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Morphological and taxonomic studies of *Gracilaria* and *Gracilariopsis* species (Gracilariales, Rhodophyta) from South Africa

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Southern Africa has an extremely rich and diverse seaweed flora with a wide variety of marine habitats. Increased commercial interest in these seaweed resources has been the stimulus for biodiversity studies. The Gracilariaceae (Rhodophyta) has emerged as one of the families that possess economic potential as a source of agar and as a potential feed for abalone. A lack of knowledge concerning the taxonomic status of many members of this family is a concern. Gross morphological characters have been the main means of identification and incorrect applications have led to a number of misidentifications. Consequently, a comprehensive reappraisal and revision of these species was carried out. The species count for the South African Gracilariaceae is now two *Gracilariopsis* species, and nine *Gracilaria* species. *Gracilaria crassa* has been reduced to a synonym of *G. canaliculata*. It is believed that *G. foliifera* was erroneously identified and specimens in South Africa referred to as *G. millardetii* and *G. protea* are assigned to *G. corticata*. South African *Gracilariopsis,* previously referred to as *Gs. lemaneiformis,* is confirmed to be conspecific with European *Gs. longissima*. This species occurs along the west and south coasts of South Africa, co-existing in a few habitats with *G. gracilis.* The taxonomic identity of *G. vieillardii* specimens from South Africa and the differentiation of *G. canaliculata* and *G. salicornia* has been confirmed based on morphology. Three species of *Gracilaria* (*G. aculeata*, *G. beckeri* and *G. capensis*) are endemic or near endemic to the South African coast, and a fourth species, *G. denticulata* is localised in southeast Africa.

Introduction

The genus *Gracilaria* Grev. with ca. 150 currently recognised species is an important component of the flora on most tropical to cool temperate shores. Many of the species, however, are poorly defined, minimally described and inadequately illustrated. Fuelled by the economic interest in phycocolloids, the study of the Gracilariaceae, an important source of agar, has spread rapidly throughout the world in the last decade, resulting in meticulously detailed generic descriptions (Fredericq and Hommersand 1989a, 1989b, 1990a, 1990b, Gurgel *et al*. 2003) and numerous regional floristic accounts of the genus *Gracilaria* (see e.g. Abbott 1995) mainly focussing on the representatives of the Pacific Ocean.

Diagnostic characters at the generic level in the Gracilariaceae are predominantly based on morphological and developmental characters of the female reproductive system. Yamamoto (1975) provided the concept of subgenera, which were based primarily on spermatangial configuration. However, a number of studies (Zhang and Xia 1984, Bird *et al*. 1986, Reading and Schneider 1986, Abbott *et al*. 1991) have shown that these features are not reliable for infrageneric discrimination. Species identification within the Gracilariaceae therefore remains problematic.

From the eighteenth century until 1930, collections of seaweeds in South Africa were made primarily by visiting plant collectors and studied by European phycologists (Bolton 1999). A large collection was made by Tyson (1851–1920) which was studied by Delf and Michell (1921). Becker collected prolifically at the Kowie, Eastern Cape, from 1890–1910 (Bolton 1999). Seaweeds were an integral part of the large-scale ecological and biogeographical studies of Stephenson and colleagues, culminating in a list of 280 ‘species and major varieties’ with distributions (Stephenson 1948). Working with Stephenson, Papenfuss made his prime goal the elucidation of the seaweed flora of South Africa. Papenfuss intended to produce a seaweed flora of South Africa and part of it exists in manuscript, but it was not completed (Bolton 1999). Detailed collections around the coast and a number of taxonomic studies were carried out locally between 1950 and 1970 by Pocock and Simons (Bolton

1999). Post 1980, work on the seaweeds of KwaZulu-Natal was carried out by RE Norris, while on the west coast similar work was performed by Stegenga and colleagues (Bolton 1999).

The first South African record was of *G. aculeata* (Hering) Papenf. (Hering 1841: as *Sphaerococcus aculeatus* Hering) based on material from Durban. Three more species [*G. beckeri* (J Agardh) Papenf., *G. capensis* F Schmitz. ex Mazza and *G. denticulata* F Schmitz ex Mazza] were described based on specimens collected by Becker at the Kowie (Port Alfred) in the later half of the 19th and early 20th century. By 1984, 11 species of *Gracilaria* had been reported from South Africa (Seagrief 1984): *G. aculeata*, *G. beckeri*, *G. canaliculata* Sond., *G. capensis*, *G. crassa* Harv. ex J Agardh, *G. denticulata*, *G. foliifera* (Forssk.) Børgesen forma *aeruginosa* (Turner) Børgesen, *G. millardetii* (Mont.) J Agardh, *G. protea* J Agardh, *G. salicornia* (C Agardh) Dawson, and *G. gracilis* (Stackh.) Steentoft, Irvine et Farnham [as *G. verrucosa* (Huds.) Papenf.]. In 1993, Farrell *et al*. reported *G. vieillardii* Silva occurring at Isipingo, south of Durban.

The first *Gracilariopsis* Dawson species recorded in the region was identified in False Bay, South Africa and Swakopmund, central Namibia as *Gs. lemaneiformis* (Bory) Dawson, Acleto et Foldvik by Stegenga *et al.* (1997). Recently there have been shown to be two *Gracilariopsis* species in South Africa in studies based on molecular data (Govender 2001, Iyer 2002, Iyer *et al*. 2005). The most common species is *Gs. longissima* (Gmelin) Steentoft, Irvine et Farnham, whereas a newly described species, *Gs. funicularis* Iyer, Bolton et Coyne occurs primarily in Namibia, with an isolated population in the De Mond estuary (Iyer *et al*. 2005).

The west coast and south coast of southern Africa, extending from the southern Angolan border in the north to Algoa Bay in the east, is species-poor with regard to the Gracilariaceae. Only three species have been reported in this cool temperate region (Stegenga *et al*. 1997, Govender 2001). The eastern overlap region of southern Africa, especially the Port Alfred region, boasts four endemic or near-endemic species (some extending their range to the East African coast and Madagascar), while the east coast is characterised by a mixture of tropical species.

Molecular studies (Iyer 2002) have demonstrated that the present descriptions of species of the Gracilariaceae in South Africa are misleading. Morphological plasticity within species and erroneous interpretations are the major contributing factors. Hence there is a need for a comprehensive reappraisal and revision of these species to be carried out. This study aims to provide a taxonomic and biogeographical analysis of members of the Gracilariaceae occurring in South Africa.

Materials and Methods

Approximately 50 specimens were collected from KwaZulu-Natal and the Eastern Cape over a period of four years (July 1998, August 1999, December 1999, July–August 2000, February 2001), as a result of a Bilateral Scientific and Technological Cooperation Project between the Flemish community (Belgium) and South Africa. Approximately 40 specimens were collected from the Western Cape and Namibia over a period of three years (June 1999–August 2001), as a result of a National Research Foundation seaweed biodiversity project.

For the anatomical analyses, liquid preserved specimens in 4% formaldehyde/seawater were sectioned by hand or with a freezing microtome. Sections were mounted on glass slides in a solution of 1% aniline blue, 3% 1N HCl, 50% Karo® and 46% water. Voucher specimens are deposited in BOL (Bolus Herbarium, Botany Department, University of Cape Town) and GENT (Herbarium, Biology Department, Ghent University). Photographs were taken with an Olympus DP50 digital camera mounted on a Leitz Diaplan compound microscope or Leica Wild M10 stereo microscope.

Gracilariaceae Nägeli 1847: 240, 254

A widespread family of red seaweeds, predominantly in warm temperate to tropical waters. The family contains 6 or 7 genera, of which two are parasitic. *Hydropuntia* is recognised by some authors (Fredericq and Hommersand 1990b). A detailed discussion of the taxonomy of the family is in Silva *et al*. (1996, 916–918). Only two genera have been recorded for South Africa. Two species of the parasitic genus *Gracilariophila* Setchell et Wilson have been recorded in the Indian Ocean (from Indonesia; Silva *et al*. 1996), but this genus has never been documented to occur in South Africa.

Key to the species of South African Gracilariaceae

1\. a. Thallus terete 2
   b. Thallus compressed to foliose 7
2\. a. Axes beset with whorls of spiny protrusions occurring at regular intervals . . . .**1. *G. aculeata***
   b. Axes lacking spiny protrusions 3
3\. a. Thalli large, 15–120cm long, branches less than 2mm in diameter, lacking a holdfast, ...4
   b. Thalli small, up to 7cm high, holdfast present 6
4\. a. Traversing cells absent in cystocarp, spermatangia of the *chorda*-type 5
   b. Traversing cells present in cystocarp, spermatangia of the *verrucosa*-type . . . .**7. *G. gracilis***
5\. a. Thalli slender, branches 0.6–1mm in diameter, medulla 3–4 cell layers thick . . . .**11. *Gs. funicularis***
   b. Thalli robust, branches 1–2mm in diameter, medulla 4–7 cell layers thick . . . .**10. *Gs. longissima***
6\. a. Axes irregularly constricted, branching di- to trichotomously . . . .**9. *G. salicornia***
   Axes not constricted (except at the base of the side-branches), branching subdichotomous . . . .**3. *G. canaliculata***
7\. a. Thalli large, up to 26cm long, axes foliose, usually more than 3cm wide . . . .**4. *G. capensis***
   b. Thalli small to medium sized, usually smaller than 16cm, axes not exceeding a width of 2cm 7
7\. a. Thallus dichotomously to irregularly branched, straps usually elongate, margins smooth . . **5. *G. corticata***
   b. Thallus irregularly branched, margin not smooth . .8
8\. a. Margins of the thallus fimbriate . . . . . .**2. *G. beckeri***
   b. Margins of the thallus minutely crenated to irregularly

dentate, but never fimbriate 9

9. a. Thallus surface dentate, colour usually distinctive green . . . . **6. *G. denticulata***
   b. Thallus irregularly branched with lobate ultimate axes, margins with minute dentations or crenations, colour usually dark purple . . . .**8. *G. vieillardii***

Descriptions of taxa

Gracilaria Greville 1830: liv,121

Much branched thalli, terete to flattened, branching subdichotomous to irregular; holdfast a disc or crust giving rise to one to many erect axes. Thalli red, olive, green to purple, cartilaginous or soft, smooth, fimbriate or dentate. Triphasic isomorphic life history, females with obvious swellings (cystocarps) with thick pericarp, ostiolate, and the presence of traversing tubular nutritive cells. Spermatangia in pits or shallow depressions. Sporophytes with tetrasporangia scattered in the outer cortex, cruciately divided.

1. *Gracilaria aculeata* (Hering) Papenf. 1967: 99, 100 (Figure 1)

Basionym: *Sphaerococcus aculeatus* Hering 1841: 91–92, *nom. illeg.*

Homotypic synonyms:

Gelidium aculeatum Hering in F Krauss 1846: 210, *nom. nov*.

Sphaerococcus heringii Kütz. 1849: 775.

Gigartina aculeata (Hering) Kütz. 1868: 3, pl 6: figs a, b.

Corallopsis aculeata (Hering) EM Holmes 1894: 336, pl. xviii: figs 16–20.

References

Papenfuss 1967: 99, 100. Seagrief 1977: 90. Simons 1977b: 55, fig. 164. Brown and Jarman 1978: 1256. Seagrief 1980: 26, fig. on pl. 8. Seagrief 1988: 54, fig. 5:9. Farrell, Critchley and Aken 1993: 153. Branch *et al*. 1994: 330, pl. 157.6.

Holotype: HBG

Type Locality

Durban [Port Natal], South Africa.

Distribution

Endemic to the South African east coast from Kenton to Cape Vidal.

Specimens examined

Eastern Cape, Kenton, intertidal pool (Papenfuss, 05.iii.1950, s.n.); Kleinmonde, drift (Stegenga, 27.iii.1987, SA1142); Kowie, (Becker, 16.xi.1894, BOL52997); Kowie, unknown (Becker, i.1895, BOL53049); Sharks Bay, drift (Stegenga, 03.xii.1987, SA1886); Three Sisters, intertidal pools (Stegenga, 20.iv.1987, SA1225); Three Sisters, intertidal pools (Stegenga, 15.iv.1987, SA1286).

KwaZulu-Natal, Trafalgar, intertidal (Leliaert, 20.iii.1997, FL235); Durban, infralittoral fringe (Coppejans, 20.xi.95, HEC10979); Palm Beach, intertidal pools (De Clerck, 19.viii.1999, KZN820); Palm Beach, intertidal (De Clerck and Kandjengo, 21.xii.1999, KZN1502); Mission Rocks, subtidal (De Clerck and Cocquyt, 17.viii.2000, KZN1741); Palm Beach, intertidal (De Clerck *et al*., 07.ii.2001, KZN2029).

