958: 124, fig. 1); Littler & Littler (2000: 322, fig. on p. 323); Schneider & Searles (1991: 70-71, figs 55, 56); van den Hoek (1963: 208-212, pl. 51, figs 677-682, pl. 52; 1982: 166-170, figs 318-327); van den

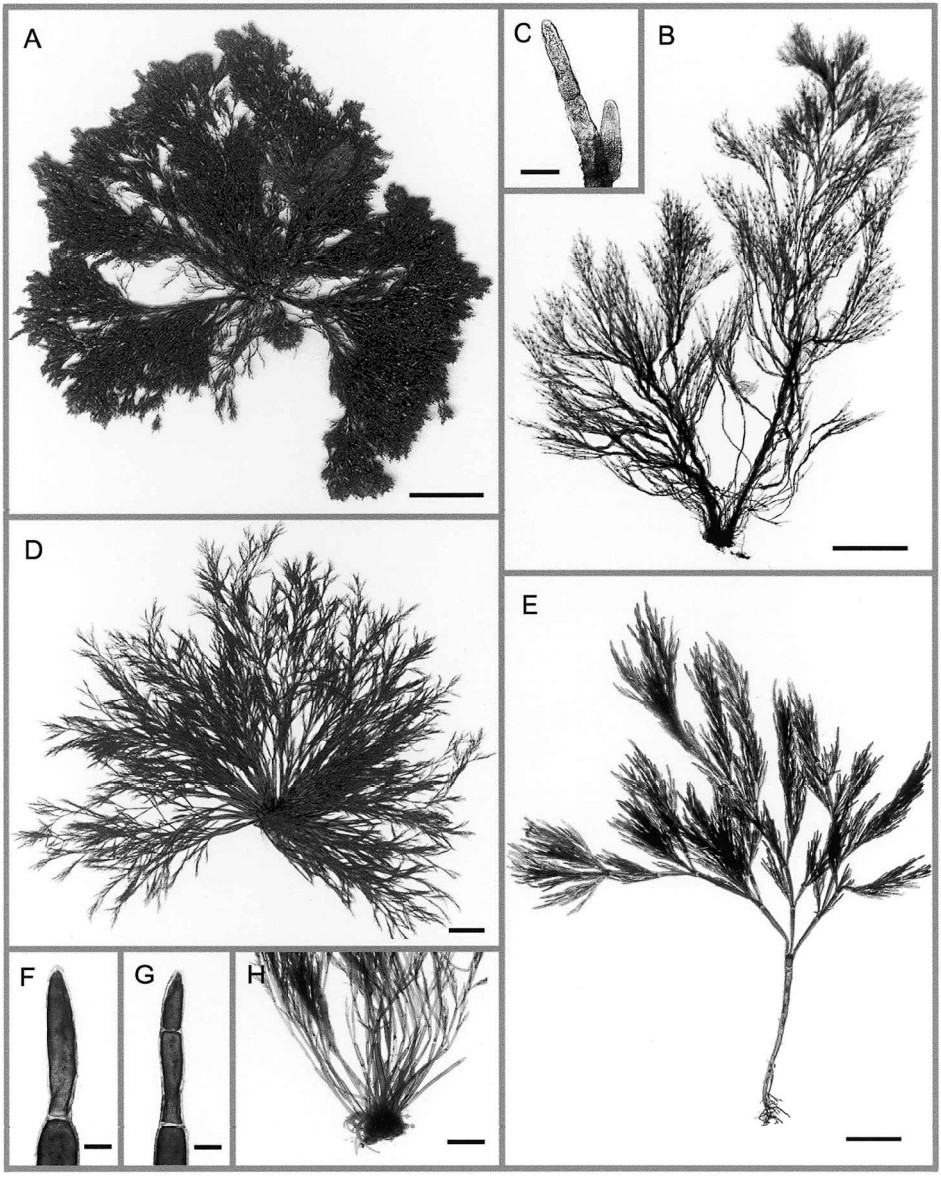


Fig. 6. A-C. *Cladophora prolifera* (KZN 533). A. Tuft composed of densely branched, fastigiate filaments, scale bar = 1 cm; B. Tuft with basal rhizoids forming a conspicuous stipe, scale bar = 5 mm; C. Apical cell, scale bar = 200 µm. D-H. *Cladophora rugulosa* (HEC 11015). D. Broom-like tuft, composed of clustered stipes, giving rise to branched filaments, scale bar = 1 cm; E. Single stipe cell giving rise to densely branched filaments, scale bar = 5 mm; F, G. Apical cells, scale bars = 200 µm; H. Densely clustered stipes, scale bar = 5 mm.

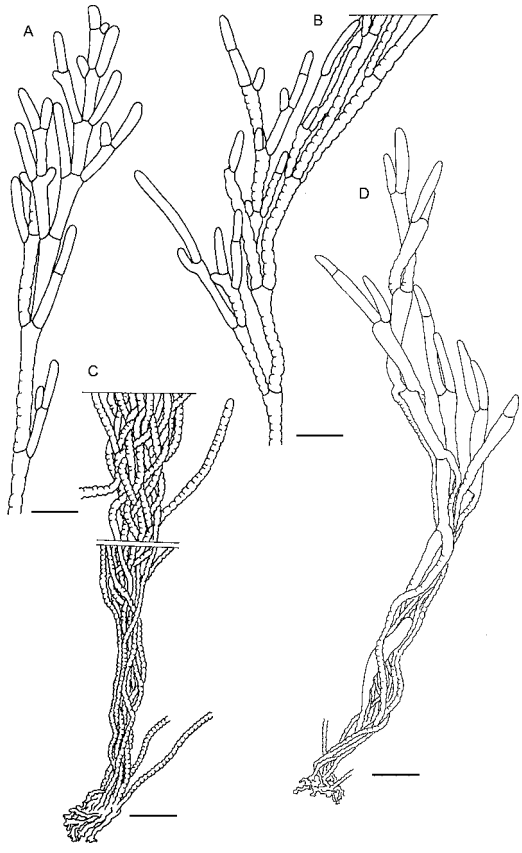


Fig. 7. *Cladophora prolifera* (KZN 533). A. Terminal branch system; B. Main branches in the middle of the thallus: cells with annular constrictions; C. Basal rhizoids with annular constrictions entangling and forming a stipe; D. Young thallus. Scale bars = 500 µm.

Hoek & Womersley (1984: 193-194, figs 62A, 63A,B); van den Hoek & Chihara (2000: 52-55, fig. 21). As *C. rugulosa* (misapplied name): Egerod (1975: 45, figs 5-7, 12); Tseng (1983: 260, fig. 4).

Description:

Thallus dark green (blackish when dried), coarse, 2-4 cm high, growing as stiff tufts composed of densely branched, fastigiate filaments. Old cells in the basal and middle part of the thallus each giving off one rhizoid with annular constrictions at their basal poles; these rhizoids grow down along the cell or cells below, where they entangle and form a conspicuous stipe that attaches to the substratum. Growth by apical cell division and subsequent cell enlargement. Branching originally acropetally organised, becoming irregular in older parts of the thallus because of intercalary

growth. Each subapical cell forms a lateral, often immediately after being cut off from the apical cell; lower down a cell may form a 2nd or sometimes a 3rd lateral. Apical cells cylindrical with rounded tip, 90-130 µm in diameter, l/w ratio 2.5-5.5; cells of the terminal branch systems cylindrical, 150-200 µm in diameter, l/w ratio 2.5-8, increasing towards base of the thallus. Cells of the main axes and basal cells elongated and club-shaped, up to 200 µm in diameter, l/w ratio 7-10, basal parts often with annular constrictions. Rhizoids 40-100 µm in diameter.

Ecology: epilithic, low intertidal, *Cladophora horii* sometimes grows as an epiphyte on this species.

