BLUMEA 35 (1991) 347–380

A TAXONOMIC REVISION OF INDONESIAN GELIDIALES (RHODOPHYTA)

A.M. HATTA[1] & W.F. PRUD'HOMME VAN REINE

Rijksherbarium / Hortus Botanicus, Leiden, The Netherlands

SUMMARY

In this study 12 taxa are treated, belonging to four different genera of Gelidiales (i.e. *Gelidiella*, *Gelidium*, *Pterocladia*, and *Porphyroglossum*) as well as one species of *Wurdemannia*, a genus of unknown affinity. One new species, *Gelidium amboniense*, and a new forma, *Gelidium latifolium* forma *elongatum*, are described. Holotype material of *Gelidium bornetii* Weber-van Bosse in the Weber-van Bosse collection in Leiden can be synonymized with *Gelidiella lubrica* (Kützing) Feldmann & Hamel, while the original sample in the herbarium in Copenhagen only contains *Gelidium pusillum* (Stackhouse) Le Jolis var *minusculum* Weber-van Bosse. In the key to the genera and species we also include the very similar genus *Ceratodictyon* Zanardini (= *Gelidiopsis* Schmitz).

INTRODUCTION

Weber-van Bosse (1921) described two groups within the genus *Gelidium* Lamouroux (Gelidiales) for Indonesia, viz. *Gelidium* without and with internal filaments. The first group, of which *Gelidium pannosum* Bornet is a representative, has been separated from the genus *Gelidium* s.s. by Feldmann and Hamel (1934) and has been included in their new genus *Gelidiella*. Fan (1961) proposed a new family (Gelidiellaceae) for this genus. The second of Weber-van Bosse's groups consisted of species now placed in the genera *Gelidium* and *Pterocladia* J. Agardh.

In the diagnosis of the monogeneric family Gelidiellaceae, Fan (1961) stated that this family is lacking internal filaments as well as a sexual phase. However, recent investigations show that internal rhizines as well as sexual reproduction may occur in this genus. Maggs and Guiry (1987) have observed internal rhizines in their new species *Gelidiella calcicola*, although only in a limited area around the attachment points. A cystocarpic plant of an unnamed *Gelidiella* species has been found in India by Rao and Trivedi (1980).

To decide whether specimens belong to *Pterocladia* or to *Gelidium* is usually not very easy. Many attempts have been made to find characters separating these genera. The characters suggested include the location of internal rhizines (Feldmann & Hamel, 1936; Loomis, 1949; Taylor, 1960), the structure of the cystocarp (Feldmann

[1] Recent address: Indonesian Institute of Sciences, Centre for Oceanological Research and Development, P.O. Box 44, Ambon, Indonesia.

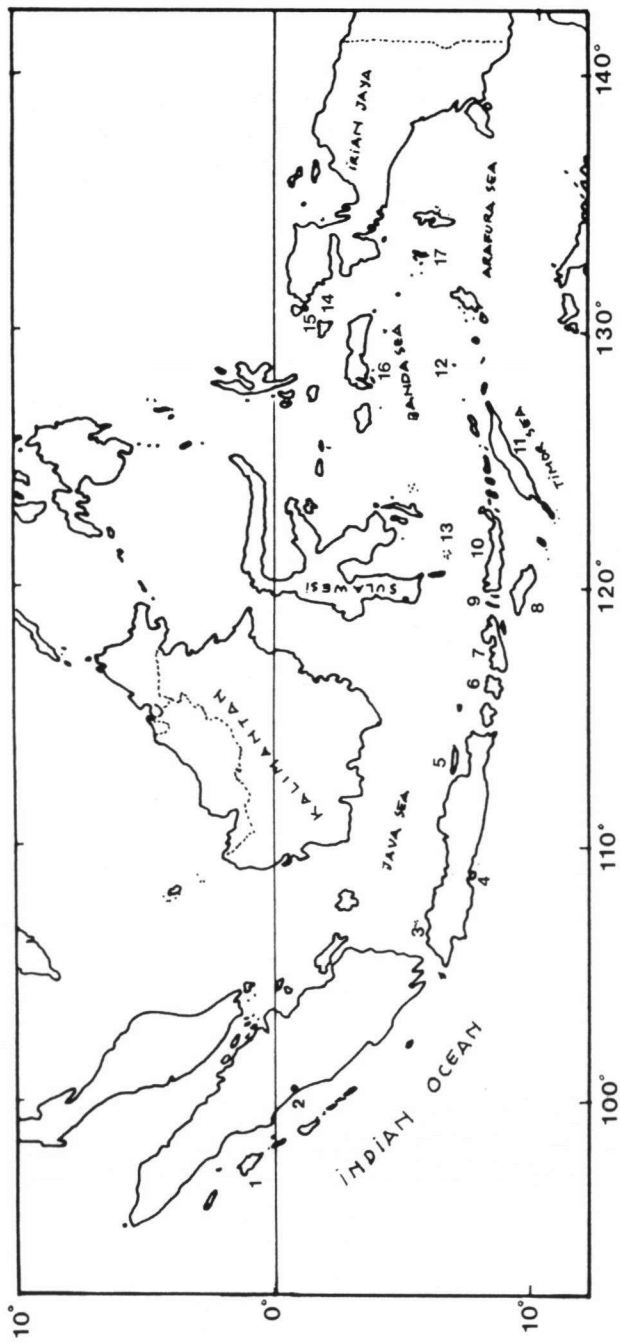

Fig. 1. Location of geographical names included in the text. 1. Nias; 2. Muara Arau (S coast of Mid Sumatra); 3. Jakarta Bay; 4. Nusa Kambangan (S coast of Mid Java); 5. Madura; 6. Lombok; 7. Sumbawa; 8. Sumba; 9. Komodo; 10. Flores; 11. Timor; 12. Damar Island; 13. Taka Bone Rate (Tiger Islands); 14. Daram Island; 15. Galewo Strait; 16. Ambon; 17. Kei Islands.

& Hamel, 1936; Fan, 1961; Santelices, 1977),the apical structure (Rodriguez & Santelices, 1987, 1988), and the morphology and dimensions of peripheral cells (Akatsuka, 1981, 1982) and of medullary cells (Loomis, 1949; Fan, 1961). However, the position of internal rhizines, the apical structure, and the morphology and dimension of cells can only be used to separate species and are not suitable to define genera. Differences in the structure of the cystocarp (usually unilocular or occasionally unequally bilocular, with only one surface provided with one or more ostioles in *Pterocladia,* and always bilocular, with one or more ostioles in each surface in *Gelidium*) have generally been accepted as differentiating characters. New genera described recently (*Pterocladiastrum* Akatsuka 1986a, and *Onikusa* Akatsuka, 1986b) share the cystocarp characters of *Pterocladia* and *Gelidium* respectively.

Literature about the taxonomy of Indonesian seaweeds is scanty and most papers about these seaweeds discuss their economic value (Eisses, 1953; Zaneveld, 1955, 1959; Soegiarto, 1978). In the years 1984–1985 the Indonesian-Dutch Snellius–II Expedition to Indonesian waters took place and in the months August and September 1984 many seaweeds have been sampled. The purpose of this study is to revise the information about Indonesian Gelidiales as based on papers by Weber-van Bosse (1926,1928) and to incorporate all available additional material. One other genus showing morphological resemblance to the Gelidiales will also be treated: *Wurdemannia* Harvey (Wurdemanniaceae, a family of unknown affinity, possibly belonging to the order Gigartinales),while in the key we also include the much resembling genus *Ceratodictyon* Zanardini (probably Gracilariaceae, Gigartinales).

MATERIAL AND METHODS

Specimens coming from the following sources have been studied:

- specimens collected during the Dutch Siboga Expedition (1899–1900) and other specimens studied by Mrs. Weber-van Bosse. It is a pity, however, that many of the specimens studied by Weber-van Bosse, apart from those of the Siboga collection, are not preserved in the Rijksherbarium or in the Herbarium Bogoriense (BO) and seem to have been lost.
- specimens collected in Indonesia before 1960 and preserved in the Rijksherbarium, the National Dutch Herbarium in Leiden.
- specimens collected during the Indonesian–Dutch Snellius–II Expedition (Aug.–Sept. 1984). Of this Snellius–II Expedition (SN–II) the A-series and the C-series (duplicates) are now in the Rijksherbarium, Leiden (L), the B- and D-series are in the Centre for Oceanological Research and Development – Indonesian Institute of Sciences, in Jakarta (JAK) and in Ambon (AMB) respectively and the E-series is in the Botanical Institute of the University of Gent, Belgium (GENT).

For herbaria recorded in the Index Herbariorum we use the standardized abbreviations.

Of all specimens their external morphology as wel as their anatomy has been studied to name these specimens according to modern classification and nomenclature. Sections of herbarium specimens have been made either by hand (razor blades) or

by freezing microtome. Aniline blue, in aqueous dye, is used to colour the sections, which are then mounted in an 80% solution of Karo or in Aquamount. A camera lucida is used in all anatomical drawings.

All descriptions are based on Indonesian specimens only, except when characters are recorded from type specimens originating from other countries. When in these descriptions layers of cells are mentioned, the numbers of cells counted on straight lines from thallus centre to thallus surface are recorded.