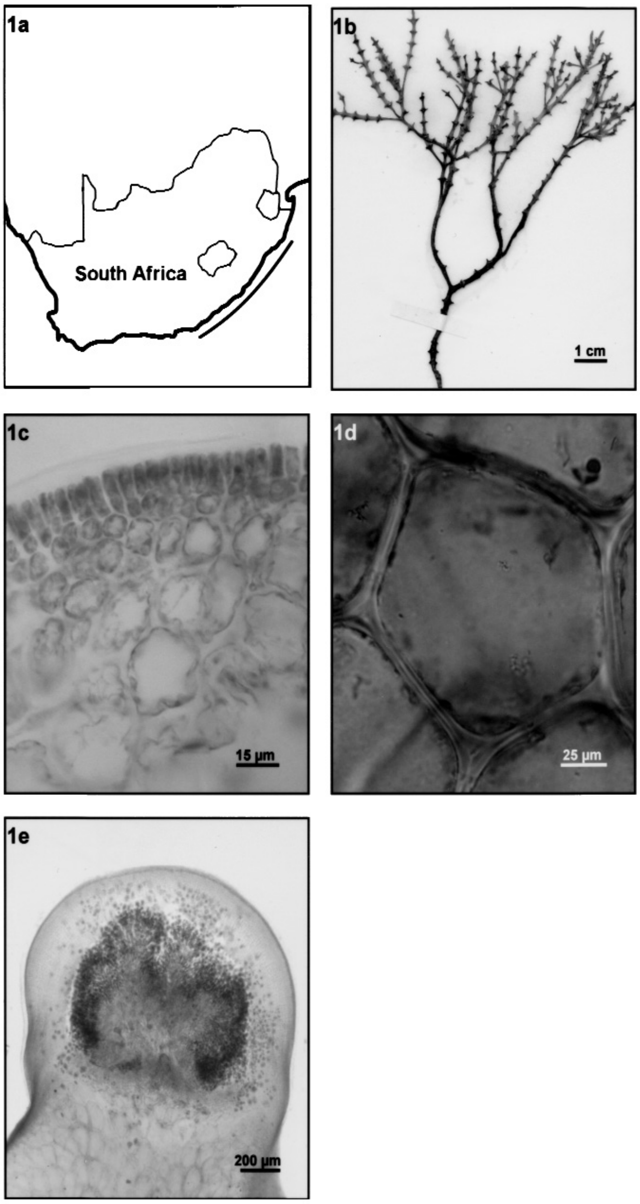

Figure 1: RSA distribution, morphology and anatomy of *G. aculeata*. (a) Distribution, (b) habit, (c) Cross-section (C/S) of cortex-subcortex, (d) C/S of medulla, (e) C/S of cystocarp

Habit

Thalli erect, up to 19cm; occurring gregariously; axes terete, stiff, cartilaginous, with prominent spiny protrusions. Holdfast a small discoid to a large crust giving rise to multiple axes. Stipe cylindrical, up to 1cm long. Branching predominantly verticillate to irregular; lowermost branches (first and sometimes second order) unconstricted, upper branches cylindrical, up to 3mm in diameter, constricted at the base (diameter to 1mm) enlarging to 2–3mm in diameter, and tapering off at the apices to an acute tip. Whorls of spiny protrusions, up to 2mm long, occur at regular intervals (3–4mm) in all branches. Fresh specimens firm in texture and light to dark red.

Vegetative structure
Transition of cell size from cortex to medulla abrupt throughout the thallus. Medullary cell walls up to 4µm thick; secondary pit connections present, but not prominent in subsurface layers, rare in outermost. Cortex of larger branches 1–3 cells thick, the cells darkly staining, up to 18µm long and 15µm in diameter. Medulla in this region up to 26 cells wide, the cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 260µm long and 240µm in diameter; medullary cells extending into protuberances, up to 50µm in diameter. Crystalline, proteinaceous crystals not observed.

Tetrasporangia (after Holmes 1894)
Tetrasporangia cruciately divided, up to 35µm long and 25µm wide. Cortex immediately surrounding tetrasporangia unmodified.

Spermatangia
Not observed.

Cystocarps
Cystocarps scattered irregularly over the surface of all branches; mature cystocarps ostiolate, up to 1.2mm high and 1.4mm wide, unconstricted at the base. Traversing cells common in mature cystocarps, rare in young cystocarps, developing from apical gonimoblast cells in a lateral and upward direction penetrating the transverse and upper pericarp, respectively; pericarp tissue up to 260µm and 26 cell layers thick; gonimoblast parenchyma sparse, basal cells up to 100µm long and 60µm wide. Carpospores densely protoplasmic, obovoid or oval, up to 50µm wide; borne terminally on gonimoblast filaments.

Remarks
Hering (1841) originally described material collected at Durban [Port Natal] as *Sphaerococcus aculeatus*. However, this name is a later homonym of *Sphaerococcus aculeatus* (L.) Stackh. (1797) [*Desmarestia aculeata* (L.) Lamour.]. *Gelidium aculeatum* Hering as defined in Krauss (1846) is therefore treated as a *nomen novum* in accordance with Art. 58.3 (see Silva *et al*. 1996). Holmes (1894) provided the name *Corallopsis aculeata* (Hering) EM Holmes on the basis of the constricted nature of the thallus as contrasted with the putative unconstricted condition in *Gracilaria*. Holmes also refers to the cells of the cortical stratum forming very short filaments, another characteristic used to differentiate *Corallopsis* from *Gracilaria*. Dawson (1954) concluded that there were no significant differences between *Gracilaria* and *Corallopsis*, except in external morphology, relegating this genus to synonymy with *Gracilaria*. Following Dawson's (1954) evidence that *Corallopsis salicornia* (C. Agardh) Grev. should be assigned to *Gracilaria*, Papenfuss (1967) decided that *Corallopsis aculeata* should also be a species of *Gracilaria*.

Gracilaria aculeata is easily distinguished from other subtropical species of *Gracilaria* by its characteristic gross morphological features. The distinctive whorls of spiny protrusions, conspicuous verticillate branching added to its terete aspect provide for easy identification of this species. Furthermore, *G. aculeata* lacks the morphological variability observed in other east coast *Gracilaria* species.

Gracilaria aculeata is endemic to the South African south and east coast extending from Kenton (Eastern Cape) in the south to Cape Vidal (KZN) in the north. The habitat of this species is interesting in that it overlaps the southernmost range of the *G. salicornia* habitat. Molecular studies (Iyer 2002) show that these two species are closely related, and based on this evidence it has been hypothesised that *G. aculeata* evolved from a *G. salicornia*-like ancestor. The terete aspect of these species is a trait which suitably distinguishes *G. aculeata* from *G. capensis* and *G. beckeri*, which are also endemic to the south coast of South Africa. This similarity in morphology supports the argument that *G. aculeata* may be closely related to *G. salicornia* (Iyer 2002).

2. *Gracilaria beckeri* (J Agardh) Papenf. 1952: 175–176 (Figure 2)
Basionym: *Tyleiophora beckeri* J Agardh, 1890: 36 ('*becheri*').
Homotypic synonym: *Tylotus beckeri* (J Agardh) Kylin 1932: 60, pl. 22: fig. 55.

References: Barton 1893: 143. Barton 1896: 197. Mazza 1907 [1905–1918]: 141–142. Delf and Michell 1921: 108. Millard and Harrison 1954: 175. Seagrief 1977: 90. Simons 1977b: 37, fig. 100. Seagrief 1988: 54, fig. 5:9. Stegenga 1988: 382.

Holotype: LD

Type Locality
The Kowie (Port Alfred), South Africa.
(Note: 'The Kowie' was the name used often for a collecting site for seaweeds. The name refers not to the Kowie River, but generally to the rocky shores around Port Alfred).

Distribution
Endemic to South Africa from Kenton (Eastern Cape) to Port Edward (KZN); Madagascar?

Specimens examined
Eastern Cape, Kenton, (Simons, 01.v.1950, BOL53043); Kenton, lower intertidal (Stegenga, 02.xii.1987, SA1932); Kowie, unknown (Becker, 12.viii.1892, BOL47333); Kowie, unknown (Becker, 10.i.1894, BOL47345); Kowie, unknown (Becker, 24.viii.1894, BOL47344); Kowie, unknown (Becker, 23.xi.1895, BOL35311); Kowie, unknown (Becker, 28.i.1893, BOL47338); Kowie, unknown (Becker, 26.xi.1895, BOL47339); Kowie, drift (De Clerck, 27.x.1999, KZN1259); Piano Rocks, infralittoral fringe (Stegenga, 23.ix.1987, SA1809); Riet river, drift (Seagrief and Lambert, 05.ii.1975, BOL53052); Salt Vlei Bay, sheltered gully (Simons, 18.iv.1950, BOL53046); Salt Vlei Bay, infralittoral fringe (Stegenga, 17.iii.1987, SA1125); Sharks Bay, drift (Stegenga, 03.xii.1987, SA1883); Three Sisters, lower inter-

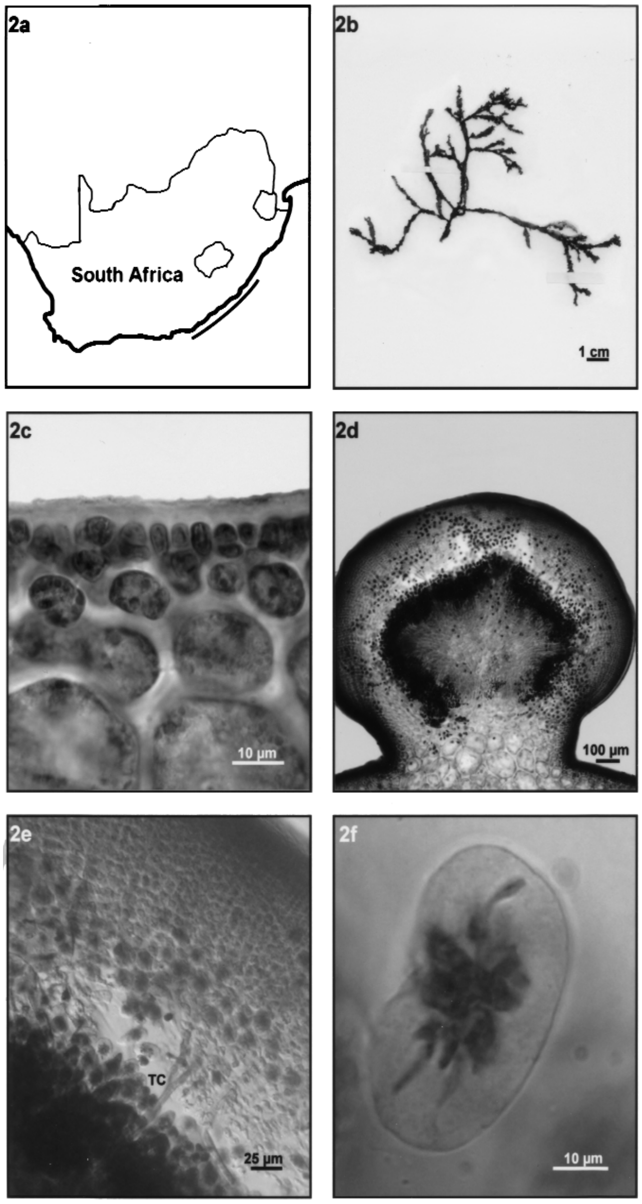

Figure 2: RSA distribution, morphology and anatomy of *G. beckeri*. (a) Distribution, (b) habit, (c) C/S of cortex-subcortex, (d) C/S of cystocarp, (e) C/S of transverse pericarp (TC = traversing cell), (f) carpospore

tidal (Stegenga, 05.iii.1987, SA1050); Three Sisters, rock pool in cave (Stegenga, 11.viii.1987, SA1602); Three Sisters, intertidal pool (Stegenga, 28.iv.1987, SA1263).

Habit

Thallus erect, up to 25cm in length, arising singly from a discoid holdfast, or multiple axes from a crustose holdfast. Stipe cylindrical, up to 1cm long. Branching often irregular, to 5–7 orders. Axes compressed, somewhat constricted at the base, irregularly linguiform with a variable width of the blades resulting in a gnawed appearance, up to 23cm long, and up to 8mm wide at any point on the blade. Margins of young blades papillate, older blade margins conspicuously fimbriate, apices often proliferating as a result of mechanical damage (e.g. grazing). Fresh specimens purple and firm but pliable; dried specimens dark purple.

Vegetative structure

Transition of cell size from cortex to medulla abrupt throughout the thallus, except for the stipe where there is a gradual transition. Medullary cell walls up to 4µm thick; secondary pit connections present, but not prominent in subsurface layers, rare in outermost. Cortex of larger blades 2–3 cells thick, isodiametric to spherical, the cells darkly staining, up to 12µm long and 10µm in diameter. Medulla up to 6 cells wide, the cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 340µm long and 160µm in diameter. Lower portion of the stipe consisting of up to 20 layers of isodiametric to rectilinear cortical cells, up to 24µm long and 12µm in diameter; medulla up to 10 cells wide, polygonal to spherical, gradually increasing in size towards the centre, 140µm long and 120µm in diameter. Thickness of the cortex decreasing gradually away from the stipe base.

Tetrasporangia

Occurring singly bordered by sterile tissue. Tetrasporangia up to 42µm long and 23µm wide, occurring on both sides of the frond; not aggregated, evenly distributed in sori. Tetrasporangia cruciately divided.

Spermatangia

Not observed.

Cystocarps

Localised prominently on the surface of 3–7 order blades; mature cystocarps ostiolate, up to 1.2mm high and 1.8mm wide, slightly constricted at the base. Traversing cells common in mature cystocarps, rare in young cystocarps, developing from apical gonimoblast cells in a lateral and upward direction, penetrating the transverse and upper pericarp, respectively; pericarp tissue up to 230µm and 16 cell layers thick; gonimoblast parenchyma dense, central cells up to 80µm long and 60µm wide. Carpospores densely protoplasmic, obovoid or oval, up to 40µm wide; borne terminally on gonimoblast filaments.

Remarks

On the basis of material from South Africa, J Agardh established the new genus and species *Tyleiophora beckeri*. During a study of *Tyleiophora* and *Tylotus*, Kylin (1932) could not find sporangia in J Agardh's material of *Tylotus obtusatus* (Sond.) J Agardh, the type of this genus. He concluded that J Agardh had erroneously reported zonately divided sporangia in this species. Kylin therefore united these two genera under the name *Tylotus*, as this genus in other respects agreed with *Tyleiophora*. Dawson (1954) found that J Agardh had been correct in describing the sporangia of *Tylotus obtusata* as zonately divided. Hence the unification of *Tyleoiphora* with *Tylotus* was incorrect, and the former had to be excluded from the Gracilariaceae (Papenfuss 1952). Dawson (1949) also reported that the genus *Gracilaria* contains numerous flat species showing the complete series of gradations from tetrasporangia borne in a completely unmodified cortex to tetrasporangia borne in well-developed nemathecia. Papenfuss (1952) argued that since *Tyleiophora* differs from *Gracilaria* only in having its sporangia in nemathecia, it becomes clear that *Tyleiophora* cannot be maintained. He argued further that the genus is congeneric with *Gracilaria* due to the presence of nutritive filaments (traversing cells) in *Tyleiophora beckeri* as illustrated by Kylin (1932).