Specimen examined from South Africa: Rabbit Rock, Kosi Bay: KZN 533 (13/08/1999).

Other specimens examined: Finike, Turkey: HEC 1790 (10/1973); Cap Le Dramont, France: HEC 2707 (07/08/1976); Point Lonsdale, Victoria, Australia: ODC 519 (07/07/1996).

Geographic distribution: *C. prolifera* is widely distributed in tropical and warm-temperate seas (van den Hoek & Chihara, 2000: 54). Along the East African coast *C. prolifera* has been collected in Mozambique (Isaac & Chamberlain (1958: 124); Tanzania (Jaasund 1976: 7, fig. 13, as *C. saviniana* (misapplied name); Jaasund 1977 as *C. rugulosa*), and Kenya (Isaac 1967: 76). The species has been recorded several times from South Africa (Krauss 1846: 215; Areschoug 1851: 12; Eyre & Stephenson 1938: 33; Stephenson 1939: 533; 1944: 300) but possibly this species was confused with *C. rugulosa* (see below).

6. **Cladophora rugulosa** G. Martens, 1868: 112, pl. II: fig. 3 Figs 6D-H, 8

Lectotype locality: Port Natal [Durban], South Africa according to Papenfuss (1943: 80).

Apjohnia rugulosa (G. Martens) G. Murray, 1891: 209

References: Bolton & Stegenga (1987: 168); Farrell et al. (1993: 149); Papenfuss (1943: 79-80); Papenfuss & Chihara (1975: 313, figs 12, 13); Seagrief (1967: 22, pl. 5; 1980: 21, fig. on pl. 1; 1988: 37, 40, fig. 5:2); Simons (1969: 246, fig. *s.n.*; 1977: 17, fig. 23).

Description:

Thallus dark green (dark brown when dried), 3-13 cm high, forming stiff, broom-like tufts, composed of densely clustered stipes giving rise to pseudodichotomous or oppositely branching main filaments and densely branched, often fasciculate terminal branch systems. Thallus attached to the substratum by branched, clumped rhizoids developing from the basal part of the stipe. Stipe composed of a single clavate cell with basal annular constrictions. Growth by apical cell division and subsequent cell enlargement. Terminal branch systems acropetally organized. Each new cell, after having been cut off from the apical cell, produces a lateral at its apical pole, either immediately when it has become the subapical cell or when it has become the 2nd cell below the apical cell. Subsequently (when the cell has become the 2nd-3rd cell below

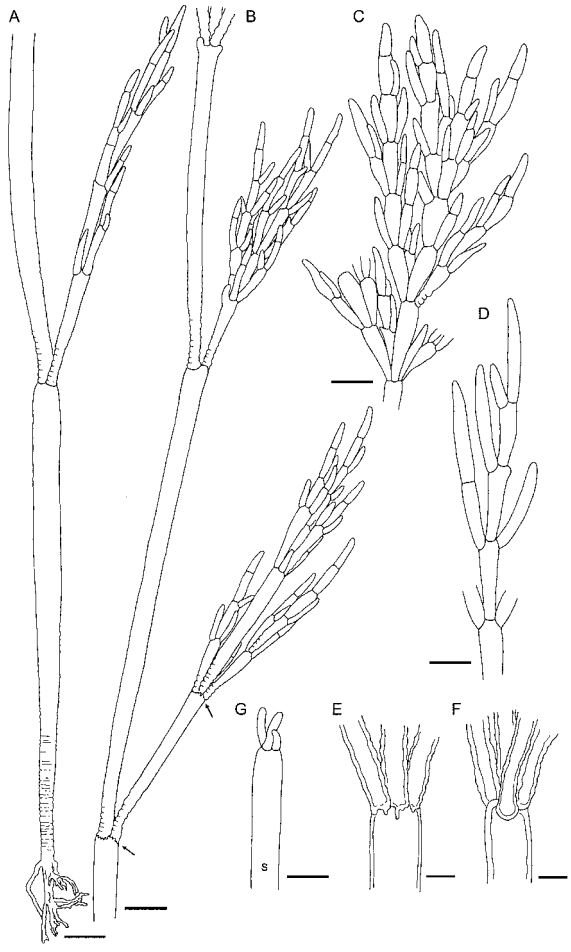


Fig. 8. *Cladophora rugulosa.* A-F (KZN 2039). A. Stipe cell with basal branches and fasciculate terminal branch-system, scale bar = 1000 µm; B. Main filaments with fasciculate terminal branch-system; basal poles of the older cells with annular constrictions and rhizoid-like processes (arrow), scale bar = 1000 µm; C, D. Terminal branch-systems, scale bars = 500 µm; E. Protuberances at the basal poles of the old cells, scale bar = 300 µm; F. Basal poles of old branches with annular constrictions, scale bar = 300 µm; G. Apical part of a young thallus (s = stipe cell) (KZN 819) scale bar = 1000 µm.

the apical cell) a second lateral is formed, resulting in a typical opposite branching pattern in the terminal, fasciculate branch-systems. At increasing distance from the apex a 3rd, 4th and 5th lateral may be produced. Young laterals are inserted with a steeply inclined cross wall cutting it off from the parent cell. Angle of ramification 10°-35°. Cells in basipetal direction becoming longer, increasingly club-shaped, with distinct annular constrictions at the base. The basal poles of the old cells often have distinct protuberances (short rhizoid-like processes) that attach to the parent cell below (fig. 7B, E). Apical cells tapering, with rounded tips, (105-) 130-260

(-285) µm in diameter, l/w ratio 2-8; cells of the terminal branches 220-415 µm in diameter, l/w ratio 2,5-12; cells of basal branches and main axes 380-550 µm in diameter at their distal end, 230-325 µm at the base, l/w ratio 5-25 (-50), up to 18 mm in length. Stipe cell 600-700 µm in diameter at the distal end, 230-350 µm at the base, 12-18 mm in length. Cell walls 12-50 µm thick in apical cells and terminal branches, up to 130 µm thick in the main axes, basal cells and stipe.

Ecology: Epilithic in the shallow intertidal or infralittoral fringe; often on wave-exposed rocks. *C. rugulosa* is by far the most common *Cladophora* species along the South African East Coast. In the lower intertidal this species often covers entire rock surfaces.

Specimens examined: Haga-Haga Mouth: KM 18 (26/10/1999); Cape Morgan: KM 182 (24/10/1999), KZN 1345 (24/10/1999), KZN 1302 (25/10/1999); Double Mouth: KM 107 (25/10/1999); Ntlonyana, S of The Haven: KZN 1026.2 (16/02/1999), KZN 1206 (16/02/1999); Port Edward: KZN 1383 (24/12/1999); Palm Beach: FL 258 (22/03/1997), KZN 819 (19/08/1999), KZN 1550 (21/12/1999), KZN 2039 (7/02/2001); Port O'Call, Trafalgar: FL 225 (20/03/1997), KZN 928 (20/08/1999); Crayfish Point, Mapelane: KZN 1836 (20/08/2000); Mission Rocks: HEC 11015 (23/11/1995), KZN 1049 (8/07/1998), HB81-S62R (8/07/1998).

Geographic distribution: *C. rugulosa* is only known from the South African South and East Coast (see note below). Most records from outside South Africa are misapplied names for *C. prolifera*: Australia (Womersley 1956: 359), Thailand (Egerod 1975: 45, figs 5-7, 12), China (Tseng 1983: 260, pl. 129, fig. 4), Japan (Okamura 1912: 103, pl. 80, figs 1-7; Sakai 1964: 67-70; Segawa 1965: 10; Yoshida 1998: 67), Vietnam (Pham-Hoàng Hô 1969: 431, fig. 4.36), Philippines (Marcos-Agngarayngay 1983: 75, fig. 10), and Tanzania (Jaasund 1977: 510). Some other records could not be verified because no description or illustration was provided: Taiwan (Lewis & Norris 1987: 8), Malaysia (Phang & Wee 1991: 57).