KEY TO THE GENERA AND SPECIES OF INDONESIAN GELIDIALES AND TAXA THAT RESEMBLE THEM

1a. Plants without internal rhizines (no sexual reproduction known) 2
b. Plants with internal rhizines (sexual reproduction observed in some species) 6
2a. Distinct apical cell present in all thalli ..... **Gelidiella** (3)
b. Thalli without distinct apical cell 14
3a. Thallus usually more than 25 mm high, rigid, proximal parts of erect axes cylindrical, distal parts compressed, straight or curved abaxially. Apical cell distinctly separated from the other cells ..... **1. Gelidiella acerosa**
b. Thallus less than 25 mm high, cartilaginous, cylindrical or somewhat compressed throughout, unbranched or branching (irregularly) pinnate. Apical cell not distinctly separated from the other cells 4
4a. Thallus usually more than 10 mm high, branching bipinnate or tripinnate **3. Gelidiella myrioclada**
b. Thallus usually less than 10 mm high, the erect part unbranched or very little branched 5
5a. Only one or two layers of inner cortical cells around one tier of medulla cells **4. Gelidiella pannosa**
b. More than two layers of inner cortical cells and medulla cells not in only one tier ..... **2. Gelidiella lubrica**
6a. Mature plants usually less than 1 cm high and often crowded together forming mats 7
b. Mature plants usually more than 1 cm high 11
7a. Only one layer of inner cortical cells around one tier of medulla cells **5. Gelidium amboniense**
b. Always more than one layer of inner cortical cells present 8
8a. Erect thallus parts mostly unbranched; filiform or spatulate throughout **8. Gelidium pusillum** var. **minusculum**
b. Thallus with branched erect parts 9
9a. Erect parts compressed throughout 10
b. Erect parts cylindrical or distally becoming compressed. Branching irregular, often trifid and not in one plane **9. Gelidium pusillum** var. **cylindricum**
10a. Branching of erect parts irregular or scarce. Always sterile. Juveniles of **7. Gelidium pusillum** var. **pusillum**
b. Branching of erect parts pectinate. Cystocarps unilocular, sometimes arranged in series ..... **12. Pterocladia caloglossoides**

11a. Small ramuli present, arranged in longitudinal rows on the surface of the flattened erect parts of the thallus ..... **10. Porphyroglossum zollingeri**
b. Small ramuli absent or not arranged in longitudinal rows 12
12a. Erect parts with scarce or irregular branching, proximal erect parts constricted, distally flattened throughout (up to 1000 µm in width) **7. Gelidium pusillum** var. **pusillum**
b. Erect parts pinnate or with opposite branches 13
13a. Branching of erect thallus opposite, often pinnate with pyramidal outline, rigid; apical cell sunken or exposed .. **6. Gelidium latifolium** forma **elongatum**
b. Branching of erect thallus pinnate, not pyramidal in outline, cartilaginous; apical cell exposed ..... **11. Pterocladia caerulescens**
14a. Tetrasporangia zonately divided. Cortical cells and medulla cells in cross section are almost isodiametric ..... **13. Wurdemannia miniata**
b. Tetrasporangia cruciately or tetrahedrally divided. Innermost cortical cells larger than cells of outer cortex and than medulla cells ..... **Ceratodictyon**

A detailed study of Indonesian *Ceratodictyon* will be published separately.

GELIDIELLA

Echinocaulon Kützing (1843) 405, nom. illeg., non *Echinocaulon* Spach (1841) 521 (a genus of flowering plants); *Gelidiella* Feldmann & Hamel (1934) 529, nom. nov. — T y p e: *Echinocaulon spinellum* Kützing (1843) 406 = *Gelidiella acerosa* (Forsskål) Feldmann & Hamel.
Acrocarpus Kützing (1843) 405, nom. illeg., non Wight (1839) 198 (a genus of flowering plants). — L e c t o t y p e: *Acrocarpus lubricus* Kützing = *Gelidiella lubrica* (Kützing) Feldmann & Hamel.

For description and discussion see Fan (1961: 340) and Maggs & Guiry (1987: 431–433). For Indonesian species see also Table 1.

1. Gelidiella acerosa (Forsskål) Feldmann & Hamel – Fig. 2

Fucus acerosus Forsskål (1775) 190. — *Echinocaulon acerosum* Børgesen (1932) 5. — *Gelidiella acerosa* Feldmann & Hamel (1934) 533; Dawson (1954) 422; Rao (1970) 64, t. 1; Santelices (1977) 63; Lawson & John (1982) 172, t. 21, f. 2. — T y p e: Mokka, Yemen (C, not seen).
Fucus rigidus Vahl (1802) 46, nom. illeg., non Turra (1780) 68. — *Sphaerococcus rigidus* C. Agardh (1822) 285, nom. nov. — *Gelidium rigidum* Greville (1830) LVII. — *Echinocaulon rigidum* Kützing (1868) 14, t. 40, f. a–d. — *Gelidiopsis rigida* Weber-van Bosse (1904) 104; (1928) 42. — T y p e: St. Croix, Virgin Islands (not seen).
Fucus spinaeformis Lamouroux (1805) 77, t. 36, f. 3 & 4. — *Gelidium spiniforme* Lamouroux (1813) 129. — T y p e: Mauritius (not seen).
Echinocaulon spinellum Kützing (1843) 406, (1868) 14, t. 38, f. d & e. — T y p e: Marianen, *Gaudichaud* in herb. Kunth (L 941,27-215).
Echinocaulon ramelliferum Kützing (1868) 14, t. 39, f. d–f. — T y p e: New Caledonia, *Vieillard 2061* (L 941,11-63; not L 941,11-9, which is *Gracilia* spec.).
Gelidiopsis acerosa var. *semipinnata* Weber-van Bosse (1928) 428 (Indonesian material only, see note 1). — No type selected.
Gelidiella acerosa forma *minima* Rao (1970) 67, t. 1, f. c. — T y p e: Adatra, Okha, India, in Central Salt and Marine Chemicals Institute, Bhaunagar, India (CSMRI - 4223 - D, not seen). (See note 2).

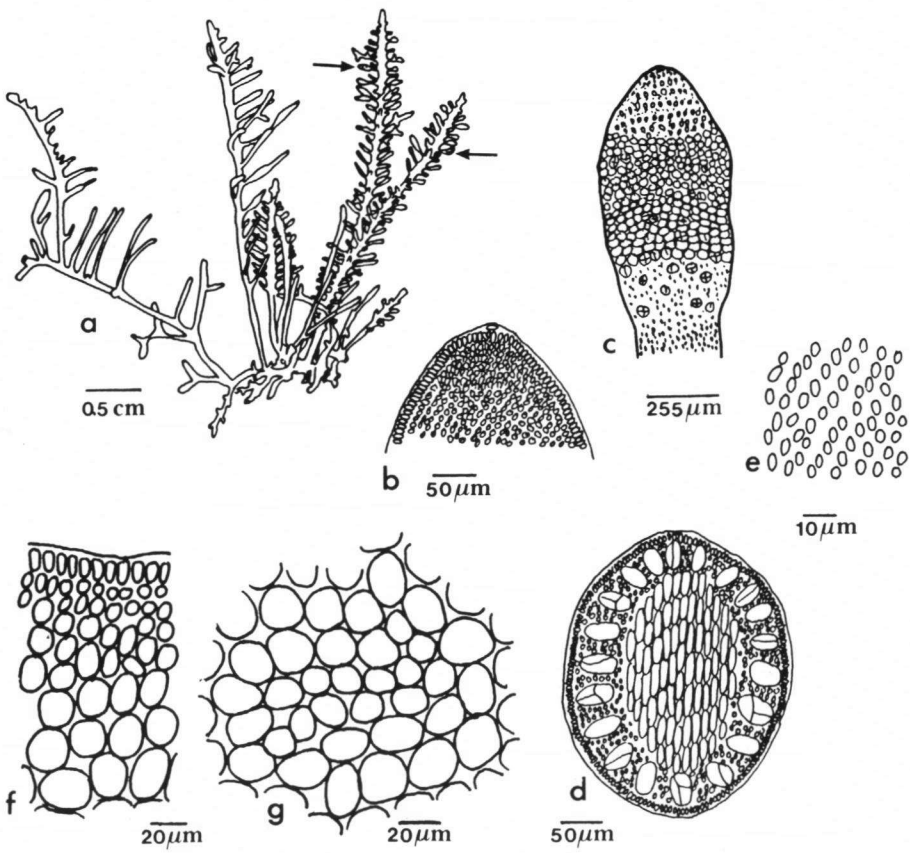

Fig. 2. *Gelidiella acerosa*. a. Habit (arrow: stichidia); b. surface view of the apex of an erect thallus; c. stichidium, densely covered with tetrasporangia; d. cross section of a stichidium with tetrasporangia; e. surface view of cortical cells; f & g. cross sections of erect thallus parts, f. with external and inner cortical cells, g. with small medulla cells surrounded by large innermost cortical cells (a, c–e Komodo Is., *SN-II, 10850*; b Galewo Strait, L 940,355-78; f, g Komodo Is., *SN-II, 10812*).

Mature plants tufted, 0.5–9 cm high; consisting of cylindrical prostrate axes (diam. 100–320 μm), attached to the substratum by disk-like haptera issued at irregular intervals and with erect, rigid, branched or unbranched, straight or abaxially curved thallus parts, proximally cylindrical (diam. 100–400 μm) and distally compressed (450–600 × 300–350 μm in cross section) (fig. 2a). Branching pectinate or pinnate, opposite, alternate, or secund; small terminal ramuli filiform or spatulate (fig. 2a). Apex of axes and branches conical or attenuate; apical cell separated from the other cells but not very conspicuous (fig. 2b). External cortical cells in surface view diagonally arranged, thick-walled and rectangular in cross section, 2–5 × 4–8 μm, anticlinally elongate (fig. 2e, f); inner cortical cells in cross section rounded, diameter inwards grading from 3 to 26 μm (fig. 2f, g). Medulla cells rounded in cross section and smaller than innermost cortical cells, diameter 15–20 μm (fig. 2g),

longitudinally elongate. Tetrasporangia in swollen conical stichidia located in the terminal ramuli (fig. 2a, arrow); stichidia 150–180 × 300–350 µm and densely or sparsely, regularly or irregularly covered with tetrasporangia (fig. 2c). Proximal tetrasporangia usually in a more advanced stage than distal ones, ovate in surface view (c. 20 µm in width), oblong in cross section of the stichidia (30–42 × 23–28 µm) (fig. 2d).

Distribution. World: in warm temperate and tropical seas all over the world. Indonesia: common in all Indonesian seas.

Discussion. This species can be distinguished easily from other Gelidiales by its external morphology. It occurs in the littoral zone on wave-exposed shores as well as in tidal pools, in the shallow sublittoral and even in water of 30 m depth (Komodo Island, *SN-II, 10980*). The 41 Indonesian samples did not show morphological discontinuities; variation in dimensions is the only striking element. These dimensions range in our samples from 8.5 mm high (Timor, L 941,27-253) up to 9 cm high plants (Galewo Strait, Irian Jaya, L 940,355-78).

