*Bothalia*. 9, 1: 153–156.

# The Genus Ceramium in South Africa

*by*

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## Abstract

A revision of the genus *Ceramium* in South Africa has been undertaken. The morphology of the genus is discussed, and a key to the ten species which are recognised is provided. The following new taxa and new combinations are published: *Ceramium* **arenarium,** *C.* **papenfussianum,** *C. diaphanum* (Lightf.) Roth var. **capense,** —var. **pulchellum** (Kuetz.) (*Hormoceras pulchellum* Kuetz.), *C.* **centroceratiforme.**

*Ceramium capense* Kuetz., which was transferred to *Microcladia* by Papenfuss, is regarded as belonging to *Ceramium*.


## Introduction

### *The Delimitation of* Ceramium *and Allied Genera*

The genus *Ceramium* (family: Ceramiaceae), although used in a restricted sense for over one hundred years, is still not fully understood. Dixon (1960) studied the British forms recently and his observations together with those of Feldmann-Mazoyer (1940) are detailed and informative. But certain problems, some highlighted by South African forms, remain and, although the present author has attempted to resolve some of them, it cannot yet be claimed that the genus *Ceramium* is satisfactorily delimited.

One of these problems concerns the attachment of tetrasporangia. According to Dixon (1960), and some other authors, they arise from unspecified cells of the cortex. The inference is that any cortical cell may act as the supporting cell of a tetrasporangium. The present author was able to trace the origin of many tetrasporangia in five out of the ten species listed in this paper. In every case they were attached to pericentral cells. No other supporting cell was indicated. Where the actual derivation was not directly observable the tetrasporangia always occupied positions such that attachment to the pericentrals was not only feasible but highly likely. If this derivation is as constant as the present author suggests it might be then it must be regarded as of fundamental importance and any interpretation of *Ceramium* should take it into account. Obviously more information is required on this subject before its value can be properly assessed.

The occurrence in South Africa of *Ceramium centroceratiforme* Simons, sp. nov., raises the second problem dealt with here, namely, that of the status of the genus *Centroceras* Kuetz. From time to time species such as this one have been described which link *Ceramium* and *Centroceras*, and opinions have been divided as to their autonomy. Most authors have accepted them as different although some have done so without much conviction. The tendency of *Ceramium centroceratiforme* Simons to have an orderly arrangement of cortical cells but at the same time to have distinct genicules somewhere along its length puzzled the author because the species appeared to belong to both genera equally well. A solution seemed to be to regard *Centroceras* as synonymous with *Ceramium* as some other authors have done. It was decided instead to make a closer study of the South African form of *Centroceras clavulatum* (Ag.) Mont., the type species of *Centroceras*, to discover whether there was any justification for its separation from *Ceramium*. Certain facts emerged from this investigation which the writer regards as notable.

First, in *C. clavulatum* the regular arrangement of basipetal secondary cortical cells in a single layer is the result of their exclusively transverse segmentation. The resultant cortical files of any single articulation develop equally by what appears to be simultaneous segmentation of their apical cells. In species of *Ceramium*, on the other hand, there is no notable regularity of segmentation of cortical cells either in time or space: apical cells of the laterals of limited growth divide transversely, longitudinally and obliquely. Secondly, in *C. clavulatum* acropetal development of cortex is virtually absent; instead there is almost radial development to form a girdle of tissue raised slightly from the surface of the thallus at every node. As a result of this, all genicules retain their individuality and there is no confluence of cortical tissue from adjacent axial cells. In contrast to this, completely corticated species of *Ceramium* have a tissue which is continuous between successive nodes. Thirdly, in male plants of *C. clavulatum*, spermatangia were found confined to the terminal part of each fertile articulation, i.e. on the radially developed girdle of tissue at each node.

South African species of *Ceramium* bearing spermatangia have not been found by the writer, but Dixon (1960) and others have reported on various other species in which they found spermatangia scattered haphazardly over the surface of the cortex. Of the characteristics of *Centroceras* listed above, the most significant seems to be that relating to the development of the basipetal cortex of each articulation. The contrast of the latter with what occurs in species of *Ceramium* is sufficient, in the present author's opinion, to justify the separate generic status of *Centroceras* Kuetz., as typified by *C. clavulatum* (Ag.) Mont. The other differences seem to corroborate this view. As to the affinities of *C. centroceratiforme* Simons: its cortical development is like that of species of *Ceramium*, to which genus it, therefore, undoubtedly belongs.

A third problem has resulted from the recognition by Papenfuss (1940) of South African material as a species of *Microcladia*. The main reason for doing this seems to have been a well developed multi-layered cortex. Feldmann-Mazoyer (1940), writing of *Microcladia*, claimed that the genus was little understood and contained unrelated species. She suggested that the only justification for removing *M. glandulosa* (Soland.) Grev. to a separate genus was its unique arrangement of cells of different sizes in the innermost layer of the cortex. The latter characteristic leads to a flattened bilateral thallus. The present author's study of *Microcladia capensis* (Kuetz.) Papenf., the South African species referred to above, revealed that the thallus is not bilateral nor does it possess any other characteristic to exclude it from *Ceramium*. This species is dealt with in this paper as *C. capense* Kuetz.*

*Some Morphological Features of South African Species of* Ceramium

Commenting on the glandular cells so often found in species of *Ceramium*, Dixon (1960) stated that these cells are rather short-lived. It is interesting to note, therefore, that similar cells in one or two South African species are sometimes very persistent. In *C. glanduliferum* Kylin, for example, they are often obtrusive and so long-lived that the specific epithet was suggested by their presence. Glandular cells in *C. papenfussianum* Simons, sp. nov., were found to be almost as persistent but not nearly so obvious as those of the previous species.

* Since writing this article the author has seen the paper by Max Hommersand on the "Morphology and Classification of some Ceramiaceae and Rhodomelaceae" (University of California Publications in Botany Vol. 35, No. 2, pp. 165–366, published in 1963). In this paper Hommersand discusses the genera *Ceramium*, *Microcladia* and *Centroceras*; he upholds the separate status of these three.

*Microcladia* produces upwardly and outwardly directed cortical filaments only which entirely enclose the axial cells. This interpretation makes no mention of bilateral symmetry but does not affect my placing of *C. capense* in the genus *Ceramium*.

Hommersand's observations on the derivation of cortical filaments in *Centroceras* are essentially similar to mine and are apparently sufficient reason for a generic separation.

*Ceramium poeppigiana* Grunow, removed to the genus *Rheinboldiella* and not considered in my paper, is returned by Hommersand to the genus *Ceramium*.

Several South African species have extremely thick-walled axial cells. The mature axial cells of *C. papenfussianum* Simons (Fig. 2: 1c), for instance, have such thick lamellate walls that the central lacunae are very narrow. The thickening appears to develop centripetally in clearly demarcated layers on the inner faces of the cell walls, and the result is a likeness to the annual rings of higher plants. This characterictic no doubt leads to the comparative rigidity of these diaphanous plants.

Intercellular hyphae ramifying within the cortex of *C. planum* Kuetz. have been seen in no other South African species. Their presence adds greatly to the girth of an already thick cortex in the mature parts and renders the thallus very cartilaginous and difficult to dissect when fresh. The origin of these hyphal filaments was not traced, but they appeared sometimes to arise from a cingula-like thread of similar material encircling a median constriction of an axial cell. Attachment of this cingula to the axial cell was at times evident. Perhaps this species belongs to *Campylaephora.*

Intracellular hyphae (*Thylles* of Feldmann-Mazoyer, 1940), such as those described by Dixon (1960), have possibly been seen in only one South African species. However, they were not entirely convincing.