Gracilaria beckeri is distinguishable by the linguiform blades of uneven width providing an eroded appearance and distinctively fimbriate blade margins. The habitat range of this species extends from Kenton (Eastern Cape) to Port Edward (KZN). It is one of three non-terete species that occur in this region, the other two being *G. capensis* and *G. denticulata*. All three species are conspicuous by their compressed blades. In addition, *G. beckeri* and *G. capensis* are endemic to the Eastern Cape and the extreme south of KZN (to Port Edward). It has been postulated (Iyer 2002) that these three endemic species probably originated from a *G. vieillardii*-like ancestor which evolved to be suited to the conditions prevalent in this ecological niche (warm temperate South Africa), thus explaining their limited habitat range.

3. *Gracilaria canaliculata* Sond. 1871: 56 (Figure 3)
Basionym: *Sphaerococcus canaliculatus* Kütz. 1868: 29, pl. 82: figs d, e, *nom. illeg*.

Homotypic synonyms:
Gracilaria crassa Harv. ex J Agardh 1876: 417 (type locality: Sri Lanka).
Ceramianthemum crassum (Harv. ex J Agardh) Kuntze 1891: 887.

References: Umamaheswara Rao 1974: 677, figs 1g–j, pl. I:A, B. Withell *et al*. 1994: 301–302, figs 16–17 (as *G. canaliculata* form of *G. salicornia*). Wynne 1995: 280, fig. 17.

Holotype: *leg. Vieilliard* # 2128 1863, L 941.61…93 (tetrasporic)

Type Locality
Wagap, New Caledonia.

Distribution
Indian Ocean (South Africa to Australia); South Africa (north of Cape Vidal into Mozambique).

Specimens examined
KwaZulu-Natal, Bangha Neck, intertidal (Coppejans *et al*., 13.viii.1999, KZN542); Bangha Neck, intertidal (Coppejans *et al*., 15.viii.1999, KZN722); Mabibi, intertidal and infralittoral fringe (Coppejans *et al*., 09.viii.1999, KZN390A, B).

Habit
Thallus stiff, brittle, cartilaginous, erect, up to 55mm long, occurring as solitary individuals. Attached by a discoid holdfast giving rise to one axis or two axes. Stipe short terete, up to 6mm long, often inconspicuous. Branching is mostly subdichotomous, subsequent dichotomies 45–90° to each other; up to six orders; frequently arcuate. Lowermost branches (first and second order) constricted at base (diameter to 1mm) and enlarging apically (diameter up to 3mm); club shaped. Upper branches cylindrical, up to 3mm in diameter; with unconstricted bases and obtuse apices. Young branches appearing constricted at point of origin. Fresh specimens firm and light to dark rose.

Vegetative structure
Transition of cell size from cortex to medulla abrupt throughout the thallus. Medullary cell walls up to 6µm thick; secondary pit connections present, but not prominent in subsurface layers, rare in outermost. Cortex of larger blades 1–2 cells thick, the cells darkly staining, up to 16µm long and 6.5µm in diameter. Medulla up to 18 cells wide, the cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 370µm long and 310µm in diameter. No marginal and surface protuberances. Lower axes with a thickened cortex consisting of up to 15 layers of enlargened, isodiametric to rectilinear cortical cells, up to 40µm long and 25µm in diameter; medulla up to 13 cells

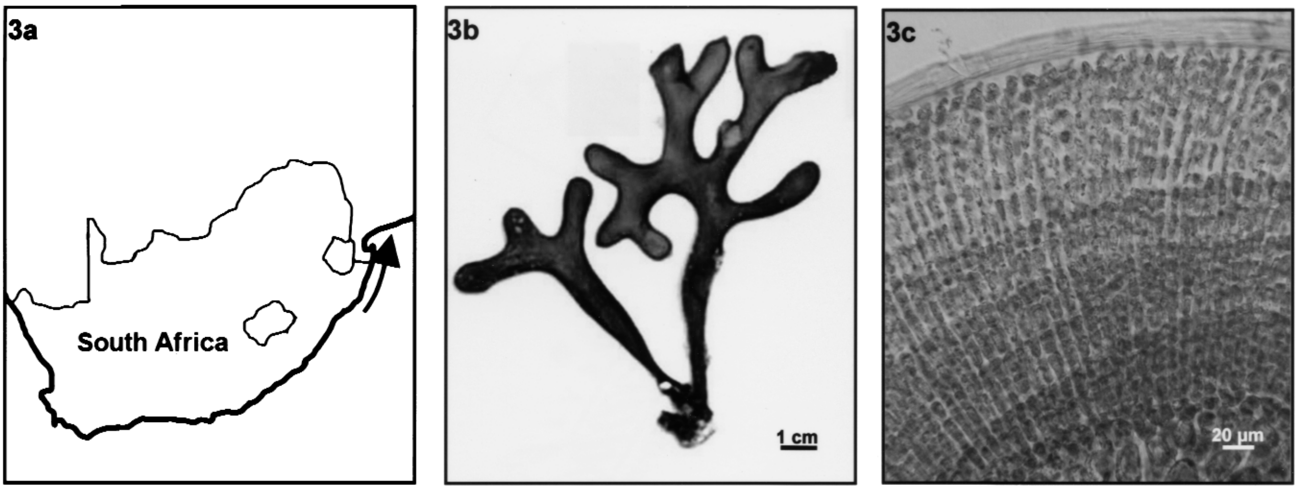

Figure 3: RSA distribution, morphology and anatomy of *G. canaliculata*. (a) Distribution, (b) habit, (c) C/S of stipe

wide, polygonal to spherical, gradually increasing in size towards the centre, up to 160µm in diameter. Depth of the cortex decreasing gradually away from the base. Crystalline, proteinaceous crystals present in cortical and medullary cells at the point of transition; inconspicuous in upper branches. Crystals up to 10µm wide and up to six per cell.

Tetrasporangia (after Withell *et al*. 1994 for material from Australia)
Cruciately divided, up to 50µm long and 25µm wide, borne in all of the branches. Cortex immediately surrounding tetrasporangia unmodified.

Spermatangia (after Withell *et al*. 1994 for material from Australia)
verrucosa-type

Cystocarps
Not observed.

Remarks
Silva *et al*. (1996) pointed out that *Sphaerococcus canaliculatus* Kütz. (1868), the intended basionym for *Gracilaria canaliculata*, is a later homonym of *S. canaliculatus* C Agardh (1822) and is thus illegitimate. He therefore treated *Gracilaria canaliculata* Sonder as a *nomen novum*.

Gracilaria canaliculata, *G. crassa* and *Corallopsis opuntia* J. Ag. were considered conspecific by Newton (1953). The combined species was merged with *G. salicornia* (C Agardh) EY Dawson by Xia (1986). Meneses and Abbott (1987) independently came to the same conclusion. Withell *et al*. (1994) provisionally accepted Xia's (1986) judgement but argued that the reasons for the merger were not evident on the basis of Australian specimens. Hence, a '*Gracilaria canaliculata* Sonder form of *Gracilaria salicornia*' was described by Withell *et al.* (1994). Wynne (1995) determined that two species can be recognised, as plants of *G. canaliculata* have non-constricted or barely constricted axes, whereas plants of *G. salicornia* have clearly and regularly constricted axes. Molecular evidence on South African material (Iyer 2002) has conclusively demonstrated that these taxa (*G. canaliculata* and *G. salicornia*) are distinct entities.

Gracilaria canaliculata is one of three sub-tropical terete *Gracilaria* species present along South African shores. Its distribution, extending north of Cape Vidal into Mozambique, overlaps with one of these species, *G. salicornia*. *Gracilaria canaliculata* is identifiable by its light to dark rose colour and subdichotomous branching, which is often arcuate. It is easily distinguished from *G. salicornia* in that branching is not articulated.

4. ***Gracilaria capensis*** Schmitz ex Mazza 1907 [1905–1918]: 134–136 (Figure 4)

Basionym: *Gracilaria capensis* F Schmitz ex Mazza 1907 [1905–1918]: 134–136
Homotypic synonym: *Tylotus capensis* (F Schmitz ex Mazza) Papenf. 1940: 220–221, fig. 14.

References: Delf and Michell 1921: 108. De Toni 1924: 261. Papenfuss 1952: 176. Seagrief 1980: 26, fig. on pl. 8. Seagrief 1988: 54, fig. 5:9. Bolton and Anderson 1990: 451. Bolton and Stegenga 1990: 234, 237.

Holotype: PAD?

Type Locality
The Kowie, Port Alfred, South Africa.

Distribution
Endemic to South African coast from Kenton to Port Edward.

Specimens examined
Eastern Cape, Kenton, gulleys (Simons, 01.v.1950, SIM5050); Kleinmonde, drift (Stegenga, 27.iii.1987, SA1150); Piano Rocks, drift (Stegenga, 23.ix.1987, SA1775); Riet River, infralittoral fringe (De Clerck, 29.x.99, KZN1254); Salt Vlei Bay, drift (Stegenga, 17.iii.1987, SA1077); Salt Vlei Bay, infralittoral fringe (Stegenga, 17.iii.1987, SA1077); Sharks Bay, drift (Stegenga, 03.xii.1987, SA1890); Three Sisters, intertidal (Stegenga, 11.viii.1987, SA1639).

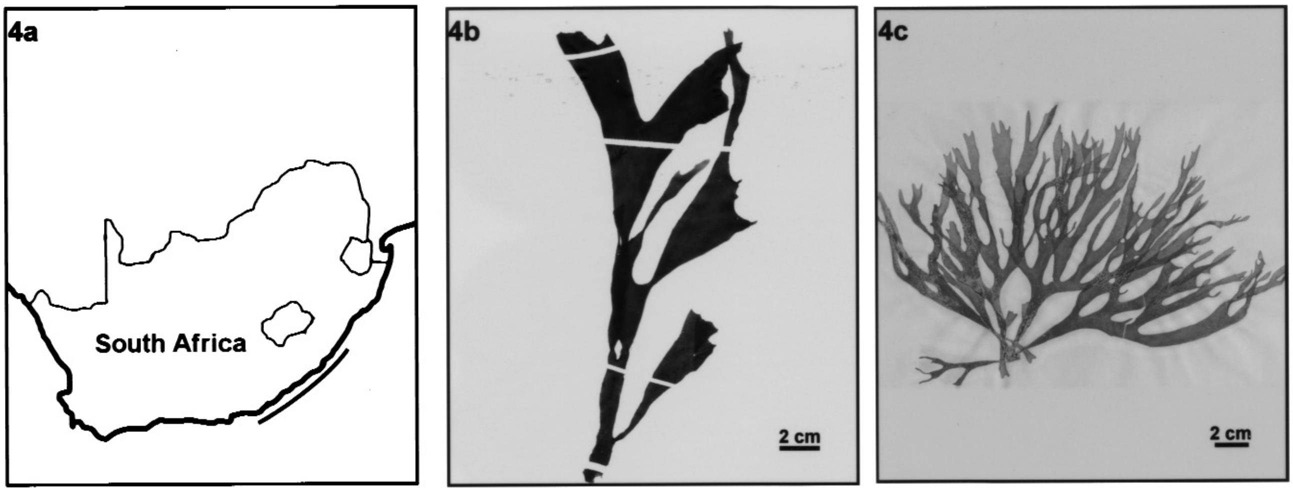

Figure 4: RSA distribution, morphology and anatomy of *G. capensis*. (a) Distribution, (b) habit (BOL12856), (c) habit (BOL508)

Habit
Thallus erect, up to 33cm in length, arising singly from a discoid holdfast. Stipe short, terete, to 1cm long. Branching irregular, up to four orders; multipartite in apical regions. Branches compressed, constricted at the base enlarging apically. Blades fan-shaped or linguiform, up to 24cm long, up to 7cm wide; apices broad and flattened or obtuse. Blade surface and margins smooth. Fresh specimens dark purple and firm but pliable; dried specimens dark purple.

Vegetative structure
Not observed.

Tetrasporangia (after Papenfuss 1940)
Tetrasporangia in sori.

Spermatangia
Not observed.

Cystocarps
Localised prominently on the surface of apical (upper) blades.

Remarks
Gracilaria capensis was described for the first time by Mazza (1907) based on material sent to him by Becker who had collected it at Port Alfred. Papenfuss (1940) confirmed that this taxon belongs to the Gracilariaceae. However, based on the formation of tetrasporangia in sori, Papenfuss (1940) argued that this species does not belong to the genus *Gracilaria*. Papenfuss also noted that the sori are localised at the tips of branches which suggested to him that it belongs to either *Curdiea* or *Tylotus*. Based on the anatomy of the thallus and the structure of the gonimoblast, Papenfuss (1940) decided that the species should be referred to *Tylotus*. Papenfuss (1952) transferred the taxon back to the genus *Gracilaria*, due to Dawson's (1949) observation that in some species of *Gracilaria*, the sporangia are localised in nemathecia.

Gracilaria capensis is easily distinguished from other members of the genus occurring in temperate waters in South Africa by the large blades, smooth margins and multipartite branching. The distribution of this species extends from Kenton (Eastern Cape) to Port Edward (KZN). Specimens are relatively elusive with only a solitary individual being collected during the period of this study.

5. *Gracilaria corticata* (J Agardh) J Agardh 1852 [1851–1863]: 602–603 (Figure 5)
Basionym: *Rhodymenia corticata* J Agardh, 1841: 14.
Homotypic synonym: *Sphaerococcus corticatus* (J Agardh) Kütz., 1849: 783.

References (reports of *G. protea*): Papenfuss 1943: 87. Seagrief 1980: 26, fig. on pl. 9. Farrell *et al*. 1993: 153.

Holotype: LUND?