Notes. 1. Specimens recorded by Weber-van Bosse (1928) as belonging to var. *semipinnata* (Piccone & Grunow) Weber-van Bosse fall in the range of variation in morphology and dimensions of this species and therefore cannot be treated as a separate infra-specific taxon. Isotype material of *Gelidium semipinnatum* Piccone & Grunow in Piccone (1884: 315) in L belongs to *Gelidiella lubrica* (Kützing) Feldmann & Hamel.

2. The dimensions of the plants of *Gelidiella acerosa* forma *minima* as described by Rao (1970) are within the range of variation of samples from Indonesia. There is no reason to consider these specimens as belonging to a separate infra-specific taxon.

2. **Gelidiella lubrica** (Kützing) Feldmann & Hamel – Fig. 3

Acrocarpus lubricus Kützing (1843) 405, t. 60 II; (1849) 761; (1868) t. 32. — *Gelidiella lubrica* Feldmann & Hamel (1934) 535, f. 3–5; Womersley & Bailey (1970) 305. — Type: Naples, Italy (L 941,46-46 and 941,46-347).

Gelidium semipinnatum Piccone & Grunow in Piccone (1884) 315. — *Gelidiopsis rigida* var *semipinnata* Weber-van Bosse (1928) 428. — Isotype: Assab Bay, Eritrea, Ethiopia, leg. A. Issel, on Patella (L 941,46-291, see note 1 to *G. acerosa*).

Gelidium bornetii Weber-van Bosse (1926) 107. — *Gelidiella bornetii* Feldmann & Hamel (1934) 535; Børgesen (1938) 210, f. 2; Dawson (1957a) 113, f. 21; Cribb (1983) 30, t. 7, f. 1. — Lectotype: Nusa Kambangan, Java, Indonesia, leg. Jensen (L 941,27-296).

Small (3–5 mm high), mat forming, saxicolous plants; consisting of cylindrical or somewhat compressed prostrate axes (diam. 90–127 µm), attached to the substratum by peg-like haptera issued at irregular intervals and opposite to the unbranched or scarcely and irregularly branched, cartilaginous, filiform or somewhat compressed, erect thallus parts, diameter 60–80 µm (fig. 3a, b). Apex of erect part attenuate; exposed apical cell not separated from the other cells and quite conspicuous. External cortical cells angular in surface view, diameter 4–7 µm, longitudinally and transversely arranged in younger parts, more irregular in older parts (f. 3d). In cross section external cortical cells quadrangular, diameter 4–8 µm; inner cortical

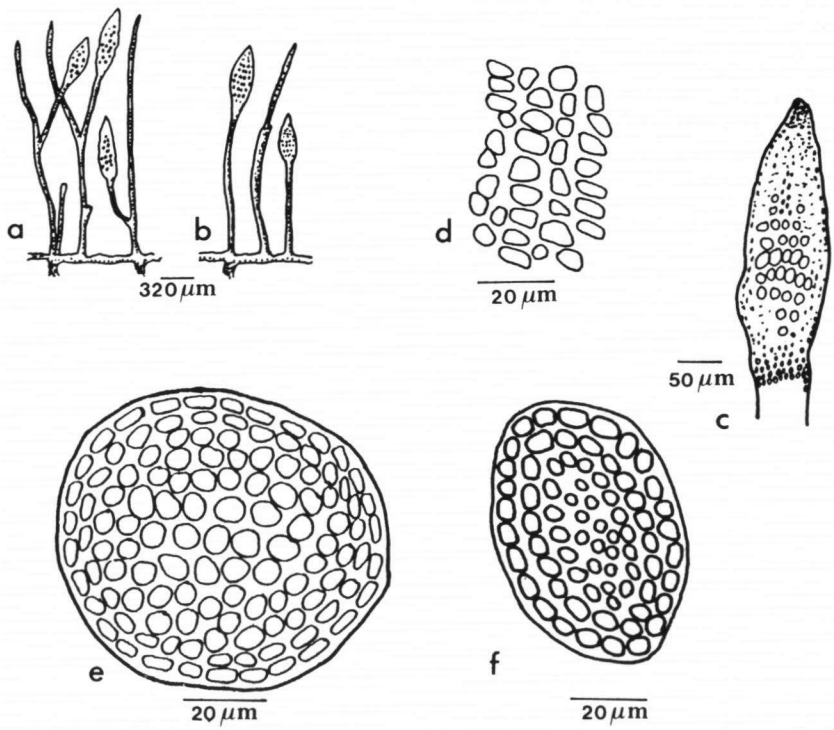

Fig. 3. *Gelidiella lubrica*. a & b. Details of plants; c. stichidium; d. surface view of external cortical cells; e & f. cross sections of erect parts, e. mature part, f. young part (a, b, d, e Noimini, Timor, L 941,27-295; c Taka Bone Rate, *SN-II, 11224*; f lectotype of *Gelidiella bornetii* from Nusa Kambangan, S coast Mid Java, L 941,27-296).

cells and medulla cells rounded, diameter often inwards grading from 7 to 12 µm (fig. 3e, f). Medulla cells are elongate in longitudinal direction, diameter as in internal cortical cells or smaller. Tetrasporangia in terminal stichidia which are slightly swollen or not, cylindrical or lanceolate and somewhat compressed (250–650 × 98–115 µm), usually densely covered with tetrasporangia (mostly cruciate and often tetrahedral) which are arranged in transverse rows or in chevrons or are irregularly scattered (fig. 3c). Proximal tetrasporangia usually more advanced than distal ones, ovate in surface view (19–32 × 10–19 µm).

Distribution. World: in warm temperate and tropical seas: Mediterranean, India, Indonesia, Marshall Islands, Solomon Islands, Great Barrier Reef. Indonesia: Nusa Kambangan (S coast of Mid Java), Noimini Bay (Timor) and Taka Bone Rate (Tiger Islands).

Discussion. These small mat-forming algae are not easily separated from *Gelidiella pannosa* and small *Gelidium* species. In *Gelidiella pannosa* there is always only one tier of medulla cells and the tetrasporangia are often regularly arranged in chevrons or transverse rows. In small *Gelidium* species the cortical cells in surface

view are smaller, more rounded and irregularly arranged, in cross section internal rhizines can be observed and the tetrasporangia are arranged in irregular groups in the stichidium. The tetrasporangia in *Gelidiella lubrica* can be arranged with 4–6 in transverse rows or in chevrons, but in other specimens, and even in other stichidia on the same plant, arrangement of tetrasporangia can be irregular. This irregular arrangement of tetrasporangia has been used by Børgesen (1938) and Cribb (1983) to separate *Gelidiella bornetii* from *G. tenuissima* (= *G. pannosa*). However, lectotype material of *Gelidiella bornetii*, labelled by Weber-van Bosse, does not differ enough from *G. lubrica* to be considered a separate species. Moreover, the description by Weber-van Bosse (1926) differs from the lectotype in dimensions, form, and arrangement of the cortical cells. Two microslides in L, labelled *'Gelidium bornetii'* by Weber-van Bosse, also conform to the description of Indonesian specimens of *G. lubrica* and again are not exactly in accordance with her description of *Gelidiella* (as *Gelidium*) *bornetii*. Erect parts of *G. lubrica* can be filiform, cylindrical or somewhat compressed and this again is not a reliable character to separate species. A sample in C, labelled *'Gelidium bornetii* n. sp., Nusa Kambangan' consists of a piece of coral on which only specimens of *Gelidium pusillum* var. *minusculum* could be detected by us. The description by Cribb (1983: 3) of *Gelidiella* species is in agreement with our concept of *G. lubrica*.

The type material of *G. lubrica* is larger (up to 3 cm high) and more profusely branched than the Indonesian specimens. However, the irregular arrangement of tetrasporangia as well as their arrangement in transverse rows occurs in these specimens and the anatomy of thalli is not different from that of Indonesian specimens.

N o t e. Kützing distributed in 1836 dried specimens collected by him during his journey to Italy. In this material, called 'Actien', he used the nomen nudum *Sphaerococcus lubricus* for specimens now to be named *Gelidiella lubrica*.

3. Gelidiella myrioclada (Børgesen) Feldmann & Hamel – Fig. 4

Echinocaulon myriocladum Børgesen (1934) 5, f. 4 & 5. — *Gelidiella myrioclada* Feldmann & Hamel (1934) 533; Børgesen (1935) 44; Dawson (1954) 422, f. 33d; Santelices (1977) 66, f. 1F–H. — T y p e: Malabar Hill, Bombay, India, *Børgesen 5235* (4 slides in C, one, fig. 5a in Børgesen 1934, has been selected as the lectotype).

Mature saxicolous plants tufted, 12–22 mm high; consisting of cylindrical prostrate axes (diam. 75–135 µm) attached to the substratum by peg-like haptera (75–450 µm in length) and with erect, branched, cartilaginous thallus parts, proximally cylindrical (diam. 80–140 µm) and distally ovate throughout in cross section (100–180 µm broad). Branching bipinnate or tripinnate, branches proximally constricted; lateral terminal ramuli 1–3.5 mm long, filiform or spatulate (fig. 4a). Apex of axes and branches attenuate; exposed apical cell not separated from the other cells and quite obvious. External cortical cells angular in surface view, often with rounded edges and not arranged in distinct rows (fig. 4c), in cross sections quadrangular, compressed (3–7 × 3–10 µm); first layer of inner cortex similar to the outer cortex, inwards followed by three layers of ovate cells, 7–10 µm wide (fig. 4d). Medulla cells in 4–5 layers, ovate in cross section, 10–14 µm wide, longitudinally elongated. Tetrasporangia in compressed lanceolate stichidia, located in the lateral ramuli;