Note: van den Hoek (1982: 169) proposed to synonymise *C. rugulosa* with *C. prolifera*, based on descriptions and illustrations of *C. rugulosa* by Papenfuss (1943), Jaasund (1976), Egerod (1975), Womersley & Bailey (1970), Sakai (1964) and Taylor (1945). Other authors had differentiated the two species. Papenfuss (1943: 80) distinguished *C. rugulosa* on the basis of longer cells, more prominent main axes, and more pronounced annular constrictions in the cells. Papenfuss & Chihara (1975: 313) argued that small rhizoid-like processes at the proximal end of the basal cells are only present in *C. rugulosa*. van den Hoek (l.c.) rejects the above arguments because rhizoid-like processes are also occasionally present in some *C. prolifera* plants and cell dimensions are too variable in *C. prolifera* to split off the coarser *C. rugulosa*. We compared the South African specimens with *C. prolifera* from Europe, Kenya and Australia. Based on our observations two species, *C. prolifera* and *C. rugulosa*, both occurring in South Africa, are not identical owing to completely different modes of attachment. *C. prolifera* is characterized by the presence of rhizoids with annular constrictions developing from the lower part of the basal cells, growing down along the cells below where they entangle with one another to form a conspicuous 'stipe' (figs 5B, 6C, D). In *C. rugulosa* this kind of rhizoids is absent (Martens 1868: Pl. 2,

Table 2. Variation in cell diameter in *C. prolifera* and *C. rugulosa.*

	Geographical region and reference	apical cell diam. (µm)	basal cell max. diam. (µm)
C. prolifera	Europe (van den Hoek 1963)	120-200	330-650
	Australia (van den Hoek & Womersley 1984)	(70-) 100-220	420
	Atlantic (van den Hoek 1982)	95-240	345
	Japan (van den Hoek & Chihara 2000)	120-220	300
	Thailand (Egerod 1975)	77-118	300
	South Africa (this paper)	90-130	200
C. rugulosa	South Africa (this paper)	(105-) 130-260 (-285)	550 (700)

fig. 3); here the plants are attached by basal branching rhizoids developing from the base of a conspicuous stipe cell with annular constrictions. The rhizoids form a basal clump giving off numerous, densely clustered stipe cells (fig. 5H). The South African *C. prolifera* also differs from *C. rugulosa* by its smaller cell diameters, but since the cell diameter of *C. prolifera* is shown to be very variable, this character is less useful in distinguishing both species (Table 2).

7. **Cladophora horii** van den Hoek & Chihara, 2000: 67-68, fig. 28 Figs 9A-C, 10

Type locality: Okinawa, Sesoko Island, Japan (leg. S. Kamura, C. van den Hoek & T. Hori; van den Hoek no. 90/8.a.4, TNS-AL-46793).

Description:

Thallus dark green, forming stiff, 2-5 cm high, broom-like tufts of densely branched fasciculate filaments; attached to the substratum by branching rhizoids developing from proximal parts of the basal cells. Growth by apical cell division in the terminal branch systems, and by intercalary cell division lower down; cells in basipetal direction becoming slightly longer and broader. Branching more or less acropetally organized. Each new cell after having been cut off from the apical cell produces a lateral at its apical pole, when it has become the 1st or 2nd cell below the apical cell; later a second lateral is often formed, resulting in an opposite branching pattern. Laterals inserted with a steeply inclined cross wall cutting it off from the parent cell. Angle of ramification acute: 5°-25°. Cells in the middle and basal parts of the thallus producing rhizoids that grow along and into the cell walls of the cells below; consequently the stem-like basal branches become completely covered by and the cell walls fused with these rhizoids. Apical cells cylindrical with rounded tip, 60-90 µm in diameter, l/w ratio 1.4-5.5; cells of the terminal branches cylindrical to slightly club-shaped, 70-120 µm in diameter, l/w ratio 3.5-5; basal cells club-shaped, up to 160 µm in diameter, l/w ratio 3-4. Cell walls 2-5 µm thick in apical cells, up to 14 µm thick in basal branches.

Ecology: Epilithic in low intertidal pools or in shallow subtidal (to 1 m deep), or epiphytic on *Cladophora prolifera* in the low intertidal.

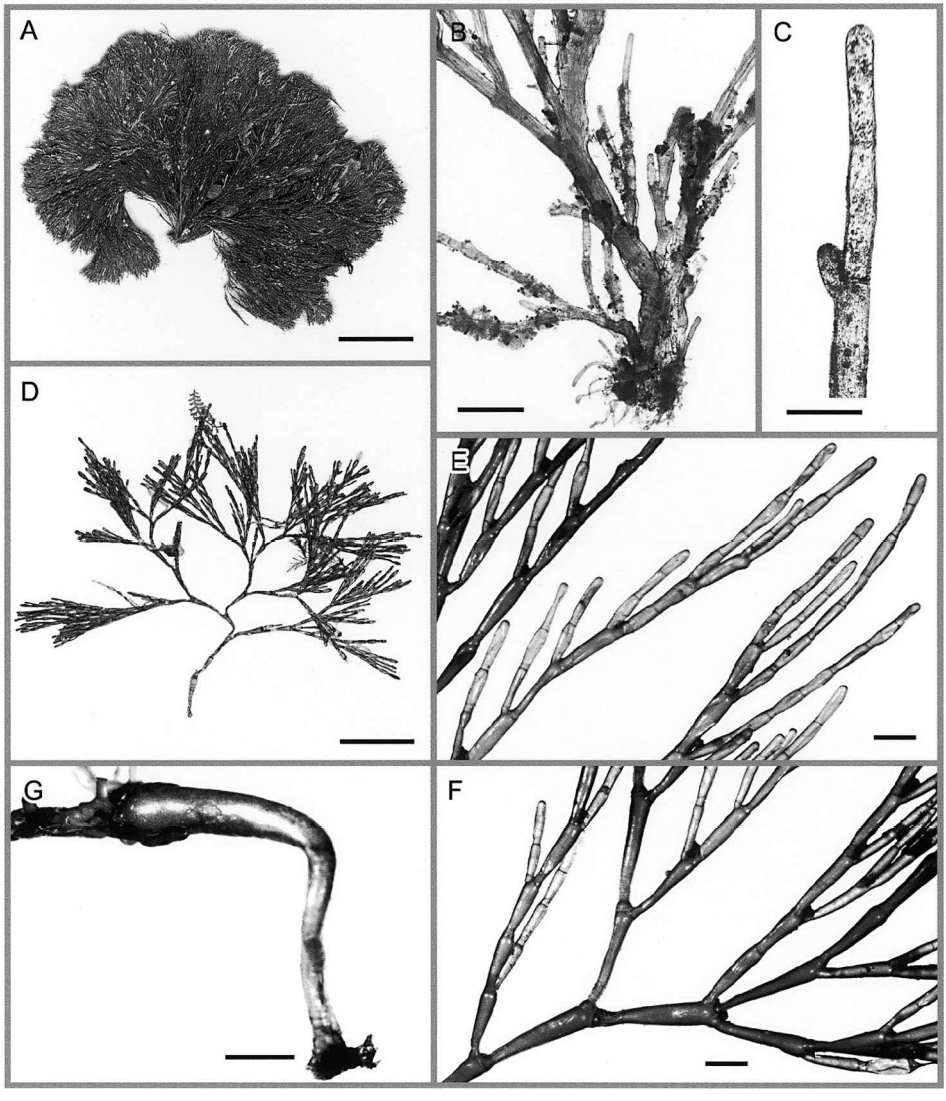


Fig. 9. A-C. *Cladophora horii.* A. Broom-like tuft, composed of densely branched, fasciculate filaments (HEC 10983), scale bar = 1 cm; B. Stem-like basal branches, completely covered by rhizoids (HEC 10983), scale bar = 5 mm; C. Apical cell (KZN 356), scale bar = 200 µm; D-G. *Cladophora dotyana* (FL 343). D. Tuft composed of a one-celled stipe, pseudodichotomously branching main axes and densely branched terminal branch systems, scale bar = 1 cm ; E. Terminal branch systems, scale bar = 1 mm; F. main axes, scale bar = 1 mm; G. Clavate, curved stipe cell, scale bar = 1 mm.