Type Locality
Sri Lanka

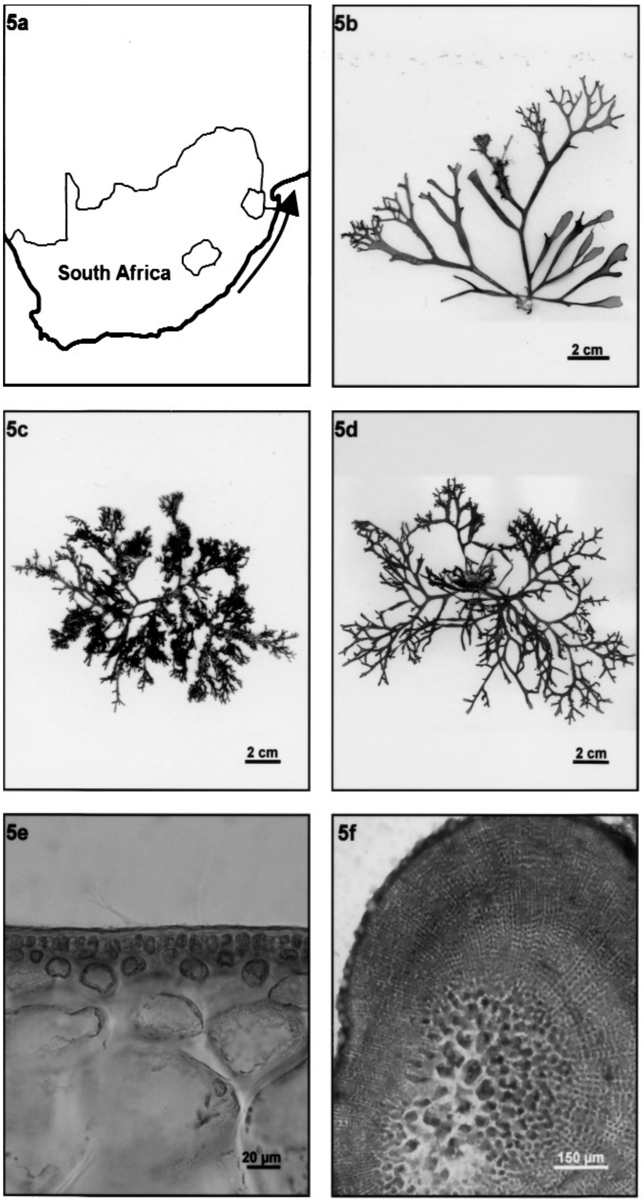

Figure 5: RSA distribution, morphology and anatomy of *G. corticata*. (a) Distribution, (b) habit (KZN1096), (c) habit (KZN1457a), (d) habit (KZN1457b) (e) C/S) of cortex-subcortex, (f) C/S of stipe

Distribution
Indian Ocean (South Africa to Indonesia); South Africa (north of Port Edward).

Specimens examined
Sri Lanka, Weligama (Halukanda Beach), intertidal (Coppejans, 07.i.1997, HEC11589).
KwaZulu-Natal, Balito, intertidal (Coppejans *et al*., 05.viii.1999, KZN186); Bangha Neck, intertidal (Coppejans *et al*., 13.viii.1999, KZN535A); Durban, infralittoral fringe (Coppejans *et al*., 03.viii.1999, KZN116); Kosi Bay, intertidal rock pools (Coppejans *et al*., 16.viii.1999, KZN740); Mabibi,

intertidal (Coppejans *et al*., 11.viii.1999, KZN495); Mabibi, infralittoral fringe (De Clerck and Cocquyt, 13.viii.2000, KZN1658); Mission Rocks, subtidal (Bolton, 08.vii.1998, KZN1095); Mission Rocks, subtidal (Bolton, 08.vii.1998, KZN1096); Mission Rocks, infralittoral fringe (De Clerck and Cocquyt, 17.viii.2000, KZN1774); Palm Beach, intertidal pools (Coppejans *et al*., 19.viii.1999, KZN812); Palm Beach, intertidal (De Clerck *et al*., 07.ii.2001, KZN2028); Sodwana Bay, intertidal (Coppejans *et al*., 09.viii.1999, KZN314); Sodwana Bay, subtidal (Coppejans *et al*., 09.viii.1999, KZN333); Trafalgar, intertidal pools (Coppejans *et al*., 20.viii.1999, KZN919); Trafalgar, intertidal rock pools (De Clerck, 23.xii.1999, KZN1457); Trafalgar, intertidal (De Clerck *et al*., 08.ii.2001, KZN2053); Zinkwazi, low intertidal pool (Coppejans *et al*., 03.viii.1999, KZN6).

Habit (Figures 6b–f and 7d)
Thallus erect, up to 14cm in length, arising singly from a discoid holdfast. Stipe very short, terete, up to 5mm long, often inconspicuous. Branching frequently, becoming more dense in upper parts of the plant; mostly dichotomous, up to many orders; rarely, fine laterals extend from the blades producing a bushy appearance; multipartite at points of damage. Axes compressed, almost cartilaginous; constricted at the base in basal branches. Blades linear, up to 15cm long, up to 4mm wide; apices generally obtuse, acute in finer branches. Blade surface and margins smooth. Fresh specimens purple to green and firm but pliable; dried specimens black to green. Large galls/tumours often evident on the surface of mature blades.

Vegetative structure
Transition of cell size from cortex to medulla abrupt throughout the thallus, except for the stipe where there is a gradual transition. Medullary cell walls up to 5µm thick; secondary pit connections present, but not prominent in subsurface layers, rare in outermost. Cortex of larger blades 1–2 cells thick, the cells darkly staining, up to 12µm long and 10µm in diameter. Medulla in this region up to seven cells wide, the cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 200µm long and 100µm in diameter. No marginal and surface protuberances. Lower portion of the stipe consisting of up to 35 layers of enlarged, isodiametric to rectilinear cortical cells, up to 18µm long and 13µm in diameter; medulla up to 18 cells wide, polygonal to spherical, gradually increasing in size towards the centre, 140µm long and 100µm in diameter. Depth of the cortex decreasing gradually away from the stipe base. Crystalline, proteinaceous crystals present in medullary cells of stipe. Crystals in stipe up to 30µm wide and up to 10 per cell. Tumour tissue extends from the medulla; medullary cells rectilinear becoming spherical at the centre, up to 130µm in diameter.

Tetrasporangia
Not observed.

Spermatangia
Not observed.

Cystocarps
Not observed.

Remarks
Rhodymenia corticata J Agardh was described on material collected in Sri Lanka. Kützing (1849) transferred the taxon to the genus *Sphaerococcus*. J Agardh (1852) supplied the name *Gracilaria corticata*, and also described two forms, *linearis* and *ramalinoides*. Umamaheswara Rao (1974) described a third form, *cylindrica*. This is the first report of *G. corticata* in South Africa.

Due to the diversity of vegetative morphologies the species has often been inadequately described. Børgesen (1938), Durairatnam (1961), and Jaasund (1976) expressed difficulty in differentiating *G. corticata* and *G. foliifera* from Mauritius, Sri Lanka, and Tanzania, respectively. Isaac (1957) described specimens in the *linearifolia* and *crenulata* forms of *G. millardetii* occurring at Xai-Xai, Mozambique. These specimens bear a marked resemblance to *G. corticata*. Furthermore he describes the *exposita* form of *G. millardetii* occurring south of Durban. Børgesen (1950) compared *G. millardetii* forma *exposita* with the *G. protea* specimens of Papenfuss (1943) and remarked that it seems to him 'to be clearly related to if not identical with certain forms of *G. millardetii* as he interprets the species'. Pocock's (1958) reference to *G. protea* is with a query, whereas Seagrief's (1980) illustration is remarkably similar to the appearance of *G. corticata*. It has been demonstrated (Iyer 2002) that thalli identified as *G. protea* in South Africa are remarkably similar to *G. corticata* based on RuBisCO spacer sequences. Consequently, specimens in South Africa have been assigned to *G. corticata*. Further studies are needed to ellucidate the taxonomic relationships between *G. millardetii*, *G. protea* and *G. corticata*, including specimens from Mauritius and Sri Lanka, the respective type localities of these species.

The diverse habit of *G. corticata* creates numerous problems in defining and identifying these specimens. Also, the differentiation of this taxon into different varieties is problematic. This is demonstrated by the habit of specimen KZN1457; one half of the plant displays the traditional *G. corticata* habit, whereas the other half has a very bushy appearance. This species can be distinguished from *G. vieillardii* in that branching is distinctively dichotomous and in a single plane rather than irregular and in multiple planes. In addition margins are characteristically smooth as opposed to minute dentations and crenations in *G. vieillardii*.

6. *Gracilaria denticulata* F Schmitz ex Mazza 1907 [1905–1918]: 138–139 (Figure 6)
Basionym: *Gracilaria denticulata* F Schmitz ex Mazza 1907 [1905–1918]: 138–139.
Homotypic synonym: *Tylotus denticulatus* (F Schmitz ex Mazza) Papenf. 1940: 221, fig. 15.

References: Delf and Michell 1921: 108. De Toni 1924: 265–266. Eyre, Broekhuysen and Crichton 1938: 100, 107. Børgesen 1943: 76. Stephenson 1948: 304. Papenfuss, 1952: 177. Isaac 1957: 97, pl. XXXI. Seagrief 1977: 90. Simons 1977b: 44, fig. 125. Seagrief 1980: 26, fig. on pl. 9. Lambert and Steinke 1986: 54. Seagrief 1988: 56, fig. 5:10.

Holotype: ?

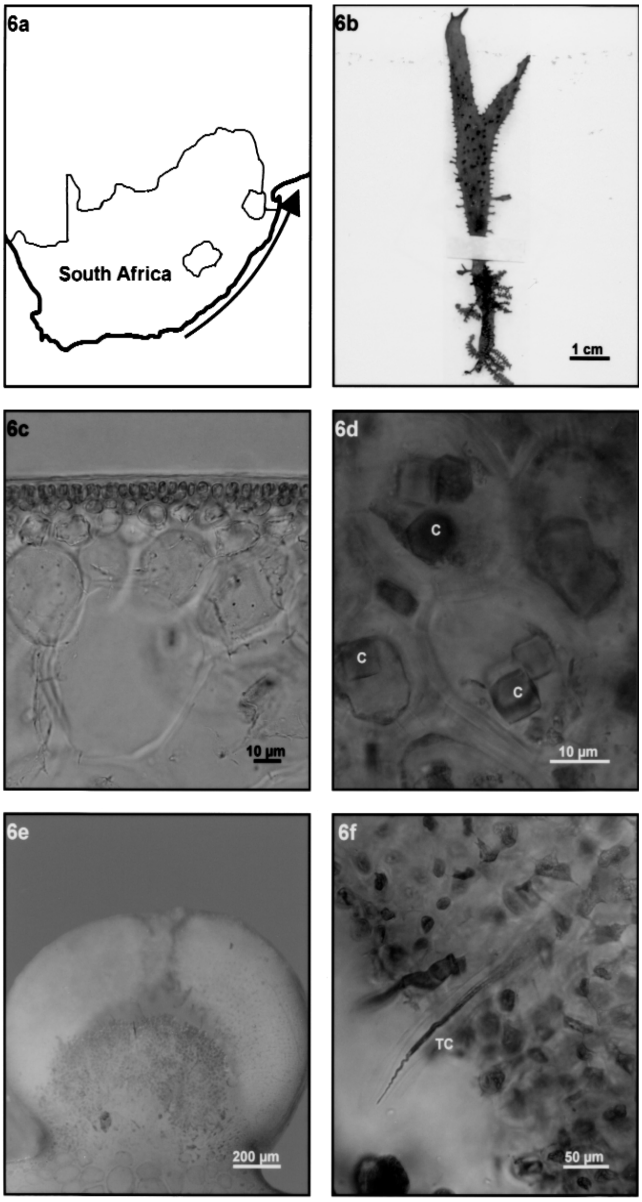

Figure 6: RSA distribution, morphology and anatomy of *G. denticulata*. (a) Distribution, (b) habit, (c) C/S of cortex-subcortex, (d) C/S of medulla (C = crystals), (e) C/S of cystocarp, (f) C/S of traverse pericarp (TC = traversing cell)

Type Locality

The Kowie, Port Alfred, Eastern Cape, South Africa.

Distribution

South Africa from Kenton (Eastern Cape) into Mozambique; Mauritius?

Specimens examined

Eastern Cape, Haga-Haga, intertidal pools (De Clerck *et al*., 26.x.1999, KZN1264, tetrasporic); Kenton, unknown (Simons, unknown, BOL53058); Kleinmonde, drift (Stegenga, 27.iii.1987, SA1155); Kowie, unknown (Becker, not specified, BOL47323); Salt Vlei Bay, subtidal (Stegenga, 17.iii.1987, SA1121); Sharks Bay, drift (Stegenga, 03.xii.1987, SA1898); Three Sisters, intertidal pool (Stegenga, 28.iv.1987, SA1222).

KwaZulu-Natal, Bangha Neck, intertidal (Coppejans *et al*., 15.viii.1999, KZN730, female); Durban, infralittoral fringe (Coppejans *et al*., 03.viii.1999, KZN82,); Kosi Bay, intertidal pools (Coppejans *et al*., 16.viii.1999, KZN739); Mission Rocks, infralittoral fringe (De Clerck and Cocquyt, 17.viii.2000, KZN1746, female); Palm Beach, intertidal (De Clerck *et al*., 07.ii.2001, KZN 2031); Port Edward, lower intertidal (De Clerck, 24.xii.1999, KZN1374); Trafalgar, intertidal pools (De Clerck, 23.xii.1999, KZN1456); Trafalgar, intertidal (De Clerck *et al*., 08.ii.2001, KZN2054).

Habit

Thallus erect, up to 12cm in length, arising singly from a discoid holdfast (rarely multiple axes occur on a crustose holdfast). Stipe short, terete, to 1cm long. Branching sparse, irregular, up to 3 orders, usually with small branchlets and short, undivided laterals arising from the blade margins; subdichotomous at tips. Branches compressed, often constricted at the base. Blades linguiform, up to 17cm long, up to 16mm wide in mid-portion, decreasing to 1–3mm wide proximal to the obtuse apices. Blade surface and margins dentate or papillate; prominent on margins, visible to the naked eye as a serrated edge; young blades often with blades and margins smooth. Fresh specimens purple to green and firm but pliable; dried specimens dark purple to dark green and slightly brittle.