*Terminology of Morphological Features*

The joints between adjacent axial cells are called *nodes.* The cortex consists of, primarily, the *pericentral cells* differentiated at the distal end of every axial cell, and, secondarily, the *laterals of limited growth* remaining closely appressed to the axial cells. The laterals of limited growth arise by segmentation of apical cells cut off acro- and basi-petally from the pericentrals. A cortical zone of common origin is referred to as a *genicule* and uncorticated zones are *intergenicules.* Unless otherwise mentioned, *length* is the dimension in the plane of the long axis of the plant, and *width* is measured at right angles to this.

## CERAMIUM

**Ceramium** *Roth* in Cat. Bot. 1: 148 (1797).
*Dictiderma* Bonnemaison (1822).
*Hormoceras* Kuetz. (1841).
*Gongroceras* Kuetz. (1841).
*Echinoceras* Kuetz. (1841).
*Acanthoceras* Kuetz. (1841).
*Chaetoceras* Kuetz. (1847), non *Chaetoceros* Ehr. (1844), nec *Chaetoceras* Kuetz. (1849).
*Trichoceras* Kuetz. (1849).
*Celeceras* Kuetz. (1849).
*Pteroceras* Kuetz. (1849).
*Ceramothamnion* Richards (1901).

Plants of pseudodichotomously or irregularly branched uniaxial filaments, partly or completely corticated by closely appressed cells in one or more layers, radially symmetrical in transverse section, cells of inner layers larger than those of outer, arising as laterals of limited growth from pericentrals, and cut off acro- and basi-petally by random segmentation. *Pericentrals* attached to, and forming a ring around the distal end of every axial cell. *Tetrasporangia* immersed in or exserted from cortex in vicinity of nodes. *Cystocarps* naked, subtended by one or more involucral branches. *Spermatangia* scattered over surface of cortex (not seen in South African species).

Without any implication as to primitiveness or derivation, the species listed here are arranged in a series decided, primarily, by the extent of tetrasporangial immersion in the cortex and, secondarily, by the degree of cortication.

Genicules distinct in lower part of plant:
Intergenicules below equal to or longer than genicules:
Tetrasporangia unilateral or whorled, exserted........................ 1. *C. glanduliferum*
Tetrasporangia whorled, partly or entirely immersed:
Tetrasporangia immersed partly:
Pericentrals at bases of genicules.................................... 3. *C. tenerrimum*
Pericentrals median in genicules; genicules contiguous in upper part of filaments 4. *C. arenarium*
Tetrasporangia immersed entirely:
Tetrasporangia patent through outer cortex; pericentrals frequently exposed and cortical cells often transversely elongated............................ 5. *C. papenfussianum*
Tetrasporangia not visible through outer cortex; pericentrals also occluded:
Plants flaccid, branches ultimately incurved strongly...... 7 (*a*) *C. diaphanum* var. *capense*
Plants setaceous, ultimately branches almost straight; apical cells patent 7 (*b*) *C. diaphanum* var. *pulchellum*
Intergenicules all shorter than genicules:
Cortical cells randomly disposed...................................... 6. *C. atrorubescens*
Cortical cells somewhat ordered into longitudinal and transverse rows in lower parts of genicules................................................... 9. *C. centroceratiforme*

Genicules not distinct in lower parts of plant:
Genicules distinct above; branch apices digitate................................ 2. *C. planum*
Genicules nowhere distinct:
Branching more or less alternate:
Branching pinnate, racemo-corymbose........................................ 2. *C. planum*
Branching pseudodichotomous, alternate; adventitious branches frequently secund 10. *C. obsoletum*
Branching on all sides, profuse............................................. 8. *C. capense*

1. **C. glanduliferum** *Kylin* in Lunds Univ. Arsskr. N.F. Avd. 2, 34, 8: 14, fig. 7A–B (1938).

*Holdfast*: prostrate filaments with distinct but weakly developed genicules of one half or one third the length of intergenicules; genicules often with single whorl of large terminal, exserted glandular cells; rhizoids numerous at nodes. *Erect system*: filaments up to 1·5 cm high, pseudodichotomously branched, adventitious branches rare, 180 $\mu$ wide at base tapering gradually to about 60 $\mu$ terminally with slightly incurved apices; axial cells up to one-and-a-half times longer than broad; genicules shortly separated above but widely so below, often up to twice as wide as long, sometimes even shorter and then pericentrals often at bases, cells angular minute (about $10\,\mu \times 5\,\mu$) most often with much larger and very conspicuous ovate (up to $30\,\mu \times 18\,\mu$), exserted glandular cells in an apical whorl; number of pericentrals variable, up to nine, often superficially visible through the cortex, more or less spherical; tetrasporangia totally exserted, mostly unilateral on inner faces of upper dichotomies; cystocarps not seen. PLATE 1: 1.

CAPE.—Mossel Bay: Tergniet, *Simons* 634. Knysna: Beacon Isle, *Isaac* B.942. East London: *Ecol. Surv.** L66. Willowvale: Dwessa, *Isaac* B. 1013. Elliotdale: Bomvanaland, *Flanagan* s.n. (*Tyson* s.n. sub BOL 27476).

NATAL.—Durban: *Ecol. Surv.* D. 100.

Typically, this species is readily identifiable by its conspicuous glandular cells but, when the latter are absent, it is not easily recognisable. The variable position of the pericentrals in the genicules, however, is a fairly reliable characteristic.

* The abbreviation "*Ecol. Surv.*" used in citations throughout this paper refers to material in the University of Cape Town collection from the ecological survey of marine, littoral fauna and flora of South Africa. This survey was directed during the period 1931–1940 by Prof. T. A. Stephenson and is now being continued under the guidance of Prof. J. H. Day, both Professors acting in their capacities as Head of the Department of Zoology, Cape Town University.

2. **C. planum** *Kuetz.* in Sp. Alg. 687 (1849); Tab. Phyc. 13: 5, pl. 11, fig. c–d (1863); Papenf. in J. S. Afr. Bot. 17: 177 (1952).

*C. cancellatum* Ag. in Syst. Alg. 136 (1824); Sp. Alg. 2: 145 (1828), non *C. cancellatum* (L.) DC. in Bull. Sci. Soc. Philom. Paris 3, 94: 264 (1804–1805). *C. flexuosum* (Kuetz.) Grunow in Alg. Nov. 64 (1867), non *C. flexuosum* Ag. in Syst. Alg. 141 (1824).

*Pteroceras cancellatum* (Ag.) Kuetz. in Sp. Alg. 690 (1849); Tab. Phyc. 13: 8, pl. 22, fig. a–b (1863). *P. flexuosum* Kuetz. in Sp. Alg. 690 (1849); Tab. Phyc. 13: 8, pl. 22, fig. c–e (1863).

*Holdfast*: short haustorium-like rhizoids produced at base of erect filaments attach plants to others. *Erect system*: up to 15 cm high, terete, about ½ mm wide; branching almost alternate and more or less distichous, racemo-corymbose; cortication either complete or interrupted in upper parts, multi-layered below, large-celled inner layer often with intercellular ramifying hyphae; pericentrals six, almost spherical; tetrasporangia exserted, frequently bilateral, or hemicyclic, attached to pericentrals; cystocarps surrounded by five or six involucral branches. PLATE 1: 2.