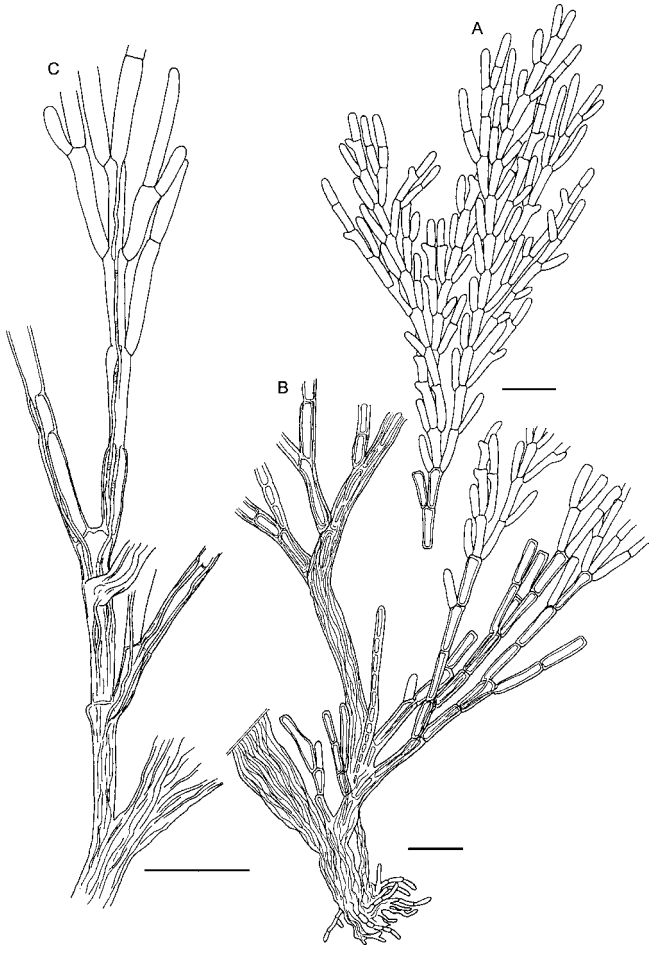


Fig. 10. *Cladophora horii* (KZN 356). A. Terminal branch systems; B. Base of thallus with stem-like branches; C. Cells in basal part of the thallus producing rhizoids at their basal poles growing along and into the cell walls of the cells below. Scale bars = 500 µm.

Specimens examined: The Bluff, Durban: HEC 10983 (22/11/1995), KZN 101 (03/08/1999), KZN 158 (04/08/1999); Mission Rocks, St. Lucia: KZN 1048 (08/07/1998); Mabibi: KZN 356 (09/08/1999), KZN 1676 (13/08/2000); Rabbit Rock, Bhanga Nek: KZN 533 (epiphytic on *C. prolifera*) (13/08/1999).

Geographic distribution: This is the first record of *C. horii* outside its type locality.

Note: This recently described species from Japan resembles young specimens of *C. prolifera* in general habit. *C. horii* can be distinguished by the lack of annular

constrictions in the stipe cell and rhizoids. The rhizoids in *C. prolifera* do not fuse with the cell walls of the cells below, like in *C. horii*, but remain loose and entangle with one another to form a distinct stipe.

Section Longi-articulatae Hamel

8. **Cladophora dotyana** Gilbert, 1965: 486-489, fig. 3 Figs 9D-G, 11

Type locality: Hokipa Park, East Maui, Hawaiian Islands (leg. Gilbert 9214, MICH).

Reference: van den Hoek & Chihara (2000: 88-91, figs 38-39).

Description:

Thalli dark green, forming erect, coarse, stiff tufts, up to 4 cm high, composed of a one- or two-celled stipe, pseudodichotomously branching main axes and densely branched terminal branch systems; attached to the substratum by basal branching rhizoids developing from the basal stipe-cell. Growth mainly by apical cell division, and few intercalary divisions lower down; cells in basipetal direction becoming longer, broader and increasingly club-shaped. Terminal branch systems organized more or less acropetally to irregularly. Each new apically formed cell giving off one lateral when arriving at the position of the 2nd to 8th cell below the apical cell; lower down a cell may occasionally produce a 2nd branch. Young laterals are apically inserted with a feebly inclined cross-wall cutting it off from the parent cell; with age these walls become almost horizontal. The basal cells of the older laterals become fused at their basal poles with the basis of the cells of the main axes. Angle of ramification ranging from 20°-30° in the terminal branch-systems to ca. 45° in the basal branches. Apical cells cylindrical with rounded tip, 250-290 µm in diameter, l/w ratio 3-6. Cells of the terminal branch systems cylindrical to slightly clavate, 280-480 µm in diameter, l/w ratio 2-6. Cells of basal branches clavate with a distinct basal bulge, diameter of cell apices 520-840 µm, diameter of the basal bulge 480-600 µm, diameter just above basal bulge 320-480, cell length 2.8-4 mm. Stipe cells clavate, often curved, diameter at cell apex 940-990 µm, diameter at lower end 380-440 µm, length 4.5-6.2 mm. Cell walls in apical cells ca. 10 µm thick, in basal filaments up to 140 µm thick.

Ecology: Epilithic, subtidal (at -19 m).

Specimens examined: Port Edward: FL 343 (24/03/1997); Salmon Banks, Shelly Beach: KZN 2003 (06/02/2001).

Geographic distribution: Up to now *C. dotyana* was only known from Hawaii (type locality) and Japan. This is the first record of the species for the Indian Ocean.

Discussion: *C. dotyana* is characterized by thick, stiff filaments, distinct clavate basal cells and a large clavate, often curved stipe cell. The South African material is in general agreement with the original description of *C. dotyana* from the Hawaiian Islands (Gilbert l.c.) and the description of the Japanese plants by van den Hoek & Chihara (2000: 88-91, figs 38, 39). A comparison of *C. dotyana* from Hawaii, Japan and South Africa is given in Table 3.

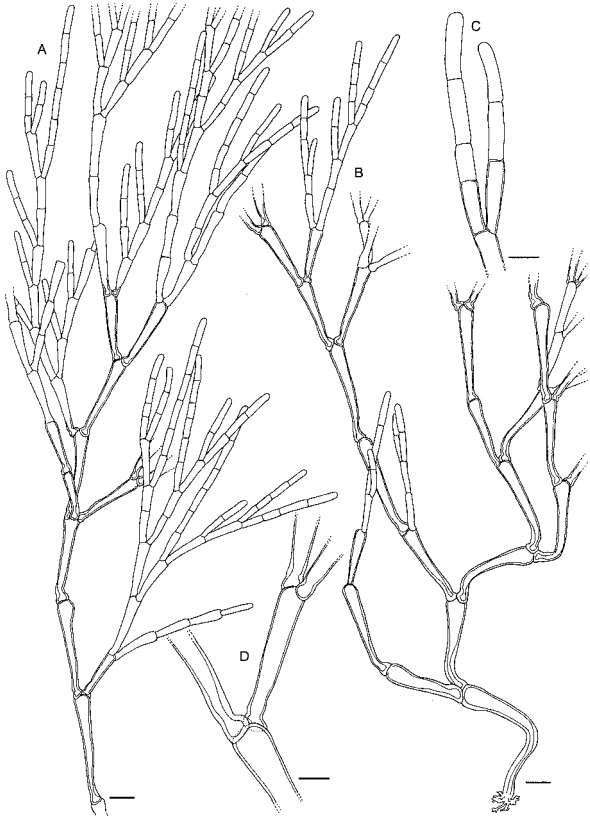


Fig. 11. *Cladophora dotyana* (KZN 2003). A. Main filaments and terminal branch-systems, scale bar = 1000 µm; B. Stipe cell and basal branches, scale bar = 1000 µm; C. Apical cells, scale bar = 500 µm; D. Clavate cells of the main filaments with basal bulges, scale bar = 500 µm.