Vegetative structure (Figure 6)

Transition of cell size from cortex to medulla abrupt throughout the thallus, except for the stipe where there is a gradual transition. Medullary cell walls up to 4µm thick; secondary pit connections present, but not prominent in subsurface layers, rare in outermost. Cortex of larger blades 1–2 cells thick, the cells darkly staining, up to 12µm long and 11µm in diameter. Medulla in this region up to seven cells wide, the cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 160µm long and 120µm in diameter. Marginal and surface protuberances simply divided, up to 3mm long; medulla extends into protuberances. Lower portion of stipe consisting of up to 30 layers of enlarged, cuboidal to rectilinear cortical cells, up to 16µm long and 12µm in diameter; medulla up to 24 cells wide, polygonal to spherical, gradually increasing in size towards the centre, 110µm long and 75µm in diameter. Depth of the cortex decreasing gradually away from the stipe base. Crystalline, proteinaceous crystals present in medullary cells; shape varies from icosahedral to cuboidal. Crystals in stipe up to 30µm wide and up to 10 per cell; crystals in blades up to 10µm wide and up to 35 per cell. Frequency of crystals greater in younger blades proximal to the apices. Density and frequency of crystals greatest in the stipe.

Tetrasporangia

Occurring singly bordered by sterile tissue. Tetrasporangia up to 35µm long and 25µm wide, occurring on both sides of the frond; not aggregated, evenly distributed in sori. Tetrasporangia cruciately divided.

Spermatangia
Not observed.

Cystocarps
Cystocarps localised on both sides of the blade surface; distribution even from the base to the apex. Traversing cells common in mature cystocarps, rare in young cystocarps; developing from basal and apical gonimoblast cells, and penetrating the gametophyte tissue basal to the carposporophyte and lower pericarp, and more frequently, in an upward direction penetrating the upper pericarp. Mature cystocarps ostiolate, up to 1.6mm high and 2mm wide, constricted at the base; pericarp tissue up to 450µm and 30 cell layers thick; gonimoblast parenchyma abundant, basal cells up to 150µm long and 50µm wide. Carpospores densely protoplasmic, obovoid or oval, up to 35µm long and 25µm wide, borne terminally on the gonimoblast filaments.

Remarks
Gracilaria denticulata was described on material provided by Becker who collected it at Port Alfred. Papenfuss (1940) supplied the name *Tylotus denticulatus* due to the formation of tetrasporangia in sori. Papenfuss (1952) transferred the taxon back to the genus *Gracilaria*, due to Dawson's (1949) observation that, in some species of *Gracilaria*, the sporangia are localised in nemathecia.

Weber-van Bosse (1928), Yamada (1938), and Børgesen (1943) have reported material from Indonesia, the Ryukyu islands, and Mauritius, respectively, under the name *G. denticulata*, making the combination from Kützing's (1869) *Sphaerococcus denticulatus*. The association by Weber-van Bosse of *S. denticulatus* with *G. denticulata* was erroneous for two reasons: (i) Mazza (1907) published the South African plant as a new species, without reference to *S. denticulatus*; and (ii) *S. denticulatus* was described based on material collected by Vieillard in New Caledonia. *G. denticulata* (Kütz.) Weber-van Bosse was renamed *G. vieillardii* by Silva *et al*. (1987).

Given the presence of both *G. denticulata* and *G. vieillardii* in South Africa, and the nomenclatural confusion between both species, it is unclear to which species the record of *G. vieillardii* by Farrell *et al.* (1993) from Isipingo Beach referred.

In terms of warm temperate members of *Gracilaria* in South Africa, *G. denticulata* has the largest distibution range. The species is endemic to the region (south eastern Africa) and seems to be suited to a range of ecological conditions as displayed by its extended distribution from Kenton (Eastern Cape) throughout KwaZulu-Natal (KZN) and into Mozambique. This species is easily distinguished by the prominent dentations, which occur on the surface and margins of blades. In addition, thalli are often characteristically green.

7. *Gracilaria gracilis* (Stackh.) M Steentoft, LM Irvine et WF Farnham 1995: 115 (Figure 7)
Basionym: *Fucus gracilis* Stackh. 1802: 100, pl. 16.
Homotypic synonyms: *Fucus confervoides* var. *gracilis* (Stackh.) Turner 1802: 329. *Flagellaria gracilis* (Stackh.) Stackh. 1809: 93. *Gracilaria confervoides* Grev. forma *gracilis* (Stackh.) Grunow 1874:42.

References*:* Isaac 1956: 173–185. Simons 1977b. Stegenga *et al*. 1997: 300–303, pl. 102.

Lectotype: BM (ex K), Hooker Herbarium

Type Locality
"Padstow (Cornwall) and elsewhere", England, but lectotype without provenance *fide* Steentoft *et al*. (1995).

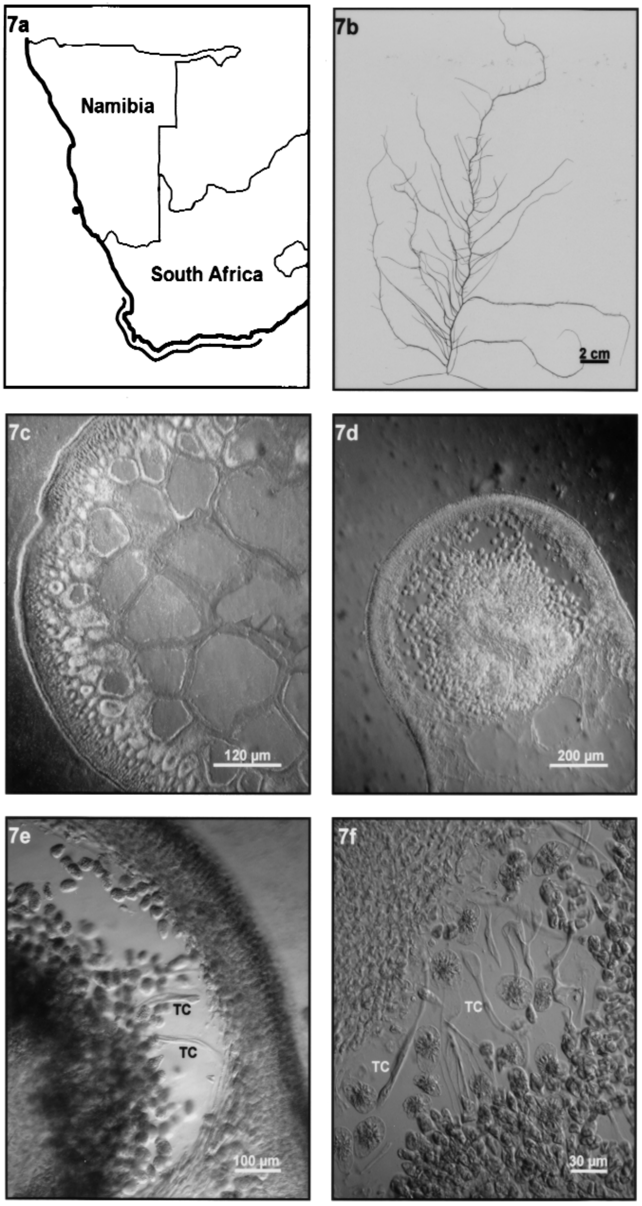

Figure 7: RSA distribution, morphology and anatomy of *G. gracilis*. (a) Distribution, (b) habit, (c) C/S of main axis, (d) C/S of cystocarp, (e and f) traversing cel (TC) within the cystocarpic cavity

Distribution
Western Europe, Australia, India, Namibia (Luderitz) and South Africa [St Helena Bay (Western Cape) to Algoa Bay (Eastern Cape)].

Specimens examined
Namibia, Luderitz, subtidal (Iyer, 23.xi.1999, LUD3); Luderitz, intertidal (Iyer, 23.xi.1999; LUD7); Luderitz, drift (Iyer, 24.xi.1999, LUD12).
Western Cape, St Helena Bay, subtidal (Govender, 23.vii.1999, HELD3); Olifants river, river mouth (Iyer, 06.vi.2000, OLI1); Saldanha Bay, subtidal (Govender, 17.v.1999, SALA1); Langebaan Lagoon, subtidal (Govender, 15.viii.1999, LANA1); Hout Bay, subtidal (Anderson, 03.iv.2001, HOB1); Keurbooms river, river mouth (Anderson, 09.x.1999, KBR3).
Eastern Cape, Swartkops river, river mouth (Bolton, 22.ii.2000, SWK1).

Habit
Thallus erect, up to 20cm (<1m depth) or 100cm (>1m depth) in length, anchored in sediment, no holdfast. Repeatedly and irregularly branched, up to four orders. Branches cylindrical, up to 2mm wide, often constricted at the base (diameter to 0.8mm); apices taper to an acute point. Fresh specimens cartilaginous, dark red to purple.

Vegetative structure
Transition of cell size from cortex to medulla abrupt throughout the thallus. Medullary cell walls up to 3µm thick; secondary pit connections present but not prominent in subsurface layers, rare in outermost. Cortex of large branches 1–3 cells thick, the cells darkly staining, up to 14µm long and 10µm wide. Subcortex 1–2 cells thick, cells lightly staining, globose, up to 80µm long and 40µm wide. Medulla in this region up to 7 cells wide, the cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 320µm long and 240µm wide.

Tetrasporangia (after Steentoft *et al*. 1995 for material from Europe)
Cruciately divided, up to 44µm long and 30µm wide, borne in all of the branches.

Spermatangia (after Steentoft *et al*. 1995 for material from Europe)
verrucosa-type

Cystocarps
Cystocarps scattered irregularly over the surface of all branches; mature cystocarps ostiolate, up to 1mm high and 1.2mm wide, unconstricted at the base. Traversing cells common in mature cystocarps, rare in young cystocarps, developing from apical gonimoblast cells in a lateral and upward direction, penetrating the transverse and upper pericarp, repectively; pericarp tissue up to 220µm and 13 cell layers thick; gonimoblast parenchyma dense, central cells up to 20µm wide. Carpospores densely protoplasmic, obovoid or oval, up to 40µm wide; borne terminally on gonimoblast filaments.

Remarks
Terete British gracilarioid material was referred to as *Gracilaria confervoides* (basionym: *Flagellaria confervoides*), and was regarded as the type species of *Gracilaria*. This name was precluded in favour of *G. verrucosa* by Parke and Dixon (1976) and South and Tittley (1986). Dixon and Irvine (1977) selected Hudson's (1762) description as lectotype. Fredericq and Hommersand (1989a, 1989b) distinguished between terete *Gracilaria* (as *G. verrucosa*) and *Gracilariopsis* [as *Gs. lemaneiformis*], which they recorded for the first time in the British Isles. Steentoft *et al*. (1991) determined that the lectotype of *G. confervoides* Grev. is a *Gracilariopsis*. In order to prevent multiple renaming of species of both *Gracilaria* and *Gracilariopsis*, and to achieve nomenclatural stability, Steentoft *et al*. (1991) proposed the conservation of *G. compressa* (C Agardh) Grev. as lectotype of the genus *Gracilaria*. The name *G. gracilis* was provided for the *Gracilaria* species which had been confused under name *G. verrucosa*. It has been demonstrated (Iyer 2002) that both *G. gracilis* and *Gs. longissima* are present in South Africa and had been previously described as a single species under the names, *G. confervoides* and, more recently, *G. verrucosa* (Isaac 1956, MacNae 1957, Simons 1977a). Simons mentions that gracilarioid thalli (as *G. verrucosa*) were collected in Table Bay by Tyson in 1894.

Gracilaria gracilis has a widespread distribution in temperate waters from Luderitz (Namibia) to Port Elizabeth (Eastern Cape), but is generally confined to sheltered embayments and estuary mouths. The species can be distinguished from *Gs. longissima* (which shares a similar distribution in South Africa) by characters of the female reproductive structures described by Fredericq and Hommersand (1989a, 1989b). However, the rarity of fertile material often leads to confusion about the precise identity of material determined by anatomical methods.

8. *Gracilaria vieillardii* P. Silva in Silva *et al*. 1987: 44 (Figure 8)
Basionym: *Sphaerococcus denticulatus* Kützing, 1869: 19, pl. 51: figs e–g.

References: Farrell *et al*. 1993: 153. Withell *et al.* 1994: 307–310.

Holotype: L?

Type Locality
New Caledonia

Distribution
Indian Ocean (South Africa and Indonesia); South Africa (KwaZulu-Natal).