CAPE.—Namaqualand: Port Nolloth, *Simons* 273; 331; *Ecol. Surv.* N. 19; *Strong* s.n. (*Tyson* s.n. sub BOL 27435); *Tyson* s.n. sub BOL 27431; Buffels River, *Ecol. Surv.* BR2H. Clanwilliam: Lamberts Bay, *Ecol. Surv.* B50. Malmesbury: Steenberg's Cove, *Ecol. Surv.* C4E; Saldanha Bay, *Simons* 594; Dassen Island, *Tyson* s.n. sub BOL 27429. Peninsula: Table Bay, *Tyson* s.n. sub BOL 27422 to 27428 incl., 27433, 27434, 27436, to 27448 incl.; Oudekraal, *Ecol. Surv.* A13; Kommetjie, *Simons* 25; False Bay, *Ecol. Surve.* F.115 in part sub *Simons* 655.

The numerous pinnate branches, arranged more or less distichously on the main filaments, make this plant unique amongst the South African *Ceramium* species, separating it clearly from *C. capense* Kuetz. especially. These two species have cortices which at times are almost indistinguishable superficially. In longitudinal section their thalli can be distinguished because the inner cells of *C. capense* are all more or less elongated longitudinally whereas those of *C. planum* are more polygonal, those in the middle of an articulation being more or less ovate and orientated so that their long axes are radial to the adjacent axial cell. The ramifying hyphae present in *C. planum* have not been seen in *C. capense*.

3. **C. tenerrimum** (*Mart.*) *Okam.* in Icon. Jap. Alg. 4: 112, pl. 179 fig. 1–7 (1921); Feldmann-Mazoyer in Céramiacées de la Méditerranée 289 (1940).

*Hormoceras tenerrimum* Mart. in Preuss. Exped. ost-Asien, Bot. Teil: Tange: 146, pl. 13, fig. 2 (1866).

*Holdfast*: prostrate lower parts of erect filaments with distinct very short genicules; numerous rhizoids attach plant to rock or other algae. *Erect system*: up to 2 cm high and 200 $\mu$ thick, branching pseudodichotomous, ultimate branches inrolled; adventitious branches occasional; genicules distinct throughout, short, up to three times wider than long; pericentrals up to seven at bases of genicules; glandular cells present, inconspicuous; tetrasporangia in single whorls on genicules of penultimate branches, apically exserted, attached to pericentrals; cystocarps of three or four gonimolobes subtended by about five branches up to five times longer than height of gonimolobes. Fig. 1: 1; PLATE 1: 3.

CAPE.—Namaqualand: Port Nolloth, *Simons* 303; Hondeklip Bay, *Ecol. Surv.* HB5B; Groen River, *Ecol. Surv.* GR4F. Clanwilliam: Lamberts Bay, *Ecol. Surv.* B70. Malmesbury: Ysterfontein, *Ecol. Surv.* YZ1F. Caledon: Hermanus, *Simons* 539; 540; Franskraal, Simons 647. Knysna: Robberg, *Isaac* B. 788.

Although present among the older collections, this species was overlooked by other workers. The specimens cited here compare well with one from the Mediterranean supplied to the present author by Mme Feldmann. The most striking thing about this species, compared with other South African species, is the basal position of the pericentrals in almost every genicule. Cell rows initiated basipetally seldom project below the bases of their pericentrals and are generally only one cell long.

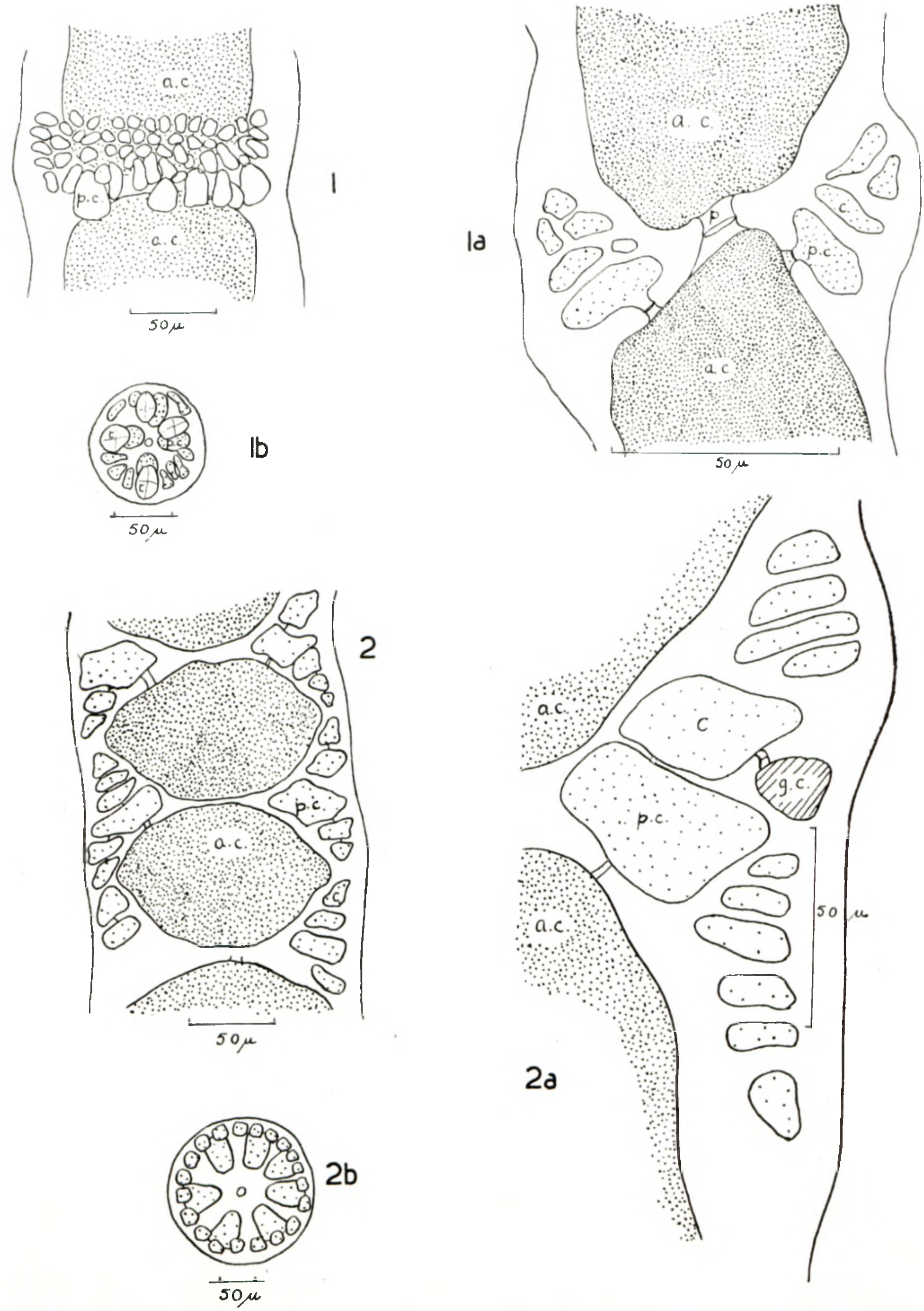


FIG. 1.—1, *Ceramium tenerrimum*, surface view of a genicule; 1a, longitudinal section through a genicule; 1b, transverse section through the pericentrals of a tetrasporiferous genicule 2, *C. arenarium*, longitudinal section through thallus near the apex of a branch; 2a, longitudinal section through a genicule of the mature portion of a thallus; 2b, transverse section through the pericentrals of a genicule.

a.c.—axial cell; c.—cortical cell; g.c.—glandular cell; p.—pit connection; p.c.—pericentral cell; t.—tetrasporangium.