Table 3. Comparison of *C. dotyana* from Hawaii (Gilbert 1965), Japan (van den Hoek & Chihara 2000) and South Africa (this paper).

	Hawaii	Japan	South Africa
Basal cell diameter	up to 600 µm	400-700 µm	480-600(-960) µm
Cell diameter of terminal branch systems	210-300 µm	180-340 µm	280-480 µm
Diameter of apical cells	ca. 220 µm (derived from Fig. 3)	160-340 µm	250-290 µm
Maximum number of laterals per cell	3 (rarely 5)	3	2
Cell shape of basal branches	cylindrical	cylindrical to slightly clavate	distinctly clavate

Fig. 12. *Cladophora* sp. (KZN 2098). A. Main filaments and terminal branch-systems, scale bar = 1000 µm; B. Main filaments with young laterals, scale bar = 500 µm.

9. **Cladophora** sp. Fig. 12

Description:

Thallus light green, forming 1.5 cm high, penicillate, densely branched tufts. Branching system organized acropetally. Growth mainly by apical cell division, each 4th or 5th cell below the apical cell giving off one lateral at its apical pole; at increasing distance from the apex a cell may give off a second and sometimes a third branch. Branches inserted at the apical cell pole with an almost horizontal cross wall, cutting it off from the parent cell. Angle of ramification ranging from 20°-40° in the basal branches to 5°-30° in the terminal branch-system. Apical cells tapering, with obtuse tip, diameter 80-95 (-125) µm, l/w ratio 10-16. Cells of the terminal branch-systems 75-110 µm in diameter, l/w ratio 9-15. Cells of the basal branches 100-300 µm in diameter, l/w ratio 5-10. The basal cell has been detached when collected.

Ecology: Epilithic, subtidal (at -12 m).

Specimen examined: 2-Mile Reef, Sodwana: KZN 2098 (10/02/2001).

Note: Only a fragment of the plant was present in our collections, lacking the basal branch system and stipe. Therefore a certain identification cannot be made. Important missing characters are the dimensions of the basal stipe cells, the number of cells composing the basal stipe, and clustering of the basal stipe cells. Based on branching pattern, insertion mode of branches and the cell dimensions of the cells in the apical parts of the thallus this specimen can possibly belong to *C. pellucidoidea* van den Hoek, *C. feredayi* Harvey, *C. japonica* Yamada var. *kajimurae* van den Hoek & Chihara or *C. sakaii* Abbott (van den Hoek pers. comm.). Table 4 gives an overview of character states of these four taxa.

Table 4. Comparison of 4 species in the section Longi-articulatae and the unidentified South African specimen.

	C. pellucidoidea	*C. feredayi*	*C. japonica* var. *kajimurae*	*C. sakaii*	*C. sp.* KZN
References	van den Hoek (1982: 179, figs 358-362) Schneider & Searles (1991: 69, figs 52-54)	van den Hoek (1963: 221-222, figs 700, 701, 706) van den Hoek & Womersley (1984: 196, figs 62 C, D, 63 D, E)	van den Hoek & Chihara (2000: 73, fig. 32)	Abbott (1972: 259-265) Abbott & Hollenberg (1976: 107-108, fig. 66) van den Hoek & Chihara (2000: 92-108, figs 41-45)	this paper
Number of laterals per cell	up to 2 (rarely 3)	up to 5	up to 4 (rarely 5)	up to 4	up to 2, sometimes 3
Diameter apical cells	50-95 µm	(35-) 40-120 (-135) µm	70-150 (170) µm	(50-) 60-150 µm	80-95 (-125) µm
Diameter stipe cells	?	350-600 (-800) µm	350-800 µm	170-250 (-300) µm	?
Number of cells composing the stipe	1-4	?	1-3	1-3 (rarely 4)	?
Clustering of stipes	stipe single?	stipes single or clustered	clustered	clustered	?
Ecology	deep-water	shallow subtidal, 1-10 m deep	shallow to deep subtidal, 1-40 m deep	deep-water	subtidal, 12 m deep
Type locality	North Carolina	Tasmania	Japan	Japan	/
Geographic distribution	North Carolina, Georgia, Curacao	Australia, Tasmania, New Zealand, Mediterranean, Canary and Salvage Islands	Japan	Japan, Korea, California	/

Section Glomeratae Kützing

10. **Cladophora flagelliformis** (Suhr) Kützing, 1849: 388 Fig. 13

Conferva flagelliformis Suhr, 1840: 294

Type locality: Cape of Good Hope, South Africa [Material of *Conferva flagelliformis* Suhr collected at "Caput bonae spei" (nos 7963-7964) is present in the Agardh herbarium (LD). It is not certain that these specimens are part of the original material

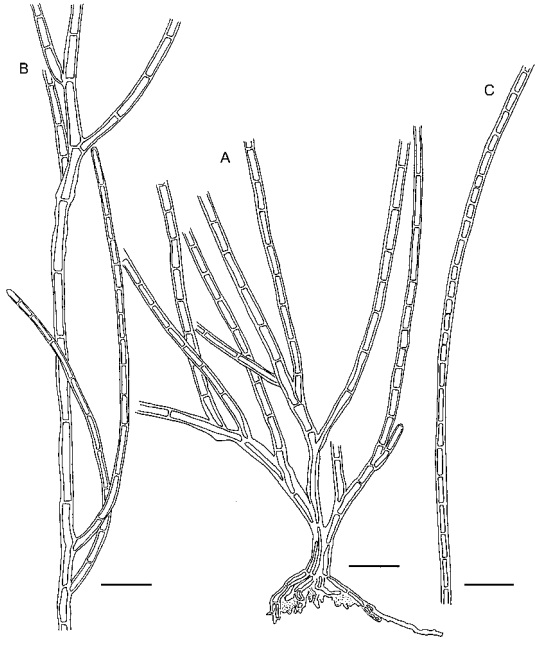


Fig. 13. *Cladophora flagelliformis* (KZN 68). A, Basal branches and rhizoidal holdfast; B. Basal branches; C. Unbranched terminal filament. Scale bars = 500 µm.

since the collector, Drége, mentioned in the original description is not mentioned on the herbarium specimens].

Taxonomic synonym: *Cladophora virgata* Kützing, 1843: 271 (type locality: Cape of Good Hope, South Africa).

References: Kützing [1853: 23, Tab. 77, fig. I (as *C. virgata*), fig. II (*C. flagelliformis*)]; Seagrief [1980: 21, fig. on pl. 1 (as *C. virgata*)]; Stegenga et al. (1997: 109, Pl. 20: 2; Colour Plate 26).

Description:

Thallus dark green, forming dense tufts of erect filaments, up to 8 cm tall; attached basally by branched, septate rhizoids developing from the proximal part of the basal cells. Growth in the main filaments mainly by intercalary cell divisions, in the young laterals also by apical cell division. Branching irregularly organized, maximum one lateral per cell, inserted by an oblique wall cutting it off from the parent cell. Branches restricted to the basal parts of the thallus, the distal part of the thallus unbranched and flagelliform. Apical cells of actively growing branches cylindrical, with rounded tip, 52-80 µm in diameter, l/w ratio 1.5-5.5; cells of branchlets 67-105 µm in diameter, l/w ratio 1.4-3.5; cells of the main filaments 60-115 µm in diameter in the basal part of the thallus, generally increasing towards the distal part up to 205 µm in diameter,

l/w ratio 3-4.8 decreasing towards the distal part to about 1.5-2.5; basal cells 85-125 µm in diameter, l/w ratio 5-34. Cell walls relatively thick throughout the thallus; ca. 5-25 µm thick in apical cells and young laterals, 12-50 µm in main filaments, up to 58 µm thick in basal cells. Fertile cells developing in long, unbranched apical parts of the thallus, 150-240 µm in diameter.