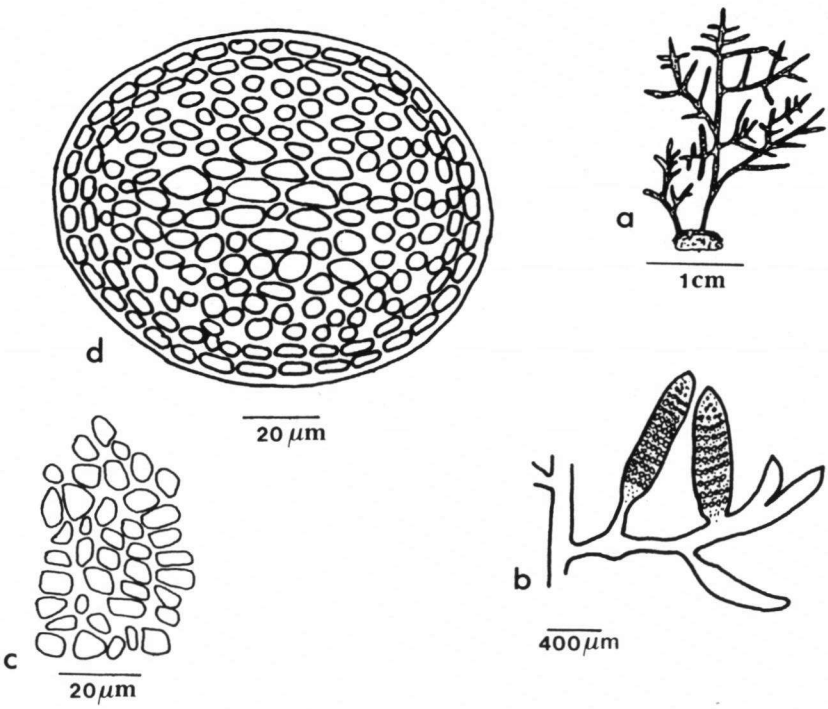

Fig. 4. *Gelidiella myrioclada*. a. Habit; b. stichidia with tetrasporangia arranged in lateral rows; c. surface view of external cortical cells; d. cross section of erect thallus part (a, c, d Taka Bone Rate, *SN-II, 11262*; b lectotype, Malabar, India).

stichidia 380–765 × 125–155 μm, with closely set rounded tetrasporangia, arranged in transverse rows (fig. 4b). Diameter of the tetrasporangia 18–20 μm in surface view (description of the stichidia is taken from the lectotype).

Distribution. World: tropical Indo-Pacific Oceans: Kenya, India, Vietnam, Indonesia, Hawaii. Indonesia: Taka Bone Rate (Tiger Islands; *SN-II, 11262*).

Discussion. Differences between the sterile specimens from Taka Bone Rate and other Indo-Pacific specimens concern bipinnate subopposite branching and smaller specimens in Vietnam (Dawson, 1954) and smaller cells in cross section in Hawaiian specimens (Santelices, 1977). The structure of the quite similarly branched *Gelidiella machrisiana* Dawson (1957b: 17, f.4B) studied in the type (from Puerto Rico, *Dawson 16745*, in LAM) proved to differ consistently from *G. myrioclada*, especially as for the dimensions and situations of the cells.

4. Gelidiella pannosa (Feldmann) Feldmann & Hamel – Fig. 5

Gelidium pannosum Bornet (1892) 267, non *G. pannosum* Grunow, which is a *Ceratodictyon*; Weber-van Bosse (1921) 233, f. 68 t. 7, f. 3 (p.p). — *Echinocaulon (?) pannosum* Feldmann (1931b) 12. — *Gelidiella pannosa* Feldmann & Hamel (1934) 534, f. 1 & 2; Cribb (1983) 31, t. 6, f. 2; Egerod (1971) 127, f. 29–31. — *Gelidiella tenuissima* Feldmann & Hamel (1936) 226,

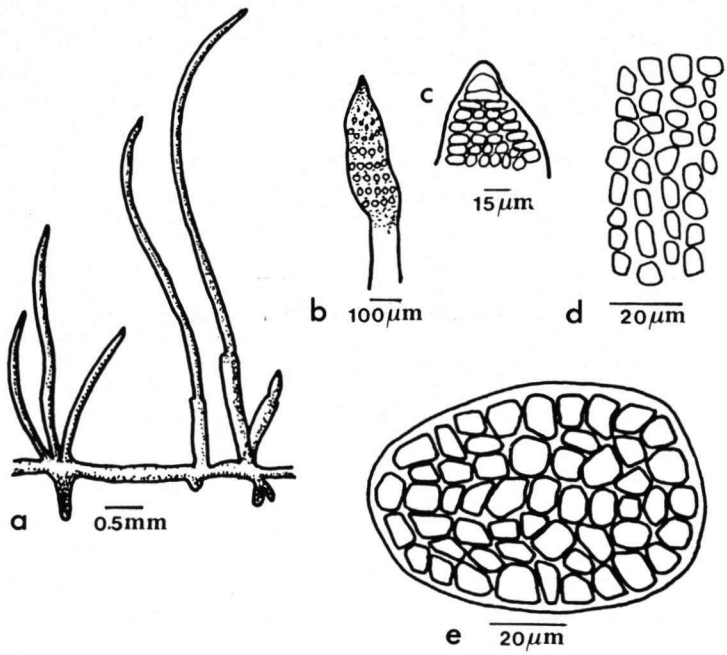

Fig. 5. *Gelidiella pannosa*. a. Habit ; b. lanceolate stichidium covered with tetrasporangia arranged in transverse rows; c. surface view of apex; d. surface view of external cortical cells; e. cross section of erect thallus part (a–e Tual Reef, Kei Islands, L 941,27-269).

superfluous nom. nov. for *G. pannosum* (Feldmann) Feldmann & Hamel, sec Fan (1961) 340, footnote; Dawson (1954) 422, f. 33e; Blomquist & Almodovar (1961) 67, t. 36; Boudouresque (1969) 783. — T y p e: Biarritz, France, herb. Bornet-Thuret in PC (not seen).

Gelidiella pannosa forma *exigua* Weber-van Bosse (1921) 233. — T y p e: Probably lost.

Small, mat-forming, saxicolous plants, 0.5–5.5 mm high, consisting of cylindrical to compressed prostrate axes (65–125 × 65–100 μm), attached to the substrate by fibrous peg-like haptera, issued at irregular intervals opposite to the usually unbranched, cartilaginous, cylindrical or somewhat compressed, erect thallus parts with a diameter 90–115 μm, or with groups of rhizoids issued from the ventral side of prostrate axes (fig. 5a). Apex of erect thallus parts attenuate, with a conspicuous apical cell (fig. 5b). Cortical cells in surface view angular, 5–15 × 3–9 μm, often higher than wide, usually arranged in longitudinal rows, not in transverse rows (fig. 5d). In cross section external cortical cells quadrangular to rounded, diameter 6–10 μm; followed by two layers of inner cortical cells of the same shape and size. Medulla cells in cross section arranged in one tier, similar to cortical cells, quadrangular to ovate and longitudinally elongate (fig. 5e). In proximal erect thallus parts the central filament is often conspicuous. Tetrasporangia in terminal, swollen, lanceolate stichidia on the erect thallus parts; stichidia 225–535 × 115–160 μm, covered with tetrasporangia, often regularly arranged in chevrons of 3–5; tetrasporangia ovate in surface view, diameter 15–18 × 25- 30 μm (fig. 5b).

Distribution. World: in warm temperate and tropical seas: Puerto Rico, Canary Is., Cape Verde Is., Salvage Is., Senegal, Mauritania, Morocco, Portugal, Atlantic France, Mediterranean, Thailand, Vietnam, Indonesia, Great Barrier Reef, Marshall Islands. Indonesia: Madura, Kangean Island (E Madura) and Tual Reef (Kei Islands).

Discussion. Weber-van Bosse (1921) reported her *Gelidium pannosum* from three localities in Indonesia: Tual Reef (Kei Islands), Kambing Island (Bima Bay, Sumbawa), and Noimini (Timor), and at the same time some somewhat aber-

Table 1. Comparison of the Indonesian *Gelidiella* species.

Characters	*G. acerosa*	*G. myrioclada*	*G. pannosa*	*G. lubrica*
Height of plants	0.5–90 mm	12–22 mm	0.5–5.5 mm	3–5 mm
Erect thallus parts	proximally cylindrical, distally compressed	proximally cylindrical, further ovate throughout	cylindrical throughout	filiform or somewhat compressed
Branching	pectinate, opposite or alternate	pectinate, tripinnate	unbranched	scarcely branched or unbranched
Apical cell	separate, inconspicuous	conspicuous	conspicuous	conspicuous
Apex of erect parts	conical or attenuate	attenuate	attenuate	attenuate
Ext. cortical cells (s.v.)	diagonally arranged, rectangular, 2–5 × 4–8 µm	not in distinct rows, angular, often with rounded edges 3–7 × 3–10 µm	mostly longitudinally arranged, angular, often higher than wide, 5–15 × 3–9 µm	mostly longitudinally and transversely arranged, often higher than wide, 3–7 × 5–8 µm
In cross section:				
Ext. cort. cells	rectangular	quadrangular	quadrangular to rounded	quadrangular
Inn. cort. cells	rounded,inwards grading to larger in diam., more than 5 layers	first layer quadrangular & compressed, followed by 2–3 layers of ovate cells	quadrangular to rounded, 2 layers	rounded, inwards grading to larger diam.
Medulla cells	rounded, smaller than innermost cortical cells	ovate, larger than innermost cortical cells	quadrangular to ovate, in a single tier	elongate, diam. as in inner cortical cells or smaller
Tetrasporangia	in conical stichidia	in lanceolate stichidia	in lanceolate stichidia	in lanceolate stichidia or on unchanged erect thallus parts
– form in s.v.	ovate	rounded	ovate	ovate
– arrangement	compact	in transverse rows	often in chevrons	occasionally in transverse rows or chevrons

s.v. = surface view.

rant specimens (described as a new forma, f. *exigua*) from Nias. In the collections of the Rijksherbarium only herbarium specimens from Tual (labelled as *Gelidium crinale*) could be located, together with additional herbarium specimens from Madura and from Kangean Island. Furthermore there were microslides (quite badly preserved) with specimens from Kambing Island and Noimini, and liquid preserved specimens also from Kambing Island. Cribb (1983) discussed the differences between *Gelidiella bornetii* (= *G. lubrica*) and *G. pannosa*, and on the basis of the description by Weber-van Bosse of her specimens from Kambing Island, he suggested that her material may belong to *G. bornetii*. A detailed study of her collections from Kambing Island and from Noimini confirms Cribb's suggestion. Her *Gelidium pannosum* specimens from Tual, however, have to be considered as actually belonging to *Gelidiella pannosa*. This is, according to the descriptions, also the case for the specimens from Nias, on which the new forma *exigua* has been based, but of which no specimens could be located. However, dimensions of plants alone cannot be considered as acceptable characters for a separate forma. Differences between *G. lubrica* and *G. pannosa* exist in the arrangement and dimensions of cortical cells and in the structure of the medulla. Børgesen (1938) and Cribb (1983) used the arrangement of tetrasporangia in the stichidia as a character to separate the two species. However, in both species a regular arrangement of tetrasporangia can occur, as well as irregular arrangements. It is true that regular chevrons of tetrasporangia occur more often in *G. pannosa*, but stichidia with irregularly arranged tetrasporangia may occur in the same plants, and these irregular arrangements have often been described in literature [compare Blomquist & Almodovar (1961) and Boudouresque (1969)].