Besides Japan, the Mediterranean and the Cape, there appears to be only one other recorded locality for this species, viz. N. Pacific (Dawson, 1962, p. 49). Such disjunctions seem strange and it is probable that *C. tenerrimum* will be found elsewhere.

4. **C. arenarium** *Simons*, sp. nov.

Thallus usque ad 3 cm altus, pileum formans, inferne circa 150 μ latus pro parte repens cum rhizoidibus multis ex geniculis excurrentibus, sursum quoque ramorum gradatim gracilior; rami ultimi circinati; genicula superne contigua, inferne multo distincta intergeniculis quam genicula triplo longioribus; cellulae pericentrales c. 7 cellulis corticalibus occlusae, plus minusve in medio geniculorum dispositae; tetrasporangia in ramulis superioribus monoverticillata dimidio superiore exserto; cystocarpia subapicalia, geminata ramulis nunc paucis nunc saepius quinque vel sex incurvatis involucrata. Fig. 1: 2; Plate 1: 4.

Type: Namaqualand, Port Nolloth, *Isaac* B.676 sub *Simons* 632 (PRE, holo., spirit material only).

*Holdfast*: prostrate basal filaments with many rhizoids at each genicule entwining neighbouring filaments and attaching plant to substratum; genicules distinct, half as long as wide; intergenicules up to four times longer but of same width as genicules. *Erect system*: up to 3 cm high, filaments dichotomously branched, frequently producing adventitious branches in the axils in a plane at right angles to dichotomies, 150 μ thick or more, narrowing slightly at each dichotomy to about 100 μ subapically, ultimately circinately inrolled; pericentrals about seven completely obscured in the mature parts, more or less median in genicule; genicules contiguous in upper half of filaments, separated below and then about one-and-a-half times wider than long, intergenicules becoming progressively longer abapically until about three times longer than genicules; tetrasporangia in a whorl at each of the upper genicules, upper half exserted when mature; cystocarps subapical, two gonimolobes, involucral branches up to six, sometimes absent.

South West Africa.—Luderitz, *Simons* 432.

Cape.—Namaqualand: Port Nolloth, *Isaac* B. 662; B. 676; *Simons* 632. Clanwilliam: Lamberts Bay, *Ecol. Surv.* B. 13. Peninsula: Table Bay, *Simons* 117.

The characteristic circinate apices, the contiguous genicules above and the more or less median pericentrals separate this species from *C. tenerrimum* (Mart.) Okam. with which it shares the habit of partially exserted tetrasporangia. The epithet chosen for this species is suggested by its sandy habitat amongst other low-growing turf-forming algae.

Transverse sections of axial cells frequently showed thick-walled cellular inclusions. Their true shape could not be deduced nor could their origin because longitudinal sections provided no evidence of their presence. There appeared to be seven such bodies circular in outline and closely appressed to the inner wall of the axial cells in which they were seen. Their diameter was approximately equal to half the greatest dimension of the pericentrals. It is possible that these structures may be similar to the intracellular filaments referred to by Dixon (1960, p. 338) and Feldmann-Mazoyer (1940, p. 161).

5. **C. papenfussianum** *Simons*, sp. nov.

*C. pulchellum* sensu Kylin in Lunds. Univ. Arsskr. N.F.Avd.2, 34, 8: 14 fig. 7C–E (1938); non *Hormoceras pulchellum* Kuetz. (=*C. diaphanum* var. *pulchellum* (Kuetz.) Simons, comb. et stat. nov., see p. 162).

Plantae parvae usque ad 2·5 cm altae, in aliis algis habitae, ramosissimae paene fastigiatae, ramis supra hamatis; genicula usque ad 150 $\mu$ lata, omnibus praeter terminalia distinctis; cellulae pericentrales plerumque 6 patentes; cellulae corticales angulatae, basi-petalibus praecipue in geniculis superioribus saepe transverse elongatis; tetrasporangia monoverticillata, immersa, patenti; cystocarpia ramulis 5 vel 6 involucrata. Fig. 2: PLATE 2: 1.

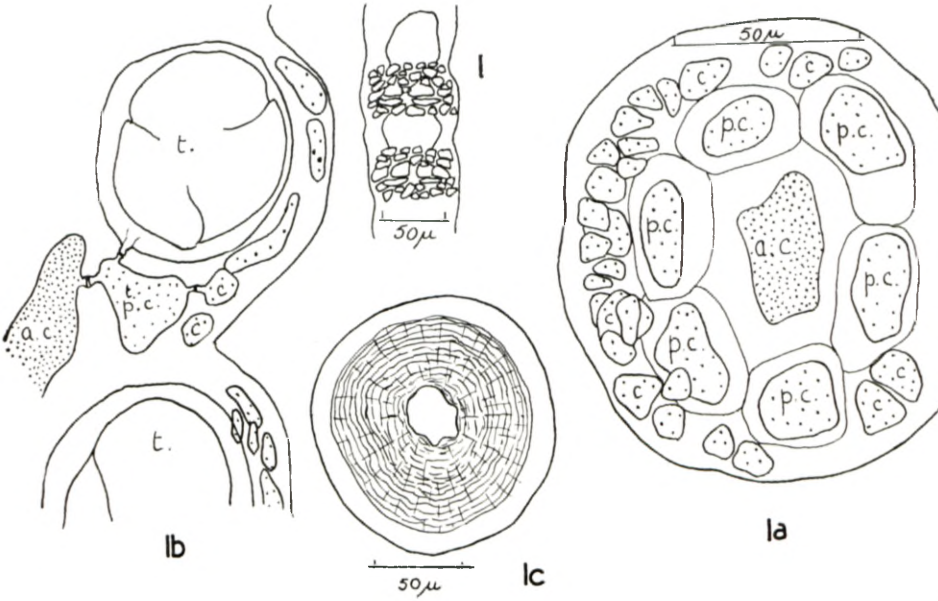


FIG. 2.—1, *Ceramium papenfussianum*, surface view of two genicules; 1a, transverse section through the pericentrals of a mature genicule; 1b, longitudinal section through a tetrasporiferous genicule showing attachment of tetrasporangium to pericentral cell; 1c, transverse section through intergenicule showing curious wall thickening.

a.c.—axial cell; c.—cortical cell; p.c.—pericentral cell; t.—tetrasporangium; t.p.c.—tetrasporiferous pericentral cell.

Type: Peninsula, Sea Point, *Simons* 694 (PRE, holo.; iso. in spirit collection).

*Holdfast*: prostrate lower filaments with widely spaced genicules from which numerous rhizoids arise to attach plant to others. *Erect system*: filaments up to 3 cm high, branching pseudodichotomous, almost fastigiate, terminal branches more or less straight but hooked inwards at the tips; adventitious branches absent; genicules distinct except terminally, widely separated below, about as wide as long; intergenicules up to four times longer than wide; pericentrals usually six, median in genicules, often clearly visible between outer smaller cortical cells; cortical cells angled, basipetal cells frequently transversely elongated especially in upper genicules; glandular cells sometimes conspicuous as an apical whorl on genicules, distinctly angled, and of same size as other cortical cells; tetrasporangia whorled, subapical, immersed but patent, as high as parent genicules, attached to pericentrals; cystocarps surrounded by five or six involucral branches up to twice as high as gonimolobes.