Specimens examined
KwaZulu-Natal, Bangha Neck, intertidal (Coppejans *et al*., 13.viii.1999, KZN538); Bangha Neck, intertidal (Coppejans *et al*., 15.viii.1999, KZN731); Cape Vidal, intertidal pools (De Clerck and Cocquyt, 18.viii.2000, KZN1822); Kosi Bay, intertidal pools (Coppejans *et al*., 16.viii.1999, KZN743); Mabibi, infralittoral fringe (De Clerck and Cocquyt, 13.viii.2000, KZN1659);

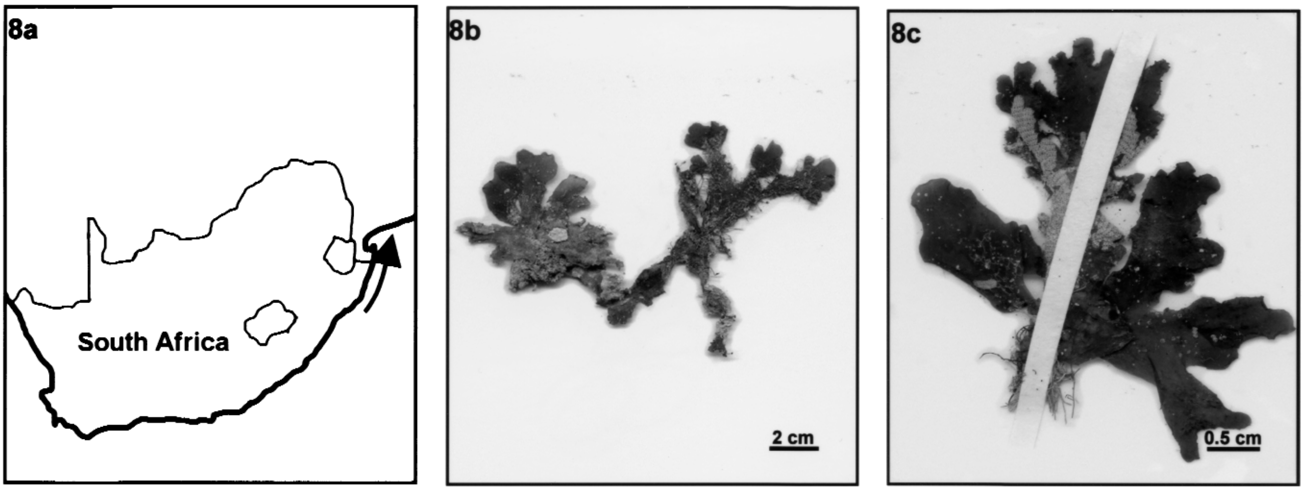

Figure 8: RSA distribution, morphology and anatomy of *G. vieillardii*. (a) Distribution, (b and c) habit

Habit
Thallus erect, up to 8cm long, cartilaginous, dark-purple in colour. Attached by means of a discoid holdfast. Axes cylindrical near the base, compressed to foliose above, up to 6 times irregularly branched in multiple planes. Blades undulate and generally up to 1(–2)cm wide; ultimate axes lobate. Margins entire and smooth or with minute dentations and crenations.

Vegetative structure
Internal structure consisting of 1–3 layers of pigmented outer cortical cells surroundinga large-celled medulla with cells of up to 150μm in diameter; medullary cells decreasing in size towards the periphery, polygonal to spherical in shape.

Tetrasporangia
Not observed.

Spermatangia
Not observed.

Cystocarps
Not observed.

Remarks
Earlier reports of *G. vieillardii* from South Africa are difficult to trace due to the nomenclatural confusion with *G. denticulata*. The species was traditionally known as *G. denticulata* (Kützing) Weber-van Bosse, a later homonym of *G. denticulata* Schmitz ex Mazza renamed *G. vieillardii* by P. Silva (Silva *et al*. 1987).

9. *Gracilaria salicornia* (C Agardh) Dawson 1954: 4, fig. 3 (Figure 9)
Basionym: *Sphaerococcus salicornia* C Agardh 1820: pl. VII.
Homotypic synonyms: *Corallopsis salicornia* (C Agardh) Grev. 1830: liii.
Heterotypic synonyms: *Corallopsis dichotoma* Rupr. nom illeg. 1850: 000.
Corallopsis cacalia J Agardh 1852 [1851–1863]: 583 (type locality: Red Sea).
Corallopsis opuntia J Agardh 1872: 40.
Corallopsis concresens Reinbold 1907: 571, pl. LVII: fig. 3.
Gracilaria cacalia (J Agardh) Dawson 1954: 2.
Corralopsis salicornia (C Agardh) Grev. var. *minor* Sond. 1871: 56, pl. III: figs 6–11 (type locality: Cape York, Queensland, Australia).
Gracilaria minor (Sond.) Durair. 1961: 64, pl. XIV: figs 1–3.

References: Pocock 1958: 26 (with query). Isaac 1971: 18. Seagrief 1980: 26. Farrell *et al.* 1993: 153. Withell *et al.* 1994: 297–301, figs 14–15. Wynne 1995: 281–2, fig. 18.

Holotype: LUND?

Type Locality
Manila, Philippine Islands *fide* Dawson 1954: 4.

Distribution
Indian Ocean (South Africa to Australia); South Africa (north of Cape Vidal into Mozambique).

Specimens examined
KwaZulu-Natal, Adams Reef, intertidal (Coppejans *et al*., 09.viii.1999, KZN285); Bangha Neck, intertidal (Coppejans *et al*., 13.viii.1999, KZN601); Mabibi, intertidal and infralittoral fringe (Coppejans *et al*., 09.viii.1999, KZN399); Mabibi, infralittoral fringe (De Clerck and Cocquyt, 13.viii.2000, KZN1637); Sodwana Bay, intertidal pools (Coppejans *et al*., 08.viii.1999, KZN214).

Habit
Thallus erect, up to 6.5cm long, occurring as solitary individuals. Irregularly discoid holdfast giving rise to one to two axes. Thalli consisting of up to 6 articulated segments, the segment base attenuated, the apex obtuse, often dilated or club-shaped. Generally di- to trichotomously arranged, but sometimes either singly or umbellately, the latter of up to 4 segments; lacking laterally derived segments. Medium sized

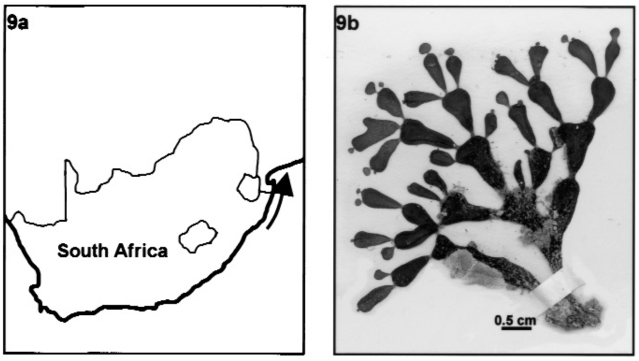

Figure 9: RSA distribution, morphology and anatomy of *G. salicornia*. (a) Distribution, (b and c) habit

thalli with first and second order segments of major axis elongated or cylindrical, up to 3mm in diameter and to 17mm long; articulations poorly defined or absent. Higher order (3–6) branch segments obovoid to obipyriform; up to 6mm in diameter and to 12mm long; conspicuously constricted articulations, 0.5–2mm in diameter. Thalli firm; colour variable, yellow to red when fresh, drying darker.

Vegetative structure
Not observed.

Tetrasporangia
Not observed.

Spermatangia (after Xia 1986)
verrucosa-type

Cystocarps
Not observed.

Remarks
Sphaerococcus salicornia was first described by C Agardh (1820) from specimens collected by Chamisso during a voyage on the Russian exploring ship *Rurik*. These specimens were believed by C Agardh (1820) to have come from Unalaska in the Pacific subarctic, although Chamisso was uncertain of their origin. Dawson (1954) collected specimens matching the original description of *S. salicornia* from Manila Harbour and decided that this is most probably the actual type locality, since the *Rurik* had spent 6 weeks there and *G. salicornia* is a tropical species unrecorded from sub-arctic waters.

Sphaerococcus salicornia was made the type species of *Corallopsis* by Greville (1830), who distinguished the genus from *Gracilaria* by the former's extreme branch constrictions. Dawson (1954) considered articulation or constriction of branches to be insufficient reason for a generic segregation.

This species is distinguished by its articulated branches and often displays a characteristic yellow to orange colour. Its South African distribution is similar to *G. canaliculata* and *G. vielliardii*, occurring north of Cape Vidal.

Gracilariopsis Dawson 1949: 40
Thallus erect, irregularly branched, terete with or without a disc-like holdfast from which one or many uprights are produced, dark red, olive green or purple, soft to slightly cartilaginous, smooth. Triphasic, isomorphic life history. Females with obvious swellings (cystocarps) with thick pericarp, ostiolate, traversing tubular nutritive cells absent. Spermatangia in surface sori. Sporophytes with tetrasporangia scattered in the outer cortex, cruciately divided.

10. *Gracilariopsis longissima* *Gracilariopsis longissima* (Gmel.) Steentoft, Irvine et Farnham 1995 (Figure 10)
Basionym: *Fucus longissima* Gmel. 1768: 134, pl. 13.
Homotypic synonyms: *Gracilaria verrucosa* (Hudson) Papenf. 1950: 195. *Flagellaria verrucosa* (Hudson) Stackh.: 1809: 92. *Fucus verrucosus* var. *simplex* (Stackh.) Stackh. 1816: 13, pl. 15. *Gracilaria confervoides sensu* Grez. 1830: 123.
Heterotypic synonyms: *Fucus confervoides sensu* Stackh. 1802: 96, pl. 15. *Fucus longissimus sensu* Stackh., *British Fuci named*: 8. *Gracilaria confervoides* var. *procerrima sensu* Grez. 1830: 123.

References: Govender 2001.

Neotype: OXF, Dillenius Herbarium (after Steentoft *et al*. 1995)

Type Locality
Sheerness (Kent).

Distribution
Western Europe, South Africa [St Helena Bay (Western Cape) to Algoa Bay (Eastern Cape)].

Specimens examined
Eastern Cape, Port Elizabeth, abalone farm (Anderson, 22.ii.2001, XPE3).
Western Cape, Knysna estuary, subtidal (Bolton, 29.vi.1999, KNY1); Langebaan Lagoon, subtidal (Govender, 15.xiii.1999, LANF1); St Helena Bay, subtidal (Govender, 23.vii.1999, HELA1); Simonstown, subtidal (Anderson, 04.iv.2001, SMT1).

Habit
Thallus erect, up to 20cm (<1m depth) or 100cm (>1m depth) in length, anchored in sediment, no holdfast. Repeatedly and irregularly branched up to 4 orders. Branches cylindrical, up to 2mm wide, often constricted at the base (diameter to 0.8mm); apices taper to an acute point. Fresh specimens cartilaginous, dark red to purple.

Vegetative structure
Transition of cell size from cortex to medulla abrupt throughout the thallus. Medullary cell walls up to 3µm thick; secondary pit connections present but not prominent in subsurface layers, rare in outermost. Cortex of large branches 1–3 cells thick, the cells darkly staining, up to 18µm long and 10µm wide. Subcortex 1–2 cells thick, cells lightly staining, globose, up to 60µm long and 40µm in diameter. Medulla up

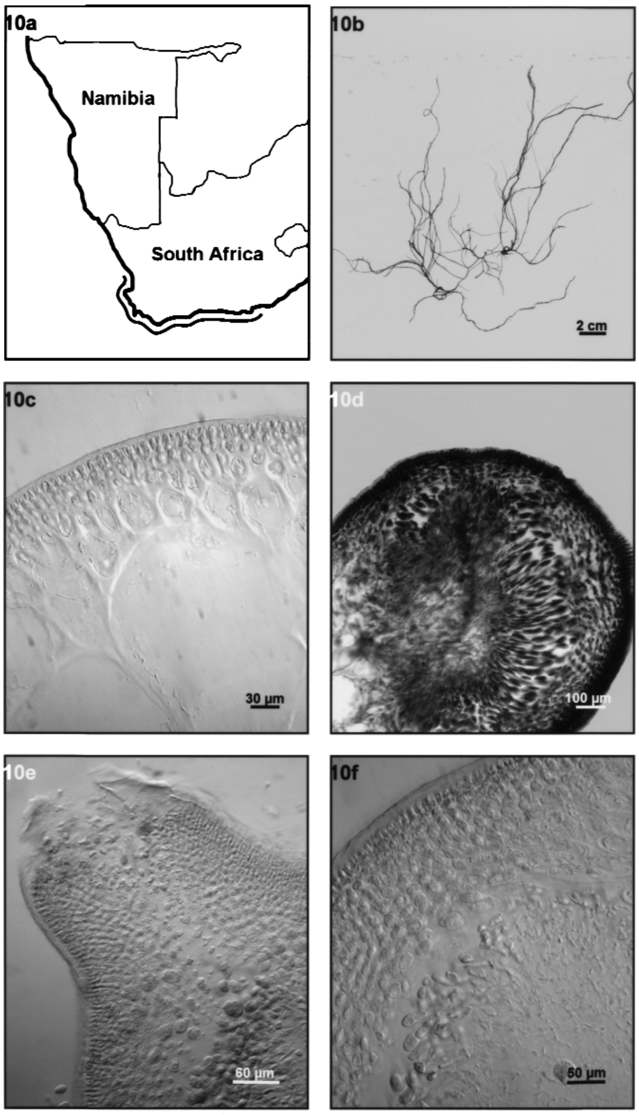

Figure 10: RSA distribution, morphology and anatomy of *Gs. longissima*. (a) Distribution, (b) habit, (c) C/S of main axis, (d) C/S of cystocarp, (e) C/S of upper pericarp, (f) C/S of traverse pericarp

to 7 cells wide, the cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 380µm long and 260µm wide.

Tetrasporangia (after Steentoft *et al*. 1995 for material from Europe)
Cruciately divided, up to 54µm long and 35µm wide, borne in all of the branches.

Spermatangia (after Steentoft *et al*. 1995 for material from Europe)
Chorda-type.

Cystocarps
Cystocarps scattered irregularly over the surface of all branches; mature cystocarps ostiolate, up to 1.0mm high and 1.4mm wide, unconstricted at the base. Traversing cells absent; pericarp tissue up to 300µm and 18 cell layers thick; gonimoblast parenchyma dense, central cells up to 38µm wide. Carpospores densely protoplasmic, obovoid or oval, up to 40µm wide; borne terminally on gonimoblast filaments.

Remarks
Gracilaria gracilis and *Gracilariopsis longissima* are superficially similar species long confused under the name *G. verrucosa* [= *G. confervoides*]. The first identification of this species in South Africa was for material from Langebaan Lagoon and St Helena Bay (Govender 2001). Material from Simonstown (Western Cape) was identified as *Gs. lemaneiformis* by Stegenga *et al*. (1997). Molecular evidence (Iyer *et al*. 2002) demonstrates that these specimens actually are representative of *Gs. longissima*. The distribution of this species is similar to *G. gracilis*, occurring in warm and cool temperate waters from Port Elizabeth (Eastern Cape) to St Helena Bay (Western Cape). Furthermore, the morphology and anatomy of *G. gracilis* and *Gs. longissim*a are remarkably similar. Consequently these two species cannot be differentiated based on these characters.