Cribb (1983) synonymized two other *Gelidiella* species with *G. pannosa* [*G. stichidiospora* Dawson (1953) 84, t. 12, f. 4 & 5. – Type: Punta Norte, Isla Cedros, Bay of California, Mexico, *Dawson*, in LAM (not seen), and *G. adnata* Dawson (1954) 422, f. 33f; Santelices (1977) 63, f. 1D. – Type: Nha Trang, Vietnam, *Dawson 11309*, in US (not seen)]. The figures and descriptions by Dawson and the observation by recent authors on *G. pannosa* make this suggestion attractive, but a decision can only be made on the basis of a detailed study of the structure of (type) specimens.

GELIDIUM

Gelidium Lamouroux (1813) 128, nom. cons. — T y p e: *Gelidium corneum* (Hudson) Lamouroux.For description and discussion see Fan (1961) and Dixon & Irvine (1977a) 126.

5. Gelidium amboniense Hatta & Prud'homme van Reine, *spec. nov.* – Fig. 6

Species generis *Gelidii* parvae tegetes formantes cellulis medullae in sectione transversali observatis solum unoserialibus. — T y p u s: *SN-II, 10006* (holotype *10006A* in L; iso in AMB, GENT, JAK), Bay of Ambon, Indonesia, on rocks in the littoral of the inner Bay.

Small, mat-forming, saxicolous plants, 0.5–2.5 mm high; consisting of cylindrical prostrate axes (diam. 80–125 μm), attached to the substrate by peg-like haptera issued at irregular intervals and opposed to the erect, cylindrical or compressed, un-

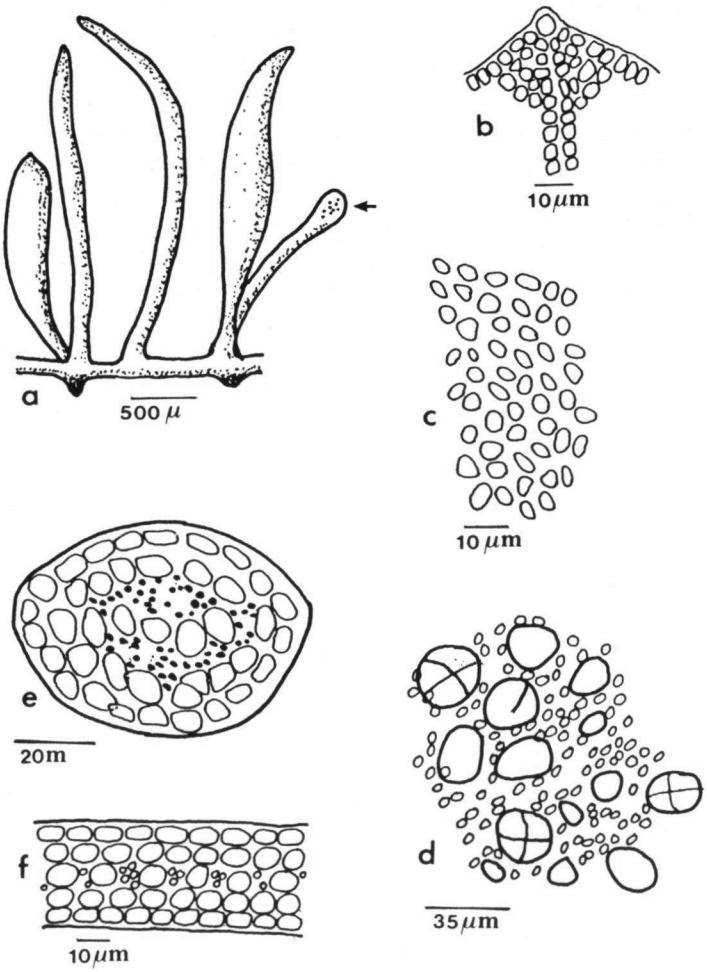

Fig. 6. *Gelidium amboniense*, type. a. Detail of a plant with tetrasporangia (arrow); b. apex with conspicuous extruding apical cell; c. cortical cells in surface view; d. detail of tetrasporangia in surface view; e. cross section of a proximal part of an erect thallus; f. cross section of a distal and compressed part of an erect thallus (a–f Bay of Ambon, *SN-II, 10006*).

branched or scarcely branched thallus parts, 40–50 × 40–230 μm in cross section (fig. 6a). Apex of axes and erect thallus parts conical, with conspicuous extruding apical cell (fig. 6b). Cortical cells rounded to ovate or somewhat irregular in surface view, 4–8 × 3–5 μm (fig. 6c). In cross section, outer cortical cells quadrangular, 6–10 × 4–5 μm; inner cortical cells in one layer, subquadrangular to rounded, diameter 7–10 μm; medulla cells in only one tier, rounded, diameter 8–10 μm, surrounded by a small number of straight internal rhizines (fig. 6e, f). Tetrasporangia in swollen apical parts of erect thallus (fig. 6a, arrow), irregularly arranged, in surface view rounded, diameter 30–35 μm (fig. 6d). Cystocarps unknown.

Distribution. Only known from the type locality.

Discussion. This species resembles much *G. pusillum* var. *minusculum* (see also table 3), but in cross section the small number of inner cortical cells as well as medulla cells is characteristic for the new species. According to Dawson (1953: 65) a similar anatomical structure has been found in what has been described as *G. crinale* var. *luxurians*, but in that taxon more complex structures can also be seen in the same thalli. In *G. amboniense* more complex structures do not occur. We agree that describing new species without having seen cystocarps is a quite tricky business, but a similar anatomical structure has been used to characterize a separate species in *Gelidiella*, and hence we propose to use that character in *Gelidium* as well.

Gelidium latifolium (Greville) Bornet

Gelidium corneum var. *latifolium* Greville (1830) 143. — *Gelidium latifolium* Bornet in Bornet & Thuret (1876) 58, t. 20, f. 8–10; Feldmann & Hamel (1936) 245; Dixon & Irvine (1977a) 127. — Lectotype: Sidmouth, England, coll. Greville (E, not seen; see Dixon & Irvine, 1977b).

Fucus corneus var. *attenuatus* Turner (1819) 146, t. 257, f. m–o. — *Gelidium attenuatum* Thuret ex Bornet (1892) 271; Feldmann & Hamel (1936) 249. — Type: no type selected.

Gelidium corneum auct. non (Hudson) Lamouroux: Taylor (1960) 356. —Type: no type selected.

In Indonesia, the specimens belong to a separate forma:

6. Gelidium latifolium forma elongatum Hatta & Prud'homme van Reine, *forma nov.* – Fig. 7

Gelidium latifolium auct. non Bornet: Weber-van Bosse (1921) 226. — Type: S coast of Mid Java, *Teijsmann 14* (L 941,27-299).

Pterocladia lucida auct. non (R. Br.) J. Ag.: Weber-van Bosse (1921) 227. — Type: Maumeri, Flores, *Weber-van Bosse 1888* (L 941,182-29).

A forma typica differt ramulis minoribus altioribusque. Ramuli terminales parvi apice emarginato.

Medium-sized (3–9 cm high), solitary, tufted, rigid plants, consisting of terete prostrate axes (diam. 250–450 µm) attached to the substratum by peg-like haptera issued at irregular intervals, and branched erect thallus parts with a pyramidal outline (fig.7a), proximally constricted and there terete or subquadrangular in cross section, diameter 300–700 µm, distally broader and compressed, 160–200 µm thick and 500–1100 µm broad.Branching opposite or bi-, tri-, or tetrapinnate; proximal laterals 7–32 mm in length, terminal ramuli spatulate or lanceolate, 100–250 µm in length. Apex of erect thallus parts emarginate or blunt, apical cell usually not exposed, often in depression. In surface view, cortical cells rounded to ovate, somewhat regularly arranged in chevrons, 3–6 × 2–3 µm (fig. 7d). In cross section outer cortical cells subquadrangular and anticlinally elongate or palissade-like (6–17 × 2–5 µm), followed by 3–5 layers of inner cortical cells, subquadrangular to ovate and inwards gradually larger, diameter 6–17 µm; medulla cells ovate, arranged in longitudinal rows, diameter 14–28 × 8–10 µm. Internal rhizines straight and congested between the inner cortical cells as well as scattered in small clusters between medulla cells

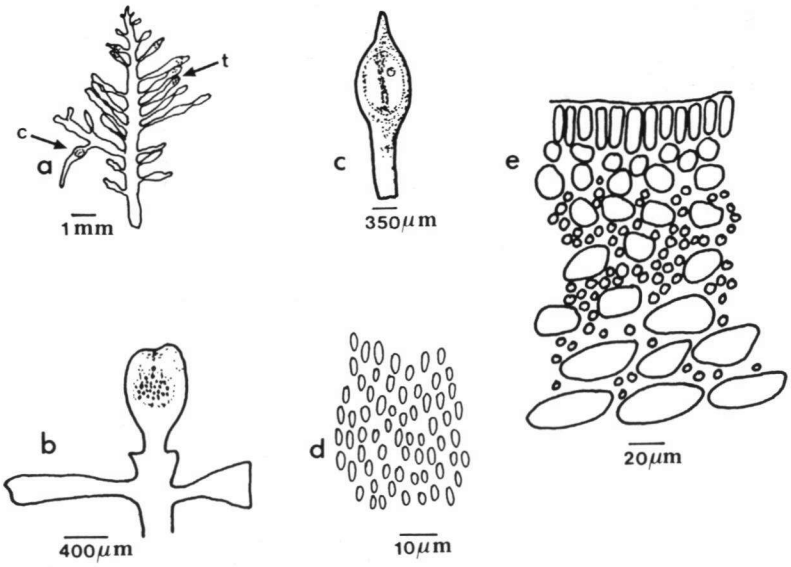

Fig. 7. *Gelidium latifolium* forma *elongatum*. a. Outline of erect thallus part bearing a cystocarp (arrow c) and tetrasporangia (arrow t); b. tetrasporangial ramulus; c. cystocarpic ramulus; d. surface view of external cortical cells; e. cross section of a secondary axis (a, b, d, e type, Mid Java, L 941,27-299; c Coast of S Java, L 19998).