CAPE.—Namaqualand: Port Nolloth, *Simons* 275; 302. Malmesbury: Paternoster, *Simons* 482; *Ecol. Surv.* P10A; Saldanha Bay, *Simons* 571; 572; 576; 581; 586; 587; 597; 609; 611; 619. Peninsula: Sea Point, *Simons* 694; *Levyns* 0170 (*Tyson* s.n. sub BOL 27470); St. James (False Bay), *Ecol. Surv.* F115. Caledon: Hermanus, *Simons* 538; 541; 542; 545. Mossel Bay: Tergniet, *Isaac* B. 949; B. 950. Knysna: Robberg, *Isaac* B. 806. Port Elizabeth, *Ecol. Surv.* E75. East London, *Ecol. Surv.* L66. Komga: Cape Morgan, *Flanagan* 111 (*Tyson* s.n. sub BOL 27471). Port St. Johns, *Isaac* B. 834. Locality not stated: *Flanagan* s.n. (*Tyson* s.n. sub BOL 27460–27463 incl.). Collector unknown (*Tyson* s.n. sub BOL 27467; 27468).

*C. papenfussianum* is common on both the west and south coasts of the Cape. The occurrence of the transversely elongated cortical cells caused earlier workers to assign this species to *C. gracillimum* Griff. et Harv., but these two species differ in the positions of their tetrasporangia, those of *C. papenfussianum* being immersed while those of *C. gracillimum* are exserted. A more recent confusion has been that of Kylin (1938) who misidentified this species as *Hormoceras pulchellum* Kuetz. The following characteristics of *H. pulchellum* Kuetz. can be deduced from Kützing's (1849, 1862) description and/or figures: first, the patent and somewhat diverging apical cells; secondly, the completely obscured pericentral cells; thirdly, the presence of many and often opposite adventitious branches. None of these characteristics is possessed by *C. papenfussianum*.

J. G. Agardh (1851) assigned *H. pulchellum* Kuetz. to *Ceramium diaphanum* (Lightf.) Roth because he could find no essential difference between the two. The present author agrees with Agardh to the point of including *H. pulchellum* Kuetz. in the species *C. diaphanum* (Lightf.) Roth, but considers it sufficiently different from the typical form to be treated as a separate variety. In this paper *H. pulchellum* Kuetz. is placed as *C. diaphanum* var. *pulchellum* (Kuetz.) Simons, comb. et. stat. nov. (p. 162).

The presence of the ring of glandular cells sometimes seen girdling the upper margin of the genicules of *C. papenfussianum* might confuse the observer but, unlike the relatively large ovate glandular cells of *C. glanduliferum* Kylin, those of this species are angled and no bigger than normal cortical cells.

The specific epithet for this species was chosen in honour of Prof. G. F. Papenfuss, who has contributed so much to the knowledge of South African marine algae.

6. **C. atrorubescens** *Kylin* in Lunds Univ. Arsskr. N.F. Avd. 2, 34, 8: 15, fig. 7F (1938).

*Holdfast*: prostrate lower parts of filaments with numerous rhizoids arising from narrowly separated genicules. *Erect system*: up to about 3 cm high and 500 $\mu$ thick below, narrowing upwards to about 100 $\mu$: branching pseudodichotomous, adventitious branches at right angles in dichotomies, often opposite; branches ultimately somewhat incurved; genicules variable in length, somewhat wider than long and scarcely separated above, up to one-and-a-half times longer than wide with intergenicules varying greatly in length below, acropetal development of cortex greater than basipetal, upper margin of genicule undefined; pericentrals more than eight, superficially scarcely visible; tetrasporangia immersed, patent, in a single whorl on every genicule throughout almost entire length of erect filaments; cystocarps subapical, subtended by four or five involucral branches somewhat longer than height of gonimolobes. PLATE 1: 5.

SOUTH WEST AFRICA.—Swakopmund, *Simons* 641; " Walfisch Bay ", *Cleverly* s.n. (*Tyson* s.n. sub BOL 27473; 27474); Luderitz, *Simons* 417; *Isaac* B. 754.

CAPE.—Namaqualand: Port Nolloth, *Ecol. Surv.* N42.

This species has a superficial resemblance to *C. circinatum* (Kuetz.) J. Ag., but its genicules are, as it were, inverted. It is also very like *C. arenarium* Simons, sp. nov. The chief difference between *C. arenarium* and *C. atrorubescens* is that the first has genicules in which the pericentrals are always median, whereas those of *C. atrorubescens* seldom are. Other differences between them are the circinate tips, the continuous cortex above, the often half-exserted tetrasporangia and the production of rhizoids for the greater length of the filaments of *C. arenarium*, all of which characteristics contrast with their counterparts in *C. atrorubescens*.

7. **C. diaphanum** (*Lightf.*) *Roth* in Cat. Bot. 3: 154 (1806); Feldman-Mazoyer in Céramiacées de la Méditerranée 306 (1940).

*Holdfast*: prostrate filaments with distinct genicules from which many rhizoids arise; litho- or epi-phyte. *Erect system*: genicules distinct throughout, often wider than intergenicules; seven pericentrals completely obscured by outer cortical tissue of large and small cells; tetrasporangia immersed, often inconspicuous; cystocarps subapical, subtended by involucral branches.

(*a*) var. **capense** *Simons*, var. nov. PLATE 1: 6.

A var. *typico* Feldmann-Mazoyer (1940), tetrasporangiis plus minusve geniculorum maturorum dimidio superiori circumscriptis, ramis ultimis valde incurvatis differt.

Type: Hopefield, Schaapen Island (Saldanha Bay), *Simons* 614 (PRE, holo., spirit collection only).

Differs from var. *typicum* Feldmann-Mazoyer (1940) by its tetrasporangia being more or less confined to upper half of mature genicules and its strongly incurved branch apices.

*Holdfast*: prostrate filaments with distinct genicules; numerous rhizoids from genicules attach plant to substratum. *Erect system*: up to 5 cm high, intergenicules about 250 $\mu$ thick in lower parts; genicules tumescent in lower parts, as much as 450 $\mu$ wide medianly and equally high, becoming relatively less swollen distally and ultimately scarcely wider than the intergenicules at about 50 $\mu$; branching mainly pseudodichotomous but adventitious branches common, branches ultimately strongly incurved; tetrasporangia immersed and obscured in upper halves of mature genicules; cystocarps not seen.

Known only from the single record cited above. This plant, like var. *pulchellum* (Kuetz.) Simons, stat. nov., shows an arrangement of cortical cells essentially similar to that described and figured for *C. diaphanum* (Lightf.) Roth by Feldmann-Mazoyer (1940). The other shared characteristics of seven pericentrals and immersed tetrasporangia have convinced the present author that it should be assigned to *C. diaphanum*. Many varieties of this species have been recognised and these two (var. *capense* and var. *pulchellum*) are sufficiently different from other varieties and from each other to deserve separate varietal rank. These two differ from each other mainly in texture and in the shapes of their ultimate branches.

(*b*) var. **pulchellum** (*Kuetz*) *Simons*, comb. et stat. nov.

*Hormoceras pulchellum* Kuetz. in Sp. Alg. 676 (1849); Tab. Phyc. 12: 23, pl. 75, fig. d–i (1862).

*Ceramium pulchellum* (Kuetz.) Kylin in Lunds Univ. Arsskr. N.F. Avd. 2, 34, 8: 14, fig. 7C–E (1938).

