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

R Iyer1, O De Clerck2, JJ Bolton*1 and VE Coyne3

1 Department of Botany, University of Cape Town, Private Bag, Rondebosch 7701, South Africa
2 Research Group Phycology, Ghent University, Krijgslaan 281/S8, B-9000 Gent, Belgium
3 Department of Molecular and Cell Biology, University of Cape Town, Private Bag, Rondebosch 7701, South Africa

* Corresponding author, email: bolton@botzoo.uct.ac.za

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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 *Gracilaria*, 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: *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 19<sup>th</sup> and early 20<sup>th</sup> 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* (Forsk.) Bergesen forma *aeruginosa* (Turner) Bergesen, *G. millardeti* (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) Stentoft, 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 Gracilariaeae. 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 Gracilariaeae 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 Gracilariaeae 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 Technological Cooperation Project between the Flemish (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<sup>®</sup> 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 Diplan compound microscope or Leica Wild M10 stereo microscope.

**Gracilariaeae** 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 Hoemmersand 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 *Gracilarioipha* 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 Gracilariaeae**

1. a. Thallus terete ..............................................2
2. a. Thallus compressed to foliose .........................7
2. b. Axes beset with whorls of spiny protrusions occurring at regular intervals ..................1. *G. aculeata*
2. b. Axes lacking spiny protrusions ........................3
3. a. Thalli large, 15–120cm long, branches less than 2mm in diameter, lacking a holdfast, ..........4
3. b. Thalli small, up to 7cm high, holdfast present ....6
4. a. Traversing cells absent in cystocarp, spermatangia of the *chorda*-type ..............................5
4. 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. *G. funicularis*
5. 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*
6. b. Axes not constricted (except at the base of the side-branches), branching subdichotomously ..........3. *G. canaliculata*
7. a. Thalli large, up to 28cm long, axes foliose, usually more than 3cm wide ..................4. *G. capensis*
7. b. Thalli small to medium sized, usually smaller than 16cm, axes not exceeding a width of 2cm ........7
8. a. Margins of the thallus fimbriate ......................2. *G. beckeri*
8. 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 subdi-
chotomous 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 (cys-
tocarps) 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.

(Figure 1)
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.

References

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 (Lelaiter, 20.iii.1997, FL235); Durban, infralittoral fringe (Coppejans, 20.xi.95, HEC10979); Palm Beach, intertidal pools (De Clerck, 19.vii.1999, KZN820); Palm Beach, intertidal (De Clerck and Kandjengo, 21.xii.1999, KZN1502); Mission Rocks, sub-

tidal (De Clerck and Cocquyt, 17.vii.2000, KZN1741); Palm Beach, intertidal (De Clerck et al., 07.ii.2001, KZN2029).

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 branch-
es 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 pro-
trusions, 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 sub-surface 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 oositolate, 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 unconfined 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 sub-tropical 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’).


**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.1989, 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, 23.i.1893, BOL47338); Kowie, unknown (Becker, 26.xi.1895, BOL47339); Kowie, drift (De Clerck, 27.x.1999, KZN1259); Piano Rocks, infralittoral fringe (Stegenga, 23.x.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-
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 obtusatus as zonately divided. Hence the unification of Tyleiophora 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:
*Ceramianthemum crassum* (Harv. ex J Agardh) Kuntze 1891: 887.


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**

**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 unconstituted 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 enlarged, isodiametric to rectilinear cortical cells, up to 40µm long and 25µm in diameter; medulla up to 13 cells

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**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_ 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.


_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, SA1690); 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 33 cm in length, arising singly from a discoid holdfast. Stipe short, terete, to 1 cm 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 24 cm long, up to 7 cm 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 Graciliariaeae. 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)
Homotypic synonym: Sphaerococcus corticatus (J Agardh) Kütz., 1849: 783.


Holotype: LUND?

Type Locality
Sri Lanka

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.vii.1999, KZN740); Mabibi,
Habit (Figures 6b–f and 7d)
Thallus erect, up to 14cm in length, arising singly from a dis- coid 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 through-out 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.

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, linears and ramalinoides. Umanaheswara 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 linearinfolia 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 Seagrie'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 elucidate 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 denticles and crenations in G. vieillardii.

6. Gracilaria denticulata F Schmitz ex Mazza 1907
[1905–1918]: 138–139 (Figure 6)


Holotype: ?

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.vii.1999, KZNN12); Palm Beach, intertidal (De Clerck et al., 07.ii.2001, KZN2028); Sodwana Bay, intertidal (Coppejans et al., 09.vii.1999, KZN314); Sodwana Bay, subtidal (Coppejans et al., 09.vii.1999, KZN333); Trafalgar, intertidal pools (Coppejans et al., 20.vii.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.vii.1999, KZN6).
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); Kleimonde, 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.vii.1999, KZN730, female); Durban, infralittoral fringe (Coppejans et al., 03.vii.1999, KZN82.); Kosi Bay, intertidal pools (Coppejans et al., 16.viii.1999, KZN739); Mission Rocks, infralittoral fringe (De Clerck and Cocquyt, 17.vii.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. Density 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 distribution 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.


**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*.](image-url)
(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 (Ludertiz) and South Africa [St Helena Bay (Western Cape) to Algoa Bay (Eastern Cape)].

**Specimens examined**

**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, LAN11); 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.i.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, obvoid 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 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 Ludertiz (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.


**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);


**Habit**

Thallus erect, up to 8 cm 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 surrounding a large-celled medulla with cells of up to 150 µm 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: iii.

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.


**Corallopsis 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.


**Holotype**: LUND?

**Type Locality**


**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 6.5 cm long, occurring as solitary individuals. Irregularly discoid holdfast giving rise to one to two axes. Thallii 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
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 obipyramidal; 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. viellardii*, 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)


**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**

*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
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. longissima* 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-
ers, columnar to spherical, up to 32 µm long and 18 µm in diameter. Medulla in this region 5–7 cells wide, cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 400 µm long and 260 µm in diameter. Crystalline, proteinaceous crystals present in medullary and subcortical cells; up to 8 per cell; generally columnar, some elongately pentagonal; up to 17 µm long and 13 µm wide. Medulla of slender thalli (especially De Mond specimens) dominated by 4–6 large medullary cells; cortex and subcortical cells; up to 8 per cell; generally columnar, some columnar to spherical, up to 32 µm long and 18 µm in diameter. Medulla in this region 5–7 cells wide, cells lightly staining, polygonal to spherical, increasing in size towards the centre, up to 400 µm long and 260 µm in diameter. Crystalline, proteinaceous crystals present in medullary and subcortical cells; up to 8 per cell; generally columnar, some elongately pentagonal; up to 17 µm long and 13 µm 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.

**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 graciarioid species. However, the morphology and anatomy of *G. gracilis, G. 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 Graciariaceae 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, Seagriff 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* (Bergesen 1938, Durairatnam 1961, Jaasund 1977) and *Gracilaria millardetii* (Isaac 1957). Furthermore, Bergesen (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. Seagriff’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 nec-
essay 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. milliaretii from G. protea in Mauritius.

Thalli from Simonstown were identified by Stegenga et al. (1997) as Gs. lemnaniformis 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 Gracilariaopsis 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. corticea, whereas Kenton serves as the cut-off point for temperate gracilaroids (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. vieillardi 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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