(fig. 7e). Tetrasporangia irregularly arranged on spatulate terminal ramuli (fig. 7a, arrow t), rounded in surface view, diameter 20–30 µm (fig. 7b). Cystocarps on lanceolate terminal ramuli (fig. 7a, arrow c), bilocular, with a single ostiole at each surface (fig. 7c).Cystocarps and tetrasporangia occasionally occurring together on a single thallus (fig. 7a, arrows).

Distribution. This forma has only been observed in Indonesia: S coast of Sumatra, coasts of Java and the Lesser Sunda Islands.

Discussion. After Weber-van Bosse (1921) identified specimens from Noimini Bay, Timor and from the S coast of Mid Java as *Gelidium latifolium*, she and Mrs. Dr. J.Th. Koster accordingly named several other specimens collected from Indonesia. However, the specimens from Indonesia differ from European specimens in being less branched and somewhat higher, and also in having an emarginate apex in terminal small ramuli. In cross section, the external cortical cells of Indonesian specimens are palissade-like. We found these characters in all 20 samples of forma *elongatum* studied, and thus we are sure that these are not only seasonal differences to be included in the normal variability of this variable species (compare Dixon & Irvine, 1977a).

In gross morphology this forma resembles growth forms of *G. reediae* Loomis and *G. micropterum* Kützing. In *G. micropterum* a disc-like holdfast is characteristic, as well as internal rhizines only occurring between the medulla cells. Differences with *G. reediae* are less obvious, but thalli of that species have a softer structure and

Table 2. Comparison of specimens of *Gelidium latifolium* and *Gelidium reediae*.

Characters	*G. latifolium* f. *elongatum* Type Mid Java	*Gelidium latifolium*		*G. reediae* Isotype Hawaii MR. 999 LAM
		Canary Islands[1]	France[2]	
Form of frond	Pyramidal	Pyramidal	Pyramidal	Pyramidal
Height (cm)	3.5	3.5	3.0	2.5
Erect thallus parts	Main axis 0.3–1 mm broad, constricted at base	Main axis 0.3–0.9 mm broad, constricted at base	Main axis 0.3–0.8 mm broad, constricted at base	Main axis 0.3–0.8 mm broad constricted at base
Branching pattern	Pinnate or opposite	Pinnate	Irregularly pinnate or opposite	Pinnate or subopposite
– degree of branching	Up to 4th order	3rd or 4th order	Up to 5th order	Up to 4th order
– origin of branching	Lateral	Lateral	Lateral or from distal part of compressed erect thallus	Lateral
Terminal small ramuli	Lanceolate or spatulate	Lanceolate	Lanceolate, very slender	Lanceolate
– apex of terminal small ramuli	Emarginate or blunt	Short conical or blunt	Conical, attenuate or blunt	Blunt
Tetrasporangia	On spatulate stichidia	Not present	On rounded or ovoid stichidia with long stalk	On lanceolate stichidia
Cystocarps	On lanceolate branches, with one ostiole at each surface	Not present	Not present	On lanceolate branches, with one ostiole at each surface
In cross section				
– external cortical cells	Subquadrangular, anticlinally elongate, 6–17 × 2–5 µm	Rounded, diam. 4–6 µm	Rounded, diam. 4–6 µm	Ovate, anticlinally elongate, 3–4 × 5–6 µm
– inner cortical cells	3–4(–5) layers, inwards grading to larger, irregularly arranged, diam. 6–17 µm	4–6 layers, ovate, inwards grading to larger, irregularly arranged, diam. 7–12 µm	4–5 layers, rounded, inwards grading to larger, irregularly arranged, diam. 6–10 µm	3–5 layers, rounded, inwards grading to larger, irregularly arranged, diam. 6–12 µm
– medulla cells	Ovate, regularly arranged, 14–28 × 8–10 µm	Ovate, regularly arranged, 16–22 × 8–15 µm	Ovate, regularly arranged 12–22 × 8–10 µm	Ovate, regularly arranged, 10–20 × 6–10 µm
– internal rhizines	Congested between inner cortical cells and scarce between medulla cells	Congested between inner cortex cells and scarce between medulla cells	Congested between inner cortex cells and scarce between medulla cells	Numerous & conspicuous in inner cortex and between the most external medullary cells

1) Isla de Alegranza, Gramonal '83, leg. W.F. Prud'homme van Reine 8048 (L 349171).
2) Port Vendres, harbour, leg. W.F. Prud'homme van Reine 706, (L 972,088-166).

a less developed medulla (table 2). We studied the holotype of *G. reediae* (Hawaii, *Loomis 82871*, in LAM) and also detected a specimen collected in Antibes (Mediterranean France) by Børgesen in Nov. 1897 (L 941,46-223, determined as *G. corneum* by Reinbold).

Gelidium pusillum (Stackhouse) Le Jolis

Fucus pusillus Stackhouse (1795) 16, t. 6. — *Acrocarpus pusillus* Kützing (1849) 762. — *Gelidium pusillum* Le Jolis (1863) 139; Weber-van Bosse (1921) 225; Feldmann & Hamel (1936) 236; Børgesen (1943) 6; Dawson (1944) 258, t. 42, f. 1–6; (1953) 62; (1954) 420; Egerod (1971) 129, f.32–49; Dixon & Irvine (1977a) 129; Santelices (1977) 71, f. 4; Stewart & Norris (1981) 275; Tanaka & Chihara (1988) 100. — T y p e: *Stackhouse s.n.*, s.l., supposedly Sidmouth, England (BM, not seen; see Dixon & Irvine, 1977b).

Fucus crinalis Turner (1819) 4, t. 198. — *Gelidium crinale* Lamouroux in Bory (1825) 191; Feldmann & Hamel (1936) 240; Dawson (1954) 420; Santelices (1977) 67, f. 2a–c. — *Acrocarpus crinalis* Kützing (1849) 761. — T y p e: *Turner s.n.*, s.l., supposedly Ilfracombe, England (BM, not seen; see Dixon & Irvine, 1977b).

Fucus corneus var. *pulchellus* Turner (1819) 146, t. 257, f. p. — *Gelidium pulchellum* Kützing (1868) 18, t. 53, f. e & f; Feldmann & Hamel (1936) 243. — T y p e: No type selected.

Gelidium pusillum var. *conchicolum* auct. non Piccone & Grunow in Piccone (1884) 316; Weber-van Bosse (1921) 225; Taylor (1960) 355; Santelices (1977) 71. — T y p e: No type selected.

Gelidium microphysa Setchell & Gardner (1930) 151, t. 9, f. 31. — T y p e: *Setchell & Gardner 173635*; *Mason 121*, Guadalupe Island, Pacific Mexico (probably in LAM, not seen; see Stewart & Norris, 1981).

KEY TO THE VARIETIES OCCURRING IN INDONESIA
(see also table 3)

1a. Plants usually less than 1 cm high, often crowded together to form mats . . . 2
b. Plants usually more than 1 cm high, distally usually compressed
7. var. **pusillum**
2a. Erect thallus parts mostly unbranched, filiform or spatulate throughout
8. var. **minusculum**
b. Erect thallus parts branched 3
3a. Erect thallus parts cylindrical or distally becoming compressed
9. var. **cylindricum**
b. Erect distal parts compressed throughout: young specimens of
7. var. **pusillum**

7. Gelidium pusillum (Stackhouse) Le Jolis var. pusillum – Fig. 8

Small, mat-forming, saxicolous plants, occasionally tufted, 2–24 mm high, consisting of cylindrical prostrate axes (diam. 120–200 μm), attached to the substrate by peg-like or disk-like haptera (disks 200–650 μm in diam.), issued at irregular intervals and often opposed to the erect thallus parts (fig.8a) which are distally terete and constricted and proximally ovate to compressed, 80–100 × 110–1000 μm in cross section. Branching irregular and not in one plane; branches distally terete and

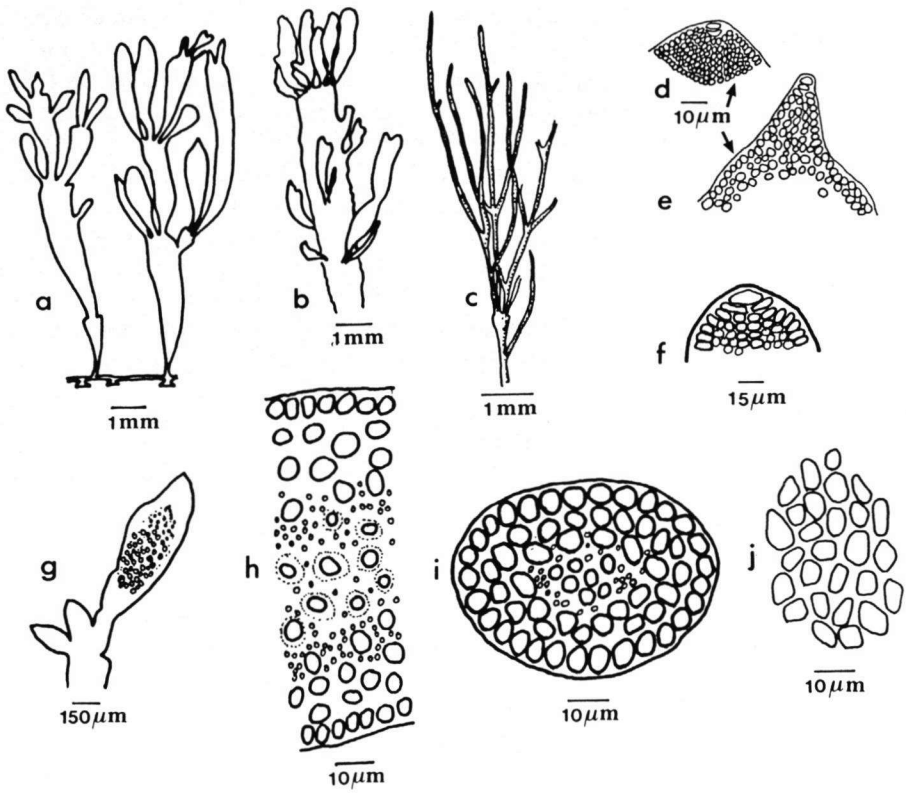

Fig. 8. *Gelidium pusillum* var. *pusillum*. a–c. Habit of plants; d–f. apices in surface view; g. terminal ramuli with tetrasporangia; h, i. cross section of erect thallus parts, h. middle part, i. proximal part of a branch; j.cortical cells in surface view (a, b, g, h Muara Arau, Mid Sumatra, L 958,169-829; c, f, i, j Pijot Bay, Lombok, L 934,263-2; d, e Damar Island, L 941,27-305).