*Holdfast*: plant epiphytic with basal haustorial attachment and prostrate filaments provided with rhizoids at genicules which are distinct and somewhat swollen. *Erect system*: filaments up to 7 cm high, about 400 $\mu$ below tapering ultimately to patent relatively large apical cells about 10 $\mu$ wide, much branched both pseudodichotomously and adventitiously; adventitious branches arising from genicules singly, oppositely or in occasional whorls, strongly divergent at first but soon becoming parallel with the parent axis, branched, all tapering upwards and downwards; ultimate dichotomies slightly incurved but apical cells remaining patent; genicules distinct throughout with intergenicules about as long as genicules; tetrasporangia immersed in whorls in penultimate and older branches; cystocarps surrounded by between three and six involucral branches somewhat longer than the height of the gonimolobes. Fig. 3: 1; PLATE 2: 2.

CAPE.—Hopefield: Schaapen Island (Saldanha Bay), *Simons* 633. Peninsula: Table Bay, *Tyson* s.n. sub BOL 27475, 27477 to 27482 incl.

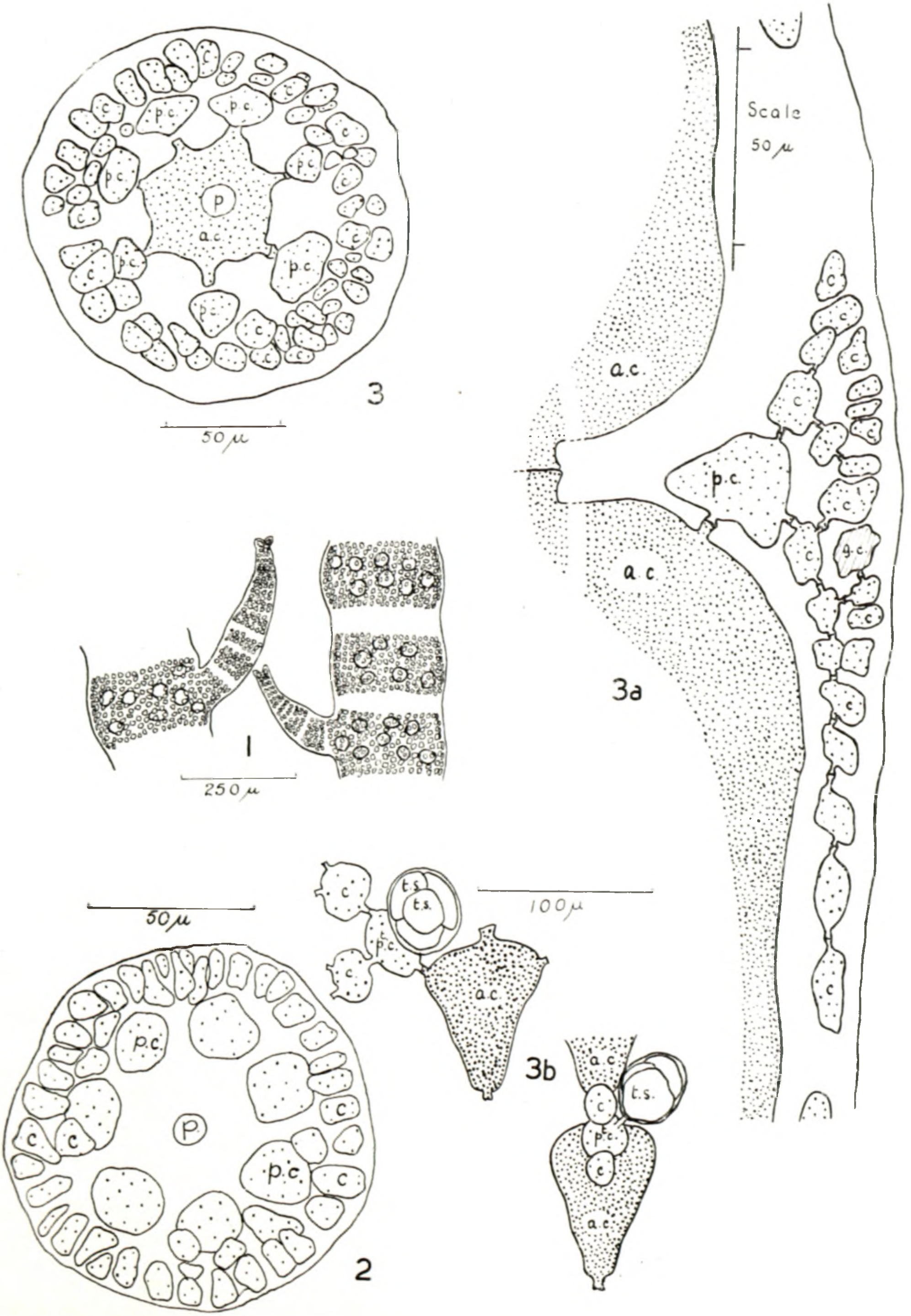


FIG. 3.—1, *Ceramium diaphanum* var. *pulchellum*, surface views of genicules bearing adventitious branches. 2, *C. capense*, transverse section through pericentrals of genicule near apex of branch. 3, *C. centroceratiforme*, transverse section through the pericentrals of a genicule; 3a, longitudinal section through a mature genicule and passing through a vertical row of cells; 3b, semi-diagrammatic representation of the oblique attachment of a tetrasporangium to a pericentral.

a.c.—axial cell; c.—cortical cell; g.c.—glandular cell; p.—pit connection; p.c.—pericentral cell; t.—tetrasporangium: t.p.c.—tetrasporiferous pericentral cell; t.s.—tetraspore.

This variety differs from var. *diaphanum* by its relatively large, patent, divergent apical cells.

All the Tyson specimens cited under this variety were designated " *C. kylinii* sp. nov. ined. G. F. Papenfuss "; a further two specimens similarly designated are of *C. atrorubescens* Kylin.

8. **C. capense** *Kuetz.* in Linnaea 15: 740 (1841); Sp. Alg. 686 (1849); Tab. Phyc. 13: 3, pl. 5, fig. c–e (1863).

*Microcladia capensis* (Kuetz.) Papenf. in Bot. Not. 223 (1940).

*Holdfast*: epiphytic plant attached by basal haustorial rhizoids. *Erect system*: plant up to 20 cm high and 1 mm thick near base, tapering downwards slightly, and upwards gradually to about 50 $\mu$ subapically; apically strongly incurved; main branching pseudodichotomous, adventitious branches frequent, often in whorls, at almost every articulation; cortication complete, multilayered when mature, outer layer of very small cells, inner layer of large elongated or isodiametric cells; seven pericentrals; articulations half as long as wide, cylindrical, translucent in upper parts, lower down one-and-a-half times longer, medianly constricted; tetrasporangia whorled, completely immersed, attached to pericentrals, often in two transverse ranks; cystocarps clasped by five or six involucral branches. Fig. 3: 2.

South West Africa.—Luderitz: Elizabeth Bay, *Simons* 257.

Cape.—Namaqualand: Port Nolloth. *Simons* 278; 313; *Isaac* B. 658; *Ecol. Surv.* N16; N20A; N40; Groen River, *Ecol. Surv.* GR4E. Clanwilliam: Lamberts Bay, *Ecol. Surv.* B12; B13; B39; B51; B52. Malmesbury: Paternoster, *Ecol. Surv.* P6A; Saldanha Bay, *Simons* 570; *Isaac* B. 31. Peninsula: Table Bay, *Tyson* s.n. sub BOL 27485–27491 incl.; Kommetjie, *Levyns* 0269 (*Tyson* s.n. sub BOL 27492).