11. *Gracilariopsis funicularis*

Gracilariopsis funicularis Iyer, Bolton et Coyne 2005 (Figure 11)

Holotype: GENT

Type locality
Swakopmund (Namibia).

Distribution (after Iyer *et al*. 2005)
Namibia [Swakopmund to Henties Bay], South Africa [De Mond].

Specimens examined
Namibia, Swakopmund, intertidal (Iyer, 24.x.99, M8-1), Swakopmund, intertidal (Kandjengo, 22.vi.01, NAM17).
Western Cape, De Mond river, subtidal (Anderson, 25.viii.99, DEM1).

Habit (after Iyer *et al*. 2005)
Thalli erect, terete, cylindrical, up to 30cm high; thalli fine in unattached estuarine specimens (up to 0.6mm in diameter) or robust in attached open shore specimens (up to 1.5mm in diameter). Multiple axes arise from a crustose holdfast; axes are prominently finer at base. No discernable stipe. Branching is frequent and irregular; up to 5 orders; branches are somewhat constricted at the bases; apices taper to an acute point. The plant ranges from dark red to dark purple.

Vegetative structure (after Iyer *et al*. 2005)
Transition of cell size from cortex to medulla abrupt throughout the thallus. Medullary cell walls 5–8µm thick; secondary pit connections present, prominent in subcortical layers, less obvious in cortex. Cortex of larger blades 1–3 cells thick, the cells darkly staining, columnar, up to 9–14µm long and 3–8µm wide, or cuboidal, 9–10µm long and 7–8µm wide. Cortex separated from medulla by 4–5 subcortical cell lay-

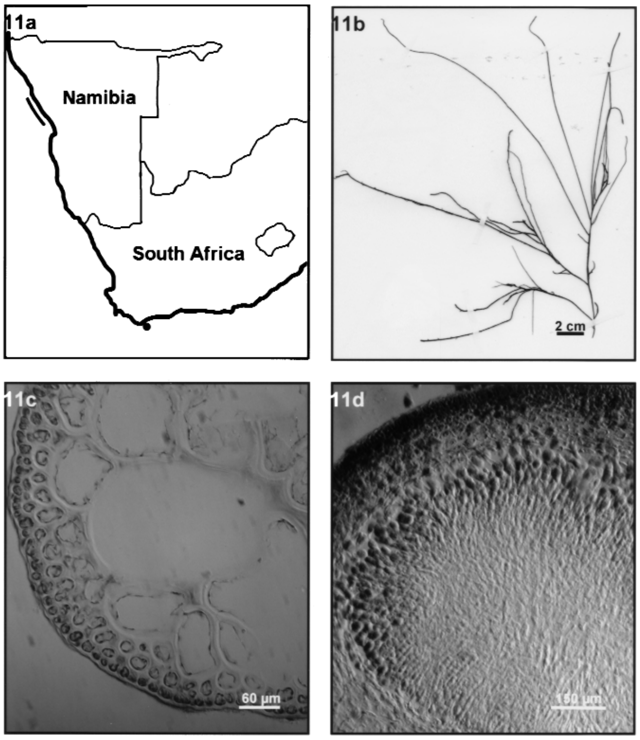

Figure 11: RSA distribution, morphology and anatomy of *Gs. funicularis*. (a) Distribution, (b) habit, (c) C/S of main axis, (d) C/S of cystocarp

ers, columnar to spherical, up to 32µm long and 18µm in diameter. Medulla in this region 5–7 cells wide, cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 400µm long and 260µm in diameter. Crystalline, proteinaceous crystals present in medullary and subcortical cells; up to 8 per cell; generally columnar, some elongately pentagonal; up to 17µm long and 13µm wide.

Medulla of slender thalli (especially De Mond specimens) dominated by 4–6 large medullary cells; cortex and subcortex each limited to 1–2 cell layers, medulla 3–4 cell layers thick.

Tetrasporangia (after Iyer *et al*. 2005)
Cruciately divided, up to 55µm long and 30µm wide, borne in all of the branches.

Spermatangia (after Iyer *et al*. 2005)
Chorda-type

Cystocarps (after Iyer *et al*. 2005)
Cystocarps occur throughout the thallus surface, randomly distibuted from the base to the apex. Mature cystocarps ostiolate, generally domoid, 1–1.2mm high and 1.8–2mm wide, unconstricted at the base; pericarp tissue 150–300µm and 10–15 cell layers thick, inner cells periclinally compressed to various degrees, maintaining radial files; gonimoblast parenchyma abundant, central cells up to 150µm long and 75µm wide. Traversing cells conspicuously absent in cystocarps. Carpospores densely protoplasmic, obovoid or oval, up to 35µm long and 25µm wide; borne terminally on gonimoblast filaments.

Remarks
Material from Swakopmund (Namibia) was identified as *Gs. lemaneiformis* by Stegenga *et al*. (1997). Molecular evidence (Gurgel *et al*. 2003, Iyer *et al*. 2005) demonstrated that these specimens are actually representatives of an undescribed *Gracilariopsis* species. The species was consequently described by Iyer *et al*. (2005) based on morphology and anatomy. The distribution of this species differs from the other South African gracilarioid species. However, the morphology and anatomy of *G. gracilis*, *Gs. longissima* and *Gs. funicularis* are remarkably similar. Consequently these three species cannot be differentiated based on these characters.

Discussion

The species count for the South African Gracilariaceae is now two *Gracilariopsis* species and nine *Gracilaria* species. Three *Gracilaria* species (*G. crassa*, *G. foliifera* and *G. protea*) and one *Gracilariopsis* species (*Gs. lemaneiformis*) have been assigned as different species. *Gracilaria crassa* was considered conspecific to *G. canaliculata* by Newton (1953). This species has been reduced to a synonym of *G. canaliculata* (Silva 1996), hence prior references (Brown and Jarman 1978, Seagrief 1980) to *G. crassa* in South Africa would now refer to *G. canaliculata*. Krauss's [1846; as *Chondrus aeruginosus* (Turner) Lamour.] and Barton's [1893; as *Gracilaria multipartita* (Clemente) Harv.] listing of *G. foliifera* forma *aeruginosa* are the only reports for this species in South Africa. There have been no subsequent descriptions, and this species was not encountered during this study. It is plausible therefore to assume that *G. foliifera* was erroneously identified.

It has been demonstrated (Iyer 2002) that specimens in South Africa referred to as *G. protea* could be assigned to *G. corticata* as known from Sri Lanka. *Gracilaria corticata* has often been inadequately described due to the diversity of vegetative morphologies assumed. This species has been confused with *G. foliifera* (Børgesen 1938, Durairatnam 1961, Jaasund 1977) and *Gracilaria millardetii* (Isaac 1957). Furthermore, Børgesen (1950) remarked that certain forms of *G. millardetii* are identical to *G. protea*. Hence it is likely that specimens of *G. millardetii* may also have erroneously been referred to as *G. protea*. The confusion as to the identification of these species is emphasised by Pocock's (1958) reference to *G. protea* with a query. Seagrief's (1980) illustration of *G. protea* bears remarkable similarity to the appearance of *G. corticata*. Oddly, *G. corticata* has never been reported in South Africa before. This is possibly due to the diverse habit of *G. corticata*, which creates numerous problems in defining and identifying these specimens. However, the differentiation of this taxon into varieties is also problematic as different morphologies often occur on a single plant.

The exclusion of *G. protea* in favour of *G. corticata* raises questions about the existence/validity of the taxon *G. protea*. Since the type locality of this species is Mauritius, it is necessary to examine specimens from that region before making decisions regarding its validity. These studies would confirm the taxonomic status of the South African species. It is interesting however that Børgesen (1950) expressed difficulty in differentiating *G. millardetii* from *G. protea* in Mauritius.

Thalli from Simonstown were identified by Stegenga *et al*. (1997) as *Gs. lemaneiformis* based on the lack of nutritive filaments in cystocarps. The species identification has proved to be erroneous based on molecular studies (Iyer 2002). The common South African *Gracilariopsis* is conspecific with European *Gs. longissima* (Iyer 2002). This species occurs along the west and south coasts of South Africa co-existing in a few habitats with *G. gracilis* (with one species generally predominating). These species are indistinguishable using vegetative morphology, and hence the previous misconception that a single species occurs. The occurrence of these two species in close proximity, added to the paucity of fertile material, ensures that it is generally impossible to confidently differentiate these two species without employing molecular methods. More recently, a third gracilarioid species, *Gs. funicularis* was described for southern Africa by Iyer *et al*. (2005). These plants are fertile on a regular basis along the central Namibian coast.

Three species of *Gracilaria* (*G. aculeata*, *G. beckeri* and *G. capensis*) are endemic to the South African coast, and a fourth species (*G. denticulata*) is localised in southeast Africa (South Africa, Mozambique and possibly Madagascar). The high species endemism within this eastern overlap region is interesting in that it points to an ecological habitat which appears to be a hotbed for species evolution. Hommersand (1986) commented that the uniqueness of the flora is striking. This has relevance for the delineation of marine reserves.

The region extending from Kenton (Eastern Cape) in the southwest to Port Edward (KZN) in the northeast is notable for its species diversity (Bolton and Stegenga 2002). Port Edward serves as the southernmost limit for the tropical species, *G. corticata*, whereas Kenton serves as the cut-off point for temperate gracilarioids (*G. gracilis* and *Gs. longissima*) which occur along the west and south coasts. Four species (*G. aculeata*, *G. beckeri*, *G. capensis* and *G. denticulata*) occur within this transition region (eastern overlap). *G. beckeri* and *G. capensis* are endemic to this region, suggesting evolutionary adaptation to this transitional ecological niche. A theory has been put forward (Iyer 2002) for the evolution of these species from an ancestral *G. vieillardii* plant.

Gracilaria aculeata is endemic to the eastern overlap and east coast of South Africa. It has been demonstrated (Iyer 2002) that this species shares greatest molecular similarity with *G. salicornia*. The implication is that *G. aculeata* probably evolved from a *G. salicornia*-like ancestor and is hence on a separate evolutionary pathway from *G. beckeri* and *G. capensis*. This is feasible biogeographically as *G. aculeata* occupies the southernmost range of the *G. salicornia* habitat. In addition, these two species are terete — the only other terete tropical *Gracilaria* species in South Africa being *G. canaliculata,* which is also closely related to these two species.

The reasons for the merger of *G. canaliculata* with *G. salicornia* by Xia (1986) and by Meneses and Abbott (1987) were not evident on the basis of Australian specimens (Withell *et al*. 1994). Wynne (1995) supported this argument stating that two species can be recognised. Molecular studies (Iyer 2002) on South African material has conclusively demonstrated that these taxa (*G. canaliculata* and *G. salicornia*) are distinguishable entities. These species are easily differentiated based on morphology (constriction of axes and branching pattern).

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References

Abbott IA (1995) A decade of species of *Gracilaria*. In: Abbott IA (ed) Taxonomy of Economic Seaweeds with Reference to some Pacific Species, V. California Sea Grant College Program, La Jolla, pp 185–194

Abbott IA, Zhang J, Xia B (1991) *Gracilaria mixta*, sp. nov. & other western Pacific species of the genus (Rhodophyta, Gracilariaceae). Pacific Science **45**: 12–27

Agardh CA (1820) Icones algarum ineditae. Fasc. 1. Lundae (Lund). pp 4, pls I–X

Agardh CA (1822) Algae, Agardh. In: Kunth CS (ed) Synopsis plantarum, quas, in itinere ad plagam aequinoctialem orbis novi, collegerunt Al. de Humboldt et Am. Bonpland. Vol. 1. Parisiis (Paris), pp 1–6

Agardh JG (1841) In historiam algarum symbolae. Linnaea **15**: 1–50, 443–457

Agardh JG (1852) Species genera et ordines algarum… Volumen secundum: algas florideas complectens. Lundae (Lund), part 2, fasc. 2, pp 505–700 + 701–720 (Addenda and Index)

Agardh JG (1872) Bidrag till Florideernes systematik. Lunds Universitets Års-Skrift, Afdelningen för Mathematik och Naturvetenskap, 8(6), pp 60

Agardh JG (1876) Species genera et ordines algarum… Volumen tertium: de Florideis curae posteriores. Part 1. Lipsiae [Leipzig]. pp VII + 724

Agardh JG (1890) Till algernes systematik. Nya bidrag. (Sjette afdelningen.) Lunds Universitets Års-Skrift, Andra Afdelningen, Kongl. Fysiografiska Sällskapets I Lund Handlingar, 26(3), pp 125, III pls

Barton ES (1893) A provisional list of the marine algae of the Cape of Good Hope. Journal of Botany **31**: 53–56, 81–84, 110–114, 138–144, 171–177, 202–210

Barton ES (1896) Cape algae. Journal of Botany **34**: 193–198, 458–461

Bird CJ, McLachlan J, De Oliveira EC (1986) *Gracilaria chilensis* sp. nov. (Rhodophyta, Gigartinales) from Pacific South America. Canadian Journal of Botany **64**: 2928–2934

Bolton JJ (1999) Seaweed systematics and diversity in South Africa: A historical account. Transactions of the Royal Society of South Africa **54**: 167–177

Bolton JJ, Anderson RJ (1990) Correlation between intertidal seaweed community composition and sea water temperature patterns on a geographical scale. Botanica Marina **33**: 447–457

Bolton JJ, Stegenga H (1990) The seaweeds of De Hoop Nature Reserve and their phytogeographical significance. South African Journal of Botany **56**: 233–238

Bolton JJ, Stegenga H (2002) Seaweed species diversity in South Africa. South African Journal of Marine Science **24**: 9–18

Børgesen F (1938) Contributions to a South Indian marine algal flora. III. Journal of the Indian Botanical Society **17**: 205–242