constricted, proximally ovate to compressed (fig. 8a–c). Apex of erect thallus parts conical, mostly with a conspicuous, often extruding apical cell (fig. 8d–f). Cortical cells somewhat angular or rounded to ovate in surface view, diameter 4–8(–11) μm, irregularly arranged (fig. 8j). In cross section, outer cortical cells rounded to ovate, 3–5 × 4–8 μm; inner cortical cells rounded, in 2–3 layers, diameter 4–8 μm; medulla cells also rounded, inwards gradually larger, diameter 4–12 μm (fig. 8h, i). Internal rhizines straight and mostly congested between innermost cortical cells and outermost medulla cells, and usually less frequent between medulla cells (fig. 8h, i). Tetrasporangia irregularly arranged in spatulate terminal ramuli (fig. 8g), rounded in surface view, diameter 20–30 μm. Cystocarps not observed in Indonesian specimens.

Distribution. World: worldwide in the tropics as well as in temperate waters. Indonesia: Muara Arau (S coast of Mid Sumatra), Jangkar Island (Jakarta Bay), Damar Island, Lombok, Flores, and Timor.

Discussion. The circumscription of the species *G. pusillum* in Europe as well as in tropical regions has always been a problem. In the N Atlantic often the suggestion by Dixon & Irvine (1977b) is followed, to consider all *Gelidium* species with predominantly cylindrical axes as belonging to *G. pusillum*. In recent papers on Gelidiales, however, usually *G. pusillum* and *G. crinale* are again considered as different taxa (Santelices, 1988; Zhang & Xia, 1988). If *G. crinale* has to be separated again, the specimens from Lombok (fig. 8c, f, i, j) would be named as such. Whether it is necessary or even possible to discern separate entities (forms or varieties) in this complex has also often been discussed. Dawson (1944), Egerod (1971), and recently Stewart & Norris (1981) refrain from separating taxa within this species, but Santelices (1977) prefers to mention the several forms separately until transplant or other kinds of experimental study throw light upon the taxonomic status of these varieties.

In the present paper we will discuss varieties as separate taxa, and therefore descriptions will follow of *G. pusillum* var. *minusculum* and *G. pusillum* var. *cylindricum*. All studied specimens of Indonesian *Gelidium pusillum* (sensu Dixon & Irvine) not included in these two separate varieties have been considered by us as belonging to *G. pusillum* var. *pusillum*. This concerns also *G. pusillum* var. *conchicola* as described by Weber-van Bosse, which name has been used for young specimens of var. *pusillum*. However, the isotype of *G. pusillum* var. *conchicola* Piccone & Grunow cannot be considered as belonging to *G. pusillum*: it most probably belongs to *Pterocladia caerulescens* and will be discussed as such. *Gelidium crinale* var. *perpusillum* Piccone & Grunow, recorded from Indonesia by Tanaka & Chihara (1988), most probably also belongs to *G. pusillum* var. *pusillum*.

Egerod (1971) stated that there are at least five species of *Pterocladia* which appear to come close to *G. pusillum* on vegetative features alone. She listed *P. musciformis* Taylor and *P. mcnabbiana, P. media, P. parva,* and *P. tropica,* all described by Dawson. Of these, the first three species were estabilished on plants lacking cystocarps, and thus a final assignment to genus would be impossible. The other two *Pterocladia* species of Egerod's list are now included in the synonymy of two other *Pterocladia* species described in the present paper, and these two species differ clearly from *G. pusillum*. The first three taxa of *Pterocladia,* whether good or not, have not been compared by us with our concept of *G. pusillum*.

8. **Gelidium pusillum** (Stackhouse) Le Jolis var. **minusculum** Weber-van Bosse Fig. 9

Gelidium pusillum var. *minusculum* ('*minuscula*') Weber-van Bosse (1921) 226; Feldmann & Hamel (1936) 238; Santelices (1977) 71. — Type: *Siboga Exp. station 165*, Daram Island (Valsche Pisang), Weber-van Bosse (L 943,5-132).

Gelidium pusillum var. *conchicola* auct. non Piccone & Grunow in Piccone (1884): Okamura (1929–1932) 42, t. 273, f. 7–10.

Small, mat-forming, saxicolous plants, 0.5–5.2 mm high, consisting of cylindrical prostrate axes (diam. 120–160 μm), attached to the substrate by peg-like haptera, issued at irregular intervals and often opposed to the erect thallus parts and by rhizoids arising solitary or in groups from the ventral side of the prostrate axes

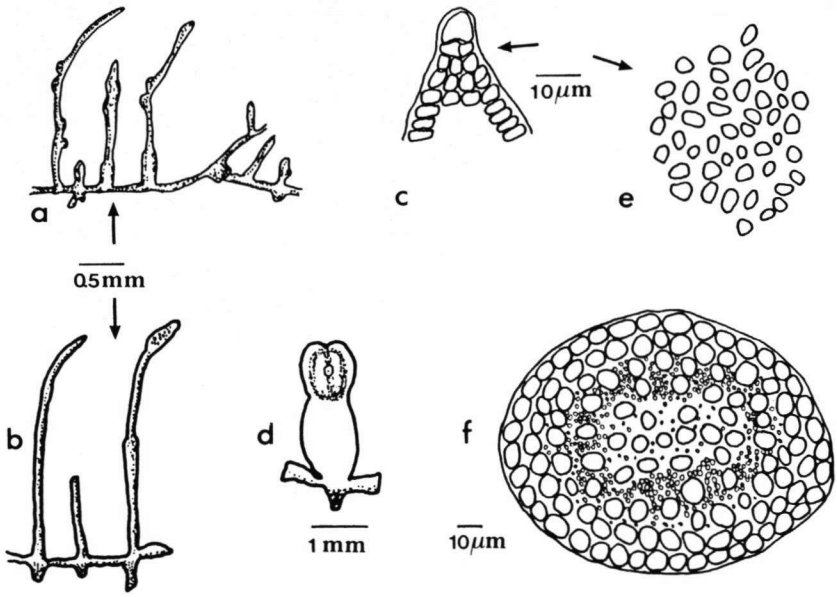

Fig. 9. *Gelidium pusillum* var. *minusculum*. a & b. Habit of plants, a. growing on mangrove, b. growing in a lagoon; c. apex of an erect thallus part in surface view; d. cystocarpic erect thallus part; e. surface view of cortical cells; f. cross section of an erect thallus part (a, c Sumba, *SN-II, 10605*; b, e, f Nusa Kambangan, Mortensen coll. in C; d Sumbawa, *SN-II, 11092*).

(fig.9a, b). Erect thallus parts unbranched and filiform, diameter 80–135 μm and occasionally with small proliferations, or spatulate, 75–85 μm thick and 380–450 μm broad (fig.9a, b). Apex of erect thallus parts attenuate to conical; apical cell conspicuous and extruding (fig. 9c). Cortical cells in surface view rounded to ovate, 3–6 × 4–9 μm, irregularly arranged (fig. 9e). In cross section, outer cortical cells quadrangular or ovate to anticlinally elongate (6–8 × 4–6 μm); inner cortical cells ovate, diameter 6–9 μm, in 2 layers; medulla cells rounded, inwards gradually somewhat larger, 5–8 μm in diameter(fig. 9f). Internal rhizines straight and abundant, surrounding the medulla cells. Tetrasporangia irregularly arranged in swollen distal parts of erect thallus, round in surface view, diameter 28–35 μm. Cystocarp rounded, diameter 350–385 μm, on spatulate distal parts of erect thallus, bilocular with one ostiole at each surface (fig. 9d).

Distribution. Possibly worldwide distributed in warm to tropical seas. Indonesia: Daram Island, Ambon, Nusa Kambangan (S coast of Mid Java), Sumba, and Sumbawa.

Discussion. The specimens from Nusa Kambangan are from the Mortensen collection in Copenhagen (C) where they were labelled as *Gelidium bornetii* Weber-van Bosse. Although they come from the type locality of *G. bornetii*, the specimens are not in accordance with the description by Weber-van Bosse, indicating absence of internal rhizines. In the specimens in this rich sample from Nusa Kam-

Table 3. Comparison of small *Gelidiums* from Indonesia.