Ecology: epilithic, subtidal (at -18 m).

Specimens examined: Cape Morgan: KZN 1350 (24/10/1999); The Bluff, Durban: KZN 68 (3/08/1999).

Geographic distribution: *C. flagelliformis* occurs along the South African West Coast (from Brandfontein to Namibia) in the lower intertidal to subtidal (to –8 m) (Stegenga et al. 1997; Leliaert et al. 2000; pers. obs.). Farrell et al. (1993: 149) recorded this species for Isipingo Beach as *C. virgata* Kützing (see Silva et al. 1996: 773 for nomenclatural note). *C. flagelliformis* has been recorded from Tristan da Cunha (Baardseth 1941: 11, fig. 2A) but the description and illustration remind one of *C. rupestris* (Linnaeus) Kützing. The Tanzanian record of *C. flagelliformis* (Gerloff 1957: 759) remains uncertain since no illustration and only a poor description are given.

Note: Our specimens are in general agreement with the description of Stegenga et al. (1997: 109) except for the maximum number of laterals per cell (4 in the West Coast plants, 1 in the East Coast plants). We compared the East Coast specimens with *C. flagelliformis* from the Cape Peninsula (voucher specimens of Leliaert et al. 2000). In these specimens the maximum number of laterals per cell varies from 2 to 4. The cell dimensions of the East Coast specimens fall within the limits of these of the West Coast plants (Table 5).

Table 5. Comparison of *C. flagelliformis* from the South African West and East Coast.

	diam. basal cells	diam. cells of main axis	diam. apical cells of actively growing branches	diam. fertile cells
West coast (Stegenga et al. 1997)	?	100-150 µm	50-70 µm	up to 400 µm
specimens Cape Peninsula	90-220 µm	100-260 µm	50-100 µm	150-270 µm
specimens East Coast	85-125 µm	60-205 µm	52-80 µm	150-240 µm

11. **Cladophora vagabunda** (Linnaeus) van den Hoek, 1963: 144 Figs 14A-B, 15

Conferva vagabunda Linnaeus, 1753: 1167

Lectotype locality: Selsey, Sussex, England [van den Hoek (1963: 19, 144) has indicated the material of *Conferva marina trichodes, lanae instar expansa* Dillenius, present in Dillenius's herbarium (OXF) as the type of *C. vagabunda*].

References: Børgesen [1935: 24-27, fig. 12, pl. 4 (as *C. monumentalis* Børgesen); 1940: 34-35, fig. 10 (as *C. fascicularis* (Mertens ex C. Agardh) Kützing); 1946: 21-

24, figs 8a,b, 9, 10 (as *C. fascicularis*)]; Jaasund [1976: 7, fig. 16 (as *C. mauritiana* Kützing); 7, fig. 15 (as *C. fascicularis*)]; Littler & Littler (2000: 324, fig. on p. 325); Schneider & Searles (1991: 74-76, figs 63-65); Sartoni (1992: 304, figs 6C, D, E); van den Hoek (1963: 144-148, pls 33, 36, 37, 39; 1982: 137-138, figs 264-294), van den Hoek & Womersley (1984: 202-203, figs 64E, 65G); van den Hoek & Chihara (2000: 180-194, figs 76-79).

Description:

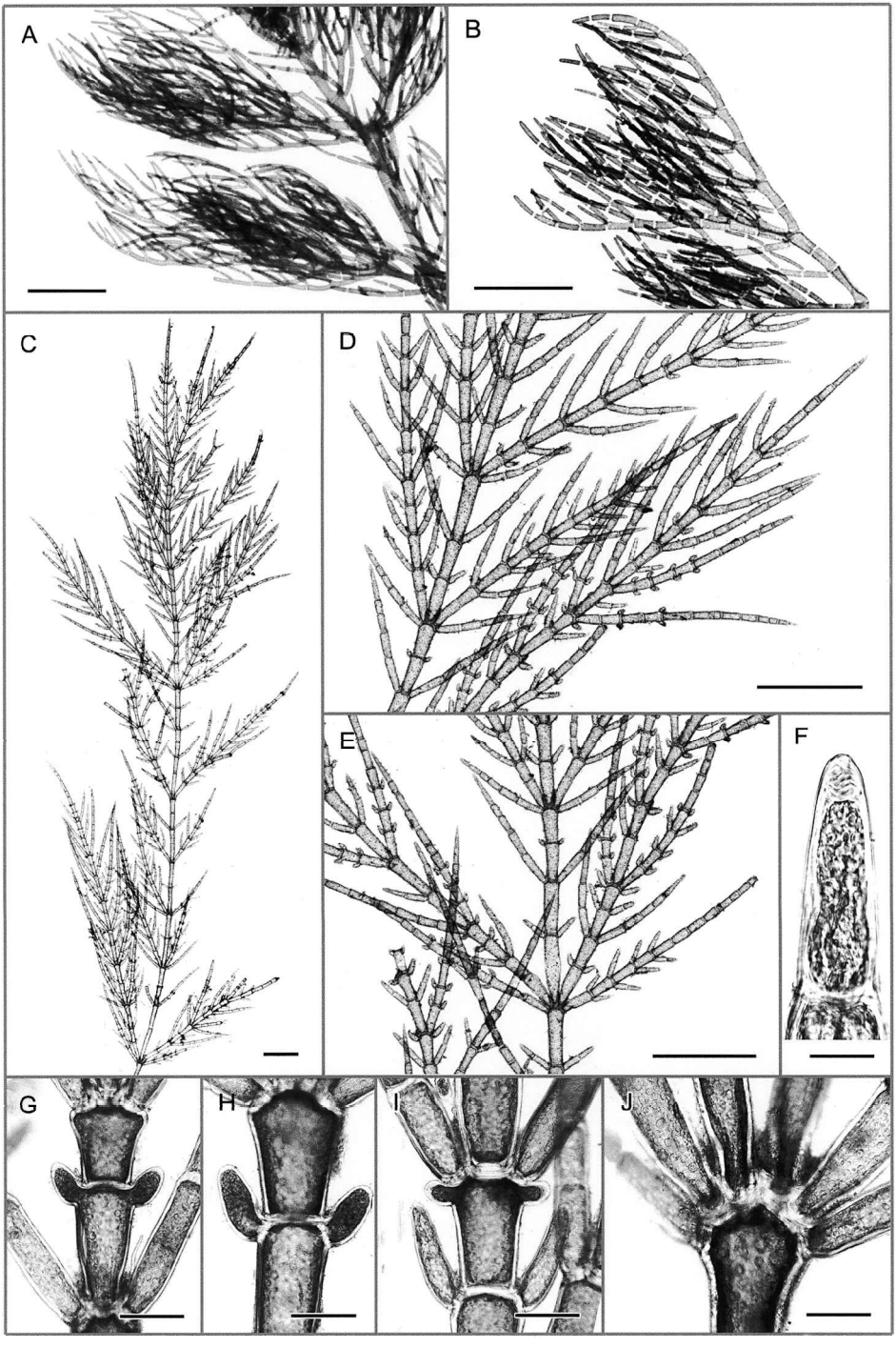
Thallus light green, forming lax tufts, 0.5 to 3 cm tall, composed of pseudo-dichotomously branching main axes ending in densely branched fasciculate terminal branch systems; attached to the substratum by basal branching rhizoids developing from the basal cells. Rhizoids also growing down from the proximal ends of the basal branches with which they partly coalesce. Growth in the terminal branch-system by apical cell division; intercalary cell divisions starting at some distance from the apex; cells in basipetal direction becoming markedly longer and broader. Terminal branch systems distinctly acropetally organized, (refracto-) falcate. Each new cell, after being cut off from the apical cell and when arriving at the position of the 3rd cell under the apex, giving off one branch at its distal pole; at increasing distance from the apex a cell may give off a 2nd, 3rd and sometimes a 4th branch. Branches inserted at the apical cell pole by an oblique wall cutting it off from the parent cell; the position of the wall becoming nearly horizontal in older branches, resulting in pseudodichtotomously branching main axes. Angle of ramification ranging from 50°-90° (-140°) in the main axes to 25°-55° in the terminal branch-systems. Apical cells cylindrical, with rounded tips or slightly tapering, diameter (35-) 45-55 µm, l/w ratio 3.5-8.5. Cells of terminal branch-systems cylindrical, 50-160 µm in diameter, l/w ratio 2.5-5.5. Cells of the main axes cylindrical, 180-210 µm in diameter, l/w ratio 4-10.