Børgesen F (1943) Some marine algae from Mauritius. III. Rhodophyceae. Part 2. Gelidiales, Cryptonemiales, Gigartinales. Kongelige Danske Videnskabernes Selekab, Biologiske Meddelelser 19(1), 85pp, 42 figs, 1 pl

Børgesen F (1950) Some marine algae from Mauritius. Additions to the parts previously published. II. Kongelige Danske Videnskabernes Selekab, Biologiske Meddelelser 18(11), pp 46, 22 figs

Branch GM, Griffiths CL, Branch ML, Beckley LE (1994) Two Oceans, A Guide to the Marine Life of Southern Africa. David Philip Publishers, Cape Town

Brown AC, Jarman N (1978) Coastal marine habitats. In: Werger MJA (ed) Biogeography and ecology of southern Africa. Monographiae Biologicae **31**: 1239–1277

Dawson EY (1949) Studies of northeast Pacific Gracilariaceae. Allan Hancock Foundation Publications Occasional Papers **7**: 1–105

Dawson EY (1954) Notes on tropical Pacific marine algae. Bulletin of the Southern California Academy of Sciences **53**: 1–7

Delf EM, Michell MR (1921) The Tyson collection of marine algae. Annals of the Bolus Herbarium **3**: 89–119

De Toni GB (1924) Sylloge algarum… Vol. VI. Florideae. Sectio V. Additamenta. Patavii (Padova). pp XI + 767

Dixon PS, Irvine LM (1977) Seaweeds of the British Isles. Vol. I (I) *Gigartinales*. British Museum (Natural History), London. pp xi + 252

Durairatnam M (1961) Contribution to the study of the marine algae of Ceylon. Fisheries Research Station, Ceylon, Bulletin 10, pp 181, including XXXII pls

Eyre J, Broekhuysen GJ, Crichton MI (1938) The South African intertidal zone and its relation to ocean currents VI. The East London district. Annals of the Natal Museum **9**: 83–112

Farrell EG, Critchley AT, Aken ME (1993) The intertidal algal flora of Isipingo Beach, Natal, South Africa, and its phycogeographical affinities. Helgoländer Meersunter **47**: 145–160

Fredericq S, Hommersand MH (1989a) Proposal of the Gracilariales ord. nov. (Rhodophyta) based on an analysis of the reproductive development of *Gracilaria verrucosa.* Journal of Phycology **25**: 213–227

Fredericq S, Hommersand MH (1989b) Comparative morphology and taxonomic status of *Gracilariopsis* (Gracilariales, Rhodophyta). Journal of Phycology **25**: 228–241

Fredericq S, Hommersand MH (1990a) Taxonomy of *Melanthalia obtusata* var. *abscissa* and its placement in the Gracilariales (Rhodophyta). Cryptogamie Botanie **2**: 4–11

Fredericq S, Hommersand MH (1990b) Diagnoses and key to the genera of the Gracilariaceae (Gracilariales, Rhodophyta). Hydrobiologia **204/205**: 173–178

Gmelin SG (1768) *Historia fucorum*. Academiae Scientarum, St Petersburg. xii + 239 + pp 6, 33 pls

Govender K (2001) Population Genetic Studies of Economically Important *Gracilaria* and *Gracilariopsis* (Rhodophyta) in the Southwestern Cape, South Africa. MSc Thesis, University of Cape Town, South Africa, 156pp

Greville RK (1830) Algae britannicae... Edinburgh. pp xxxviii + 218, XIX pls

Grunow A (1874) Algen der Fidschi-, Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe. Journal des Museums Godeffroy (Hamburg) **3**: 23–50

Gurgel CFD, Liao LM, Fredericq S, Hommersand MH (2003) Systematics of *Gracilariopsis* (Gracilariales, Rhodophyta) based on *rbc*L sequence analyses and morphological evidence. Journal of Phycology **39**: 154–171

Hering C (1841) Diagnoses algarum novarum a cl. Dre. Ferdinand Krauss in Africa Australi lectarum. Annals and Magazine of Natural History **8**: 90–92

Holmes EM (1894) New marine algae. Annals of Botany **8**: 335–342

Hommersand MH (1986) The biogeography of the South African marine red algae: A model. Botanica Marina **29**: 257–270

Hudson W (1762) Flora angelica… Nourse and Moran, London. pp viii + 506 + (22)

Isaac WE (1956) The ecology of *Gracilaria confervoides* (L.) Greville in South Africa with special reference to its ecology in the Saldanha-Langebaan Lagoon. In: Braarud T, Sorensen NA (eds) Proceedings of the Second International Seaweed Symposium, Trondheim, pp 173–185

Isaac WE (1957) Some marine algae from Xai-Xai. Journal of South African Botany **23**: 75–102

Isaac WE (1971) Marine botany of the Kenya coast 5. A third list of Kenya marine algae. Journal of the East Africa Natural History Society and National Museum **28**: 1–23

Iyer R (2002) Systematics of the Gracilariaceae (Rhodophyta) of Southern Africa. PhD Thesis, University of Cape Town, South Africa

Iyer R, Bolton JJ, Coyne VE (2005) Gracilarioid species (Gracilariaceae, Rhodophyta) occurring in southern Africa, with the description of *Gracilariopsis funicularis* sp. nov. African Journal of Marine Science (in press)

Jaasund E (1976) Intertidal Seaweeds in Tanzania. (Tromsø, Norway) University of Tromsø. pp (III +) 159, including 12 pls (= 23 photos bearing the species number), 288 figs (bearing the species number, omitting no. 165, 186, and 187)

Jaasund E (1977) Marine algae in Tanzania VII. Botanica Marina **20**: 415–425

Krauss F (1846) Pflanzen des Cap- und Natal-Landes, gesammelt und zusammengestellt von Dr. Ferdinand Krauss. (Schluss.) Flora **29**: 209–219

Kuntze O (1891) Revisio generum plantarum… Part 2. Leipzig. pp 375–1011

Kützing FT (1849) Species algarum. Lipsiae (Leipzig), pp 775–785

Kützing FT (1868) Tabulae phycologicae… Vol. 18. Nordhausen. pp (III +) 35, 100 pls

Kützing FT (1869) Tabulae phycologicae... Vol. 19. Nordhausen. pp IV + 36, 100 pls

Kylin H (1932) Die Florideenordnung Gigartinales. Lunds Universitets Årsskrift, Ny Följd, Andra Afdelningen **28**: 58–60

Lambert G, Steinke TD (1986) Rocky shore communities at Umdoni Park, Natal south coast. Transactions of the Royal Society of South Africa **46**: 51–67

MacNae W (1957) The ecology of the plants and animals in the intertidal regions of the Zwartkops River estuary near Port Elizabeth, South Africa, Part I. Journal of Ecology **45**: 113–131

Mazza A (1907) Saggio di algologia oceanica. Nuova Notarisia **18**: 133–142

Meneses I, Abbott LA (1987) *Gracilaria* and *Polycavernosa* (Rhodophyta) from Micronesia. Micronesica **20**: 187–200

Millard NAH, Harrison AD (1954) The ecology of South African estuaries. Part V. Richards Bay. Transactions of the Royal Society of South Africa **34**: 157–179, 2 figs (maps), pls V, VI; III tables

Nägeli C (1847) Die neueren Algensysteme und Versuch zur Begründung eines eigenen Systems der Algen und Florideen. Neue Denkshr. Allg. Schweiz. Ges. Naturwiss **9**: 1–275

Newton LM (1953) Marine algae. The John Murray Expedition 1933–34 Scientific Reports **9**: 395–420

Papenfuss GF (1940) Notes on South African marine algae. I. Botanisker Notiser **1940**: 200–226

Papenfuss GF (1943) Notes on South African marine algae. II. Journal of South African Botany **9**: 79–92

Papenfuss GF (1952) Notes on South African marine algae. III. Journal of South African Botany **17**: 167–178

Papenfuss GF (1967) Notes on algal nomenclature — V. Various Chlorophyceae and Rhodophyceae. Phykos **5**: 95–105

Parke M, Dixon PS (1976) Check-list of British Marine Algae. 3rd rev. Journal of the Marine Biological Association of the UK **56**: 527–594

Pocock MA (1958) Preliminary list on marine algae collected at Inhaca and on the neighbouring mainland. In: MacNae W, Kalk M (eds) A Natural History of Inhaca Island, Mocambique. Witwatersrand University Press, Johannesburg, pp 23–27

Reading RP, Schneider CW (1986) On the male coneptacles of two terete species of *Gracilaria* (Rhodophyta, Gigartinales) from North Carolina. Journal of Phycology **22**: 395–398

Reinbold T (1907) Die Meeresalgen der deutschen Tiefsee-Expedition 1898–1899. In: Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899. Vol. 2, part 2. Jena. pp 549–586, pls LV–LVIII

Ruprecht (1850) Algae ochotenses. Die ersten sicheren Nachrichten über die Tange des Ochotskischen Meeres. St. Petersburg, pp 243

Seagrief SC (1977) Seaweeds at Riet River. In: Thorpe C (ed) Tharfield: An Eastern Cape Farm. Express Litho Services, Port Elizabeth, pp 74–90

Seagrief SC (1980) Seaweeds of Maputaland. In: Bruton MN, Cooper KH (eds) Studies on the Ecology of Maputaland. Rhodes University and the Natal Branch of the Wildlife Society of Southern Africa, Durban, pp 18–41

Seagrief SC (1984) A catalogue of South African green, brown and red marine algae. Memoirs of the Botanical Survey of South Africa **47**: vi + pp 72

Seagrief SC (1988) Marine algae. In: Lubke RA, Gess FW, Bruton MN (eds) A Field Guide to the Eastern Cape Coast. Wildlife Society of Southern Africa, Grahamstown, pp 35–72

Silva PC (1996) Proposal to conserve the name *Asteronema* Delépine and Asensi (Phaeophyceae) against *Asteronema* Trevis. (Fungi). Taxon **45**: 123–124

Silva PC, Basson PW, Moe RL (1996) Catalogue of the benthic marine algae of the Indian Ocean. University of California Press, Berkeley

Silva PC, Meñez EG, Moe RL (1987) Catalog of the benthic marine algae of the Philippines. Smithsonian Contributions to the Marine Sciences 27. iv + pp 179, 2 figs, 1 table

Simons RH (1977a) The algal flora of Saldanha Bay. Transcript of the Royal Society of South Africa **42**: 462–482

Simons RH (1977b) Seaweeds of Southern Africa: Guide-lines for Their Study and Identification. Republic of South Africa, pp 37–55

Sonder OG (1871) Die algen des tropischen Australiens. Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben von dem Naturwissenschaftlichen Verein in Hamburg **5**: 33–74, VI pls

South GR, Tittley I (1986) A Checklist and Distributional Index of the Benthic Marine Algae of the North Atlantic Ocean. Huntsman Marine Laboratory and British Museum (Natural History), St Andrews

Stackhouse J (1797) Nereis britannica… xl + pp 112, XVII pls Bathoniae (Bath). Fasc. 2. pp ix–xxiv + 31–70, pls IX, 10, 11, XII

Stackhouse J (1802) Nereis britannica… fasc. 1 and 3. Hazard, Bath and White, London. pp viii + 30, pls 1–8 and pp xxv–xl + 71 + 112 + 4 + 3, pls 13–17, A–G

Stackhouse J (1809) Tentamen marino-cryptogamicum, ordinem novum, in genera et species distributum, in classe xxivta Linnaei sistens. Mémoires de la Société Impérialiste des Naturalistes de Moscou **2**: 50–97

Steentoft M, Irvine LM, Bird CJ (1991) (1015) Proposal to conserve the type of *Gracilaria*, nom. cons., as *G. compressa* and its lectofication (Rhodophyta: Gracilariaceae). Taxon **40**: 663–666

Steentoft M, Irvine LM, Farnham WF (1995) Two terete species of *Gracilaria* and *Gracilariopsis* (Gracilariales, Rhodophyta) in Britain. Phycologia **34**: 113–127

Stegenga H (1988) Notes on Ceramiaceae (Rhodophyta) from the eastern Cape Province, South Africa. I. New records and remarks on morphology. Blumea **33**: 371–393, 45 figs

Stegenga H, Bolton JJ, Anderson RJ (1997) Seaweeds of the South African west coast. Contributions from the Bolus Herbarium No. 8, University of Cape Town, 655pp

Stephenson TA (1948) The constitution of the intertidal fauna and flora of South Africa. Part III. Annals of the Natal Museum **11**: 207–324, pls XV, XVI

Turner D (1802) A Synopsis of the British Fuci. Yarmouth. pp xlvi + 400

Umamaheswara Rao M (1974) On the Gracilariaceae of the seas around India. Journal of the Marine Biological Association of India **14**: 671–696

Weber-van Bosse A (1928) Liste des algues du Siboga. IV. Rhodophyceae. Troisième partie. Gigartinales et Rhodymeniales et tableau de la distribution des Chlorophycées, Phaeophycées et Rhodophycées de l' Archipel Malaisien. Sibonga-Expeditie Monographie 59d. Leiden. pp 393–533, figs 143–213, pls XI–XVI

Withell AF, Millar AJK, Kraft GT (1994) Taxonomic studies of the genus *Gracilaria* (Gracilariales, Rhodophyta) from Australia. Australian Systematic Botany **7**: 281–352

Wynne MJ (1995) Benthic marine algae from the Seychelles collected during the R/V *Te Vega* Indian Ocean Expedition. Contributions of the University of Michigan Herbarium **20**: 261–346

Xia B (1986) On *Gracilaria salicornia* (C Agardh) Dawson. Chinese Journal of Oceanology and Limnology **4**: 100–107

Yamada Y (1938) Notes on some Japanese algae VIII. Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido University **2**: 119–130

Yamamoto H (1975) The relationship between *Gracilariopsis* and *Gracilaria* from Japan. Bulletin of the Faculty of Fisheries, Hokkaido University **26**: 217–222

Zhang J, Xia B (1984) Some problems in the taxonomy of the Chinese species of *Gracilaria* (Rhodophyta). Hydrobiologia **116/117**: 59–62

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