This species differs from *C. rubrum* (Huds.) Ag. in having seven pericentrals instead of eight (Feldmann-Mazoyer, 1940). Very similar to *C. vimineum* J. Ag., *C. capense* differs by its more extensive branching and rather shorter mature articulations. True nodes, indicated by the point of origin of lateral branches, alternate with false ones marked by transverse constrictions of the frond especially in the older parts.

The description given above applies to the plant designated by Papenfuss as *Microcladia capensis*, but it does not seem to apply well to *Ceramium capense* Kuetz. which Papenfuss has designated as the basionym of this species. For instance, the articulations of *C. capense* are all half as long as wide and the cortical cells are larger (than those of *C. rubrum*). The present author is of the opinion that *C. capense* Kuetz. is a form of *C. obsoletum* Ag., but on the available evidence hesitates to make the change because it would necessitate the erection of a new name for *M. capensis* Papenf. The missing type of *C. capense* must be found and re-examined before this matter can be satisfactorily resolved.

9. **C. centroceratiforme** *Simons*, sp. nov.

Fila prostrata, intricata, pulvinum parvum formantia; genicula distincta, pellucida, rhizoidibus numerosis: cellulae pericentrales in dimidio superiore geniculorum; corticales sub pericentralibus plus minusve longitudinaliter vel transverse seriatae, omnibus subpellucidis; fila erecta, pseudo-dichotomoso-ramosa, usque ad 2 cm alta, 300 $\mu$ lata, interdum ramis adventitiis instructa; rami ultimi suberecti, breves, divaricati et fere triangulares; genicula superiora contigua vel fere contigua, inferiora plus minusve distincta; pericentrales 6 vel 7, in partibus superioribus medianae, in partibus inferioribus in dimidio superiore geniculorum dispositae; cellulae corticales plus minusve in stratis transverse et longitudinaliter *Centrocerati* similes dispositae, praecipue in partibus geniculorum infra pericentrales; tetrasporangia verticillata subterminalia omnino immersa vix manifesta, pericentralibus orta; cystocarpia bilobata uno ramulo subtensa. Plantae subflavae vel galbanae. Fig. 3: 3; PLATE 2: 3.

Type: Caledon, Hermanus, *Simons* 555 (PRE, holo., spirit collection only).

*Holdfast*: prostrate filaments matted together forming a small cushion, rhizoids abundant at distinct genicules; pericentrals in upper half of genicules; cortical cells below pericentrals arranged more or less in longitudinal and transverse rows, all more or less colourless. *Erect system*: up to 2 cm high and 300 $\mu$ thick, branching dichotomous, adventitious branches occasional, ultimate branches short, more or less straight and somewhat triangular in contour; upper genicules contiguous or almost so, lower genicules the same or distinct and scarcely different from those of prostrate filaments, longer than intergenicules; cortex, in vicinity of articulations and sometimes elsewhere, two-layered; pericentrals six or seven, median in upper parts, in lower parts occur in upper half of genicules; cortical cells arranged more or less in transverse and longitudinal rows similar to those of the genus *Centroceras*, especially in parts of genicule below pericentrals; tetrasporangia immersed, whorled, subterminal, scarcely discernible, attached to pericentrals; cystocarps two-lobed, subtended by only one ramule. Plant yellowish or greenish-yellow.

CAPE.—Caledon: Hermanus, *Simons* 489; 555; 557. Knysna: Noetzie, *Isaac* B. 755; Robberg, *Isaac* B. 939; B. 941. Willowvale: Dwessa, *Isaac* B. 1014.

The superficial appearance of this species is so like that of a *Centroceras* that sometimes only the distinct genicules of the prostrate filaments disclose its identity. Mostly, however, the genicules in other parts of the plant are also distinct. The author's reasons for assigning this species to *Ceramium* and not to *Centroceras* have been given in the introduction to this paper.

10. **C. obsoletum** *Ag.* in Sp. Alg. 2: 145 (1828); Kuetz. in Sp. Alg. 687 (1849); Tab. Phyc. 13: 4, pl. 10, fig. a–d (1863); Papenf. in J. S. Afr. Bot. 17: 178 (1952).
*C. furcellatum* Kuetz. in Sp. Alg. 687 (1849); Tab. Phyc. 13: 4, pl. 11, fig. a–b (1863).

*Holdfast*: epiphytic on other algae, haustorial rhizoids arising from the base. *Erect system*: somewhat rigid and setaceous, up to 20 cm high, 700 $\mu$ thick below, tapering slightly to base and upwards gradually; branching pseudodichotomous, often diverging strongly; adventitious branches sparse, but numerous and secund when fertile; cortex continuous throughout, one or more layered, inner layer of large cells of almost hexagonal outline with small angular cells seeming to cover only the interstices between the larger cells; pericentrals nine or ten, more or less spherical and largest of the cortical cells; plant translucent throughout, articulations as long as or shorter than width; tetrasporangia immersed in adventitious stichidia-like branches and in penultimate branches; cystocarps on short adventitious branches subtended by about five involucral branches. PLATE 2: 4.

CAPE.—Peninsula: Kommetjie, *Simons* 692. Knysna: Robberg, *Ecol. Surv.* RR1C. Bathurst: Kowie (Shark's Bay), *Tyson* s.n. sub BOL 27483. East London: *Ecol. Surv.* L114. Komga: Cape Morgan, *Flanagan* 56 (*Tyson* s.n. sub BOL 27484).

There is a confusing amount of variation in the habit of this species: in well-developed plants the pseudodichotomies diverge at right angles to one another, whilst in other plants they converge somewhat. Ultimately, however, they are never inrolled. The most consistent features of this plant are the large cortical cells outlined by very much smaller cells and the translucent thallus. When dry the plant is more or less opaque.