Characters	*G. pusillum* var. *pusillum* [1]	*G. pusillum* var. *minusculum*		*G. pusillum* var. *cylindricum* [4]	*G. amboniense* Type Ambon Bay [5]
		From mangrove[2]	From lagoon[3]		
Height	2–3 mm	0.5–5.2 mm	0.5–2 mm	2–10 mm	0.5–2.5 mm
Haptera	Peg-like	Peg-like, very frequent	Peg-like	Peg-like	Peg-like
Branching pattern	Irregular	Lacking	Lacking	Irregular, occasionally trifid, not in one plane	Lacking or almost lacking
Erect thallus parts	Constricted and terete at the base, 110–180 µm wide, distally compressed, 200–1000 µm wide	Filiform throughout, 80–135 µm wide	Constricted at the base and distally spatulate, 380–450 µm wide	Cylindrical at proximal part, 133 × 185 µm, distally cylindrical throughout or compressed, 40–75 × 50–230 µm	Cylindrical throughout or distally compressed (40–50 × 40–230 µm)
Surface cells	Angular, irregularly arranged, diam. 4–8(–11) µm	Rounded, irregularly arranged, diam. 4–9 µm	Rounded to ovate, irregularly arr., diam. 3–6 µm	Rounded to ovate, irregularly arr., diam. 4–6 µm	Rounded, ovate, or irregular, irreg. arr., 4–8 × 3–5 µm
In cross section:					
- external cortical cells	Round to ovate, anticlinally elongate, 3–8 × 4–8 µm	Subquadrangular, anticlinally elongate, 6–8 × 4–6 µm	Ovate, anticlinally elongate, 6–8 × 4–6 µm	Subquadrangular to rounded, anticlinally elongate, 6–8 × 4–6 µm	Quadrangular, anticlinally elongated, 6–10 × 4–5 µm
- inner cortical cells	In 2 or 3 layers, rounded, diam. 4–8 µm	In 2 layers, ovate, diam. 6–9 µm	In 2 layers, ovate, diam. 6–8 µm	In 2 or 3 layers, rounded to ovate, diam. 6–8 µm	In single layer, subquadrangular to rounded, diam. 7–10 µm
- medulla cells	Rounded, inwards grading to larger, diam. 4–12 µm	Rounded, inwards grading to larger, diam. 5–8 µm	Rounded, inwards grading to larger, diam. 6–8 µm	Rounded, inwards grading to larger, diam. 6–12 µm	Rounded, in a single tier, diam. 8–10 µm
- internal rhizines	Numerous between innermost cortical cells, less frequent in medulla zone	Abundant, surrounding outer medulla cells, scanty in medulla zone	Abundant, surrounding outer medulla cells, scanty in medulla zone	Abundant, between innermost cortical cells, scanty in medulla zone	In a small number, around medulla cells
Tetrasporangia	Not present	Not present	Not present	In lanceolate or ligulate stichidia, rounded to ovate, irreg. arr., diam. 28–35 µm	In swollen apical parts of erect thallus, rounded, irreg. arr., diam. 30–35 µm
Cystocarps	Not present	Not present	In spatulate erect thallus parts, with one ostiole at each surface	Not present	Not present

1) Sikka, Flores (labelled *G. pusillum* var. *conchicola* by Weber-van Bosse, L 941,27-305). — 2) Sumba (*SN-II, 10605*). — 3) Sumbawa (*SN-II, 11092*). — 4) Kangean Reef, Madura (L 943,5-131). — 5) Ambon Bay, type (*SN-II, 10006 A*).

bangan, internal rhizines are always present and thus the specimens do belong to the genus *Gelidium*. The specimens described by Weber-van Bosse, however, must belong to the genus *Gelidiella*. See also discussion under *Gelidiella lubrica* in the present paper. For comparison with *G. pusillum* var *pusillum* (including *G. pusillum* var. *conchicola*) and *G. amboniense* see table 3.

9. Gelidium pusillum (Stackhouse) Le Jolis var. cylindricum Taylor – Fig. 10

Gelidium pusillum var. *cylindricum* Taylor (1945) 154, t. 5, f. 1; Santelices (1977) 72, f. 4 C, E; (1988) 102, f. 9. — T y p e: *Taylor 34-490 C*, Bahia San Francisco, Esmaraldas, Ecuador (probably in LAM, not seen).

Small, mat-forming, saxicolous plants, occasionally tufted, 2–10 mm high, consisting of cylindrical prostrate axes (diam. 80–150 µm), attached to the substrate by peg-like haptera, issued at irregular intervals and often opposed to the erect thallus parts, which are proximally cylindrical, diameter 135–185 µm, distally cylindrical throughout or compressed, 45–75 × 50–230 µm (fig. 10a). Branching irregular, occasionally trifid, not in one plane; branches similar to the axes. Apex of erect branches truncate, often with 2–5 proliferations, often with a conspicuous, extruding apical cell. Cortical cells round to ovate in surface view, 4–6 µm, irregularly arranged. In cross section, outer cortical cells subquadrangular to ovate, anticlinally elongate, 6–8 × 4–6 µm; inner cortical cells rounded to ovate, in 2–3 layers, cells 6–8 µm in diameter; medulla cells rounded, inwards gradually larger diameter, up to 12 µm (fig. 10b). Internal rhizines congested between innermost cortical cells and outermost medulla cells, very few between inner medulla cells (fig. 10b). Tetraspo-

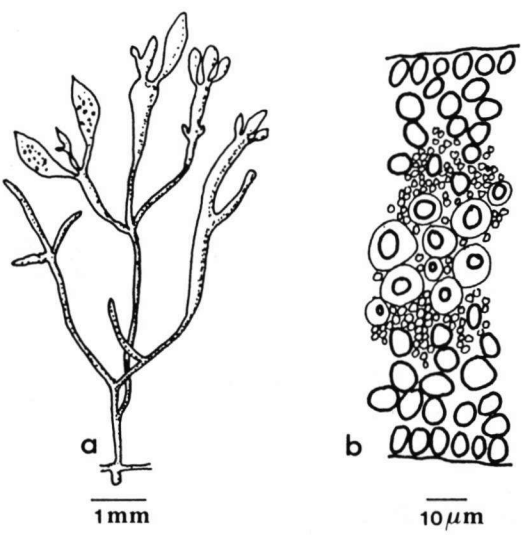

Fig. 10. *Gelidium pusillum* var. *cylindricum*. a. Habit; b. cross- section of a cylindrical part of an erect thallus (a, b Kangean Reef, E Madura Island, L 943,5-131).

rangia irregularly arranged in lanceolate or ligulate stichidia, 340–535 × 665–1560 µm, tetrasporangia rounded to ovate in surface view, diameter 28–35 µm. Cystocarps not observed.

Distribution. World: Pacific Ecuador, Costa Rica, Gulf of California, Indonesia, and possibly also Hawaii. Indonesia: Kangean Reef, E Madura.

Discussion. The description and figure by Santelices (1977) do not in all details conform with Taylor's description. Our specimens, however, agree very well with that description (Taylor, 1945).

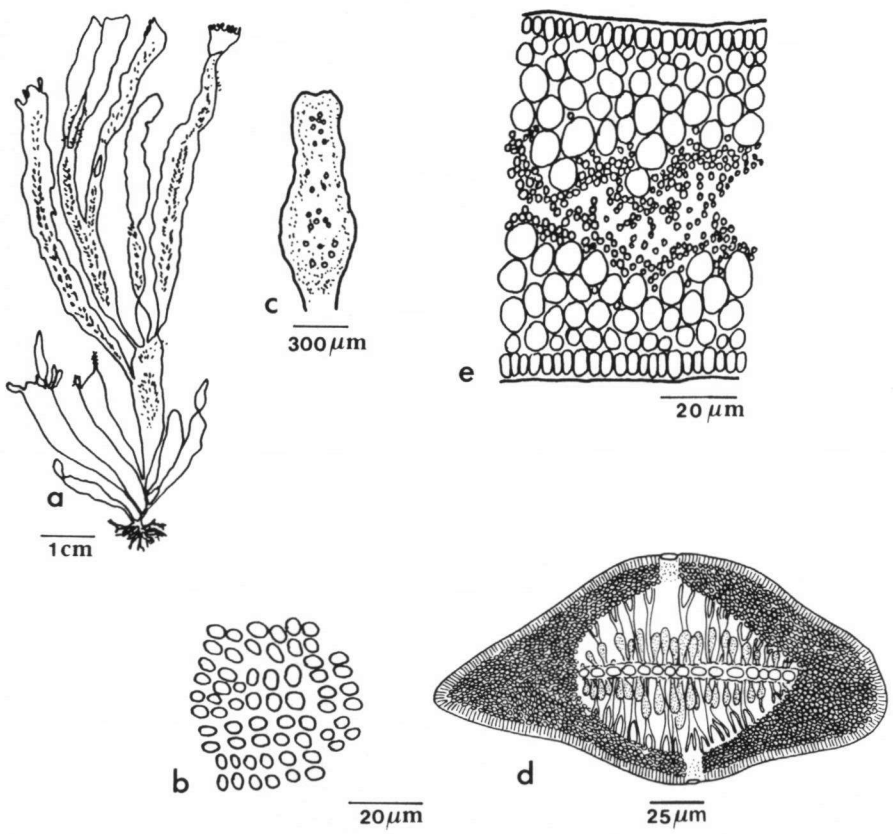

Fig. 11. *Porphyroglossum zollingeri*. a. Habit; b. surface view of cortical cells, arranged in tetrads; c. tetrasporangial ramulus; d. cross section of a cystocarp (after Weber-van Bosse, 1921); e. cross section of a young erect thallus part (a type; b, c, e Nusa Kambangan, L 942,246-270).

PORPHYROGLOSSUM

Porphyroglossum Kützing (1847) 775. — Type: *Porphyroglossum zollingeri* Kützing. For discussion, see under that species.

Table 4. Comparison of characters of the genus *Gelidium* and of *Porphyroglossum zollingeri*.

Characters	*Gelidium*	*Porphyroglossum zollingeri*
Cystocarps	Bilocular	Bilocular[1-3]
Ostioles[2]	Provided on each surface, with raised position	Provided on each surface with flat or raised position
Form of stichidia	Oblong[2]	Oblong or spatulate
Holdfast[2]	Fibrous	Fibrous
Growth pattern[2, 3]	Monopodial	Monopodial
Development of erect thallus	Initiated by a dome-shaped apical cell	Initiated by a dome-shaped apical cell
Surface cells[2]	Round to elliptic, arranged in pairs or without order	Round to elliptic, arranged in tetrads or in pairs
Histological structure	– Inner cortical cells & medulla cells are usually well differentiated	– Inner cortical cells & medulla cells are similar
	– Internal rhizines are congested in the inner cortical part or/and in the medulla	– Internal rhizines are congested in the medulla

1) Weber-van Bosse (1921).
2) Akatsuka (1986).
3) Fan (1961).

10. Porphyroglossum zollingeri Kützing – Fig. 11

Porphyroglossum zollingeri Kützing (1847) 775; (1849) 794; (1869) 17, t. 45, f. a–d; Fan (1961) 319, f. 1e, t. 33; Akatsuka (1983) 205, f. 9; (1986b) 60. — T y p e: SE Java near Malang, *Zollinger 2109* (L 941,182-77).

Plants are shrubby, erect, and somewhat complanate when all erect axes and branches are arranged in one plane, 3.5–14 cm high, consisting of short, narrow, much branched, recurved, stolon-like prostrate axes (diam. 200–300 µm), attached to the substrate by numerous peg-like haptera 250–450 µm in length, issued at irregular short intervals, and erect, irregularly branched thallus parts (fig. 11