Ecology: Epilithic, intertidal to subtidal (to 6 m deep).

Specimens examined: ¼ Mile Reef, Sodwana: KZN 2109 (10/02/2001), KZN 2152 (11/02/2001); Bhanga Nek: KZN 680 (15/08/1999).

Geographic distribution: *C. vagabunda* is a wide-spread and ubiquitous species in tropical to warm-temperate seas; along the East African coast it has been recorded from Somalia (Sartoni, l.c.), Kenya [Isaac 1968: 1 as *C. fascicularis* (Mertens ex C. Agardh) Kützing)], Tanzania (Jaasund 1976: 7, fig. 15, pl. 1 as *C. fascicularis*), and Mozambique (Coppejans et al. 2002). This is the first record for South Africa.

Note: Molecular analyses (DNA-DNA hybridisation and nuclear rDNA ITS sequences) have demonstrated that the morphological species *C. vagabunda*, occupying one huge continuous geographic area, represents at least four divergent lineages (Bot et al. 1990; Bakker et al. 1995; van den Hoek & Chihara 2000). Depending on the interpretation of these molecular data, *C. vagabunda* can be seen as a single species or a cryptic species complex (multiple species). No African representatives were included in the molecular analyses.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Section Willeella (Børgesen) van den Hoek

12. **Cladophora ordinata** (Børgesen) van den Hoek, 1982: 123-125, pl. 22: figs 235-237 Figs 14C-J, 16

Willeella ordinata Børgesen, 1930: 155-158, figs 3, 4a,b, pl. I: fig. 1

Type locality: Dwarka, Okha Port, India (leg. Børgesen, nr 5563, type in C).

References: Børgesen [1934: 17, fig. 3 (as *Willeella ordinata*)]; Lawson & John (1987: 82, pl. 6, fig. 1); Sartoni (1992: 300-302, figs 5C-F); Segawa [1938: 133-135, fig. 2, pl. 33,1 (as *Willeella japonica* Yamada & Segawa)]; van den Hoek (1982: 123-125, figs 231-237); van den Hoek & Chihara (2000: 219-224, figs 93, 94).

Description:

Thallus dark to medium green, forming 4-8 cm high, bushy, fan-like tufts with distinct main axes; attached to the substratum by branching basal rhizoids developing from the proximal part of the basal cells. Growth by division of apical and intercalary cells; diameter and length of cells basipetally increasing (cells becoming extremely elongated and slightly decreasing in diameter in the basal parts of the thallus). Branch systems mainly acropetally organized; each new apically formed cell giving off a pair of opposite laterals, when arrived at the position of the 3rd to 8th cell from the apex. At increasing distance from the apex a cell may give off a second, and sometimes a third pair of opposite laterals in the same plane, resulting in flabellate branches. All branches typically lie in one plane; sometimes this plane is slightly spirally twisted. Angle of ramification (i.e. angle between the lateral and the main axis) ranging between 35°-45° in the opposite branches, 20°-65° in flabellate branches. Apical cells conical with a small obtuse tip and an apical thickening of the cell wall (27-) 30-45 µm in diam., l/w ratio 2-3.5; cell of the terminal branch systems cylindrical, 45-120 µm in diam., l/w ratio 1-3; main axes (70-) 110-175 µm in diam., l/w ratio 2-10; basal cells cylindrical to somewhat clavate, 75-120 µm in diam., l/w ratio 15-20. Cell walls in apical cells and ultimate filaments ca. 2-5 µm thick, increasing to 7-20 µm in main filaments, and up to 45 µm thick in basal cells.

Ecology: epilithic, intertidal rock pools to subtidal (to 37 m deep).

Specimens examined: Port Edward: FL 341, FL 342, FL 344: (24/03/1997); Palm Beach: KZN 816, KZN 869: (19/08/1999); Broken Reef, Trafalgar: KZN 959 (21/08/1999); Protea Banks, Shelly Beach: KZN 1927 (4/02/2001); Boboyi Reef, Shelly Beach: KZN 1973 (5/02/2001); Uvongo Reef, Shelly Beach: KZN 2002 (6/02/2001); Mabibi: KZN 452 (11/08/1999).

Fig. 14. A, B. *Cladophora vagabunda* (KZN 2152). A, B. Densely branched fasciculate terminal branch systems, scale bars = 1 mm; C-J. *Cladophora ordinata*. C-D. Main axes and terminal branch systems with opposite to flabellate branches (KZN 1927), scale bars = 1 mm; F. Apical cell (KZN 452), scale bar = 25 µm; G-J. Intercalary cell division and formation of flabellate branches (KZN 452), scale bars = 100 µm.

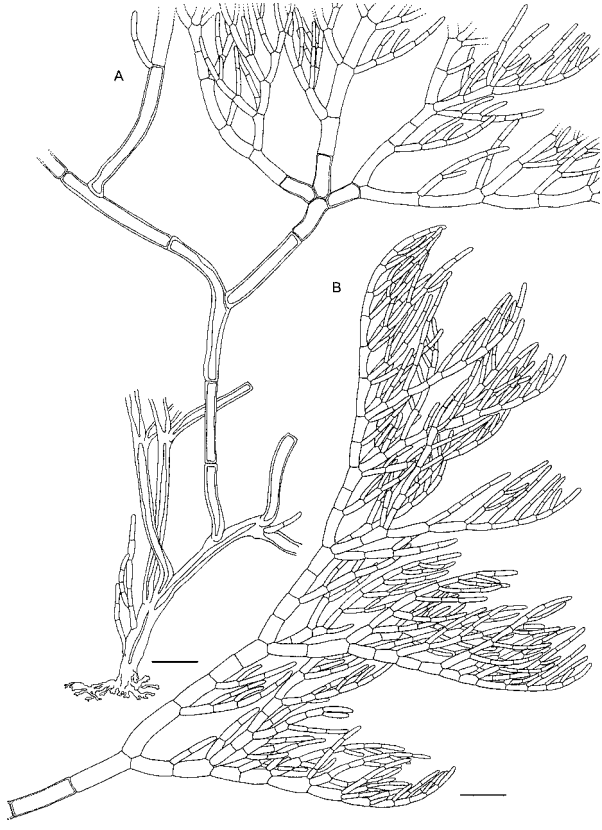

Fig. 15. *Cladophora vagabunda* (KZN 2152). A. Basal branches and rhizoidal holdfast; B. Terminal branch-system. Scale bars = 500 µm.