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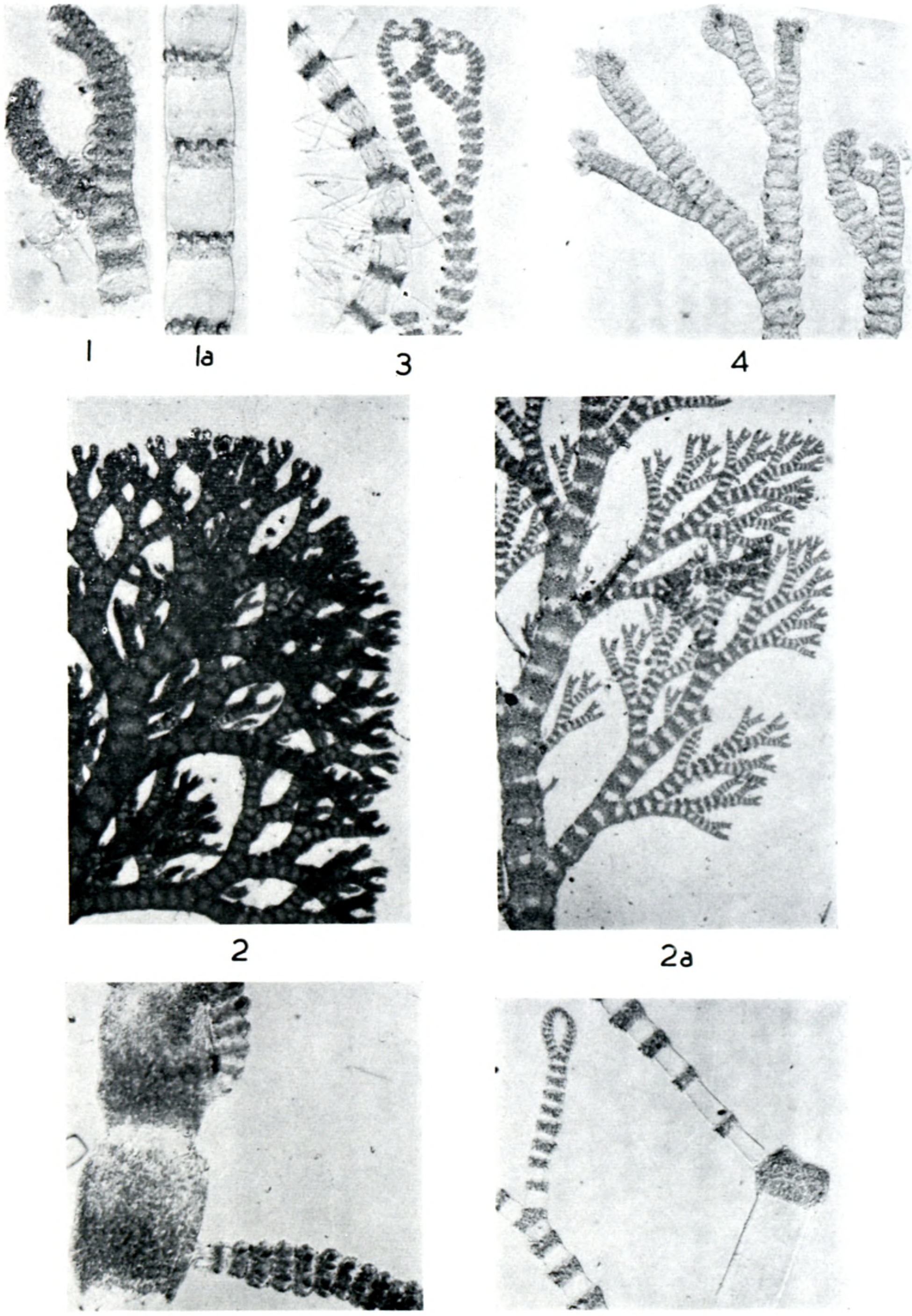


PLATE 1.—1, *Ceramium glanduliferum*, terminal fertile dichotomies, × 60 (*Isaac* B. 942); 1a, part of mature filament (refractive cells are the glandular cells), × 60; 2, 2a, *C. planum*, completely and partially corticated terminal portions of racemes, × 10 (2a, *Simons* 655); 3, *C. tenerrimum*, terminal and part of prostrate filament with rhizoids, × 30 (*Simons* 647); 4, *C. arenarium*, terminal portion of erect system (tetrasporiferous), × 30 (*Simons* 632); 5. *C. atrorubescens*, portion of a mature filament with two fertile laterals, each indicating a node, × 30 (*Ecol. Surv.* N. 42); 6. *C. diaphanum* var. *capense*, terminal portions of laterals, one attached to a mature genicule, × 30 (*Simons* 614).

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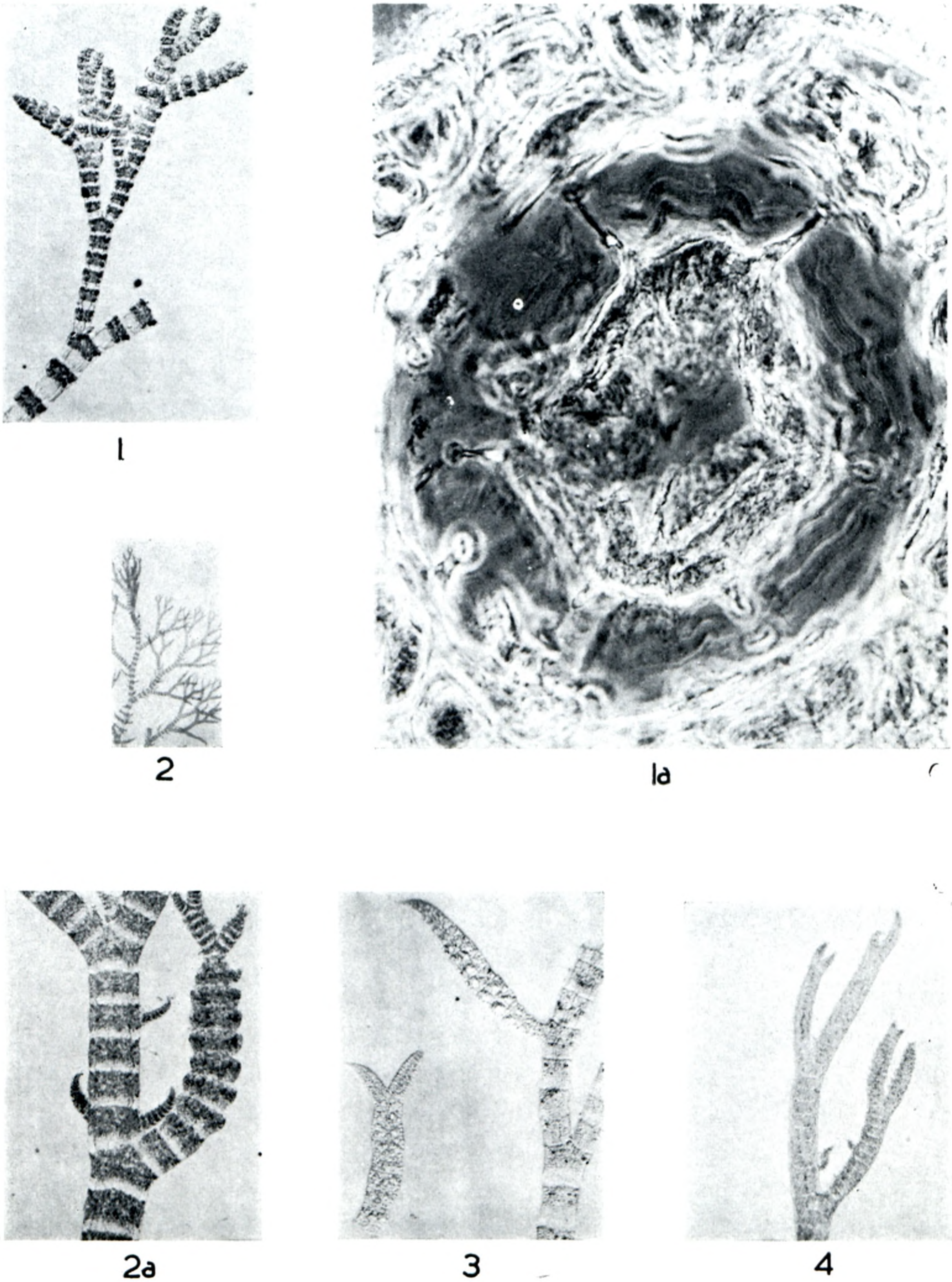


PLATE 2.—1, *Ceramium papenfussianum*, terminal tetrasporiferous portion of erect system, × 30 (*Simons* 609); 1a, transverse section through distal end of an axial cell showing several pit-connections to the ring of pericentrals, × 500 (*Ecol. Surv.* F. 115); 2, *C. diaphanum* var. *pulchellum*, general habit, × 2; 2a, detail of tetrasporiferous plant (swollen genicules indicate presence of tetrasporangia), × 30 (*Simons* 633); 3, *C. centroceratiforme*, terminal portions of filaments and portion of more mature thallus, × 30 (*Isaac* B. 939); 4, *C. obsoletum*, terminal portions of filaments (slight swelling of some genicules indicate presence of tetrasporangia), × 15 (*Ecol. Surv.* L. 114).