Geographic distribution: *C. ordinata* has a disjunct distribution pattern in the tropical to warm temperate Atlantic and Indo-Pacific Oceans. The species has been collected from India (type locality), South Africa (Papenfuss & Egerod 1957: 82-83), Ghana (Lawson & John 1987: 82, pl. 6, fig. 1), Venezuela (van den Hoek & Rios 1972), and Japan (van den Hoek & Chihara 2000: 219-224, figs 93, 94). The Somalian record (based on Sartoni 1992: 300-302, figs 5C-F) is most probably a misapplied name for *C. montagneana* Kützing.

Note: Van den Hoek (1982) reduced Børgesen's genus *Willeella*, in which *C. ordinata* was first described, to a section of *Cladophora*. Other authors (Silva et al. 1996: 787) prefer to retain the name *Willeella* and await a new classification of the Cladophorales based on molecular data. Two other species have been described for *Willeella*: *W. japonica* Yamada & Segawa and *W. mexicana* Dawson. Van den Hoek (1982) and van den Hoek & Chihara (2000) reduced the first species to a synonym

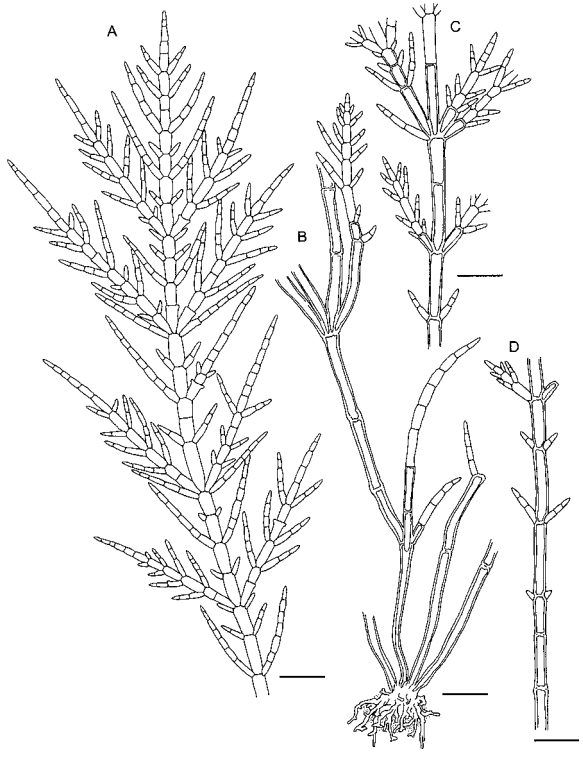

Fig. 16. *Cladophora ordinata* (KZN 2002). A. Terminal branch-system; B. Basal filaments and rhizoidal holdfast; C. Flabellate branching in main filaments; D. Main filaments with young laterals. Scale bars = 500 µm.

of *C. ordinata*. *W. mexicana* was reduced to a synonym of *Pseudostruvea robusta* (Setchell & Gardner) Egerod [= *Struveopsis robusta* (Setchell & Gardner) Rhyne & H. Robinson] by Egerod (1975: 47).

Key to the species

1a. Thallus forming cushion-like mats, composed of interwoven filaments; attached to the substratum at several places 2
1b. Thallus forming erect tufts, attached to the substratum at a single point 5

2a. Filaments short-celled (l/w ratio of the apical cells 2-5), anastomosing with one another to form compact, three-dimensional net like cushions ..... *C. liebetruthii*
2b. Filaments long-celled (l/w ratio of the apical cells 5-40), loosely entangled with one another (infrequently anastomosing) 3

3a. Thallus attached to the substratum by terminal haptera on the apical cells of decumbent axes; apical cell diameter larger than 250 µm ..... *C. catenata*

3b. Thallus attached to the substratum by rhizoids developing from the proximal poles of the stolon-like filaments; apical cell diameter smaller than 100 µm..... 4

4a. Apical cell diameter 57-75 µm.....*C. coelothrix*
4b. Apical cell diameter 25-50 µm.....*C. socialis*

5a. Thallus attached to the substratum by a conspicuous basal stipe, composed of one or two cells which are much longer than the apical cells (stipe-cells generally longer than 3 mm)..... 6
5b. Thallus lacking a conspicuous stipe, or if present composed of entangling rhizoids..... 8

6a. Stipe cell and cells of the main axes with conspicuous annular constrictions at their proximal parts..... *C. rugulosa*
6b. Stipe cell and cells of the main axes lacking annular constrictions.....7

7a. Cells of the main axes clavate, often curved, with a distinct basal bulge; apical cell diameter 250-290 µm..... *C. dotyana*
7b. Cells of the main axes subcylindrical, straight; apical cell diameter 80-125 µm..... *C.* sp.

8a. Cells in the basal part of the thallus each giving off one rhizoid at their proximal pole..... 9
8b. Rhizoids only developing from the proximal end of the basal cell..... 10

9a. Rhizoids with annular constrictions, growing down and entangling along the cells below, forming a conspicuous stipe that attaches to the substratum..... *C. prolifera*
9b. Rhizoids lacking annular constictions, growing along and into the cell walls of the cells below; basal branches becoming completely covered by and the cell walls fused with these rhizoids ..... *C. horii*

10a. Branches restricted to the basal part of the thallus, the distal part of the thallus unbranched and flagelliform..... *C. flagelliformis*
10b. Terminal branch systems densely branched..... 11

11a. Thallus with pseudodichotomous main axes, ending in acropetal, often falcate terminal branch systems..... *C. vagabunda*
11b. Erect thalli fan-like, composed of opposite to flabellate branches, developing in one plane..... ..... *C. ordinata*

Discussion

The Cladophorophyceae are believed to be an originally tropical group with members (including a large number of *Cladophora* species) that succesfully invaded the warm-temperate and even cold-temperate regions (Bakker et al. 1994; van den Hoek & Chihara 2000). However the tropical representatives of *Cladophora* remain largely unstudied. In the tropical Western Indian Ocean limited studies of the genus *Cladophora* are restricted to the publications of Sartoni (1986, 1992; Somalia), Jaasund (1976; Tanzania) and Børgesen (1940, 1946, 1948; Mauritius).

Seven distribution groups of the genus *Cladophora* have been distinguished, based on the species' northern and southern boundaries in combination with winter and summer isotherms of the sea surface (van den Hoek 1979, 1982; van den Hoek & Chihara 2000). The 11 species identified along the South African East Coast fall into three biogeographical categories: two species belong to the strictly tropical distribution group and have their southernmost boundary in northern KwaZulu-Natal (*C. catenata* and *C. horii*), eight species belong to the tropical to warm temperate distribution group, and *C. rugulosa* that was previously regarded as a synonym of *C. prolifera*, seems to be restricted to the South and East Coast of South Africa. Two

species are reported for the first time in the Indian Ocean (*C. dotyana* and *C. horii*) and three others are recorded for the first time in South Africa (*C. catenata*, *C. liebetruthii* and *C. vagabunda*).

The genus *Cladophora* is a heterogeneous assemblage of species. Based on morphological characters, van den Hoek (1982) demonstrated that the genus does not conform to the requirement that the species contained in the genus are mutually more related than with species in other genera. Some species of *Cladophora* share typical characters with other genera within the Cladophorales and, as a consequence, can easily be confused with them. *C. coelothrix*, *C. socialis* and *C. catenata* are characterized by delayed cross-wall formation and the presence of rhizoidal or hapteroidal structures, characters that typify the genus *Cladophoropsis*. *C. liebetruthii* shares common characters with the genus *Microdictyon*: anastomoses of filaments to form net-like thalli, rhizoids developing from the basal poles of the cells (van den Hoek 1982, Kraft 2000). Molecular data based on 18S rRNA (Bakker et al. 1994; Hanyuda et al. 2002) confirm the close relationship of *Cladophora* species with other genera in the Cladophorales. Evolutionary relationships in the Cladophorales based on partial LSU rRNA are currently under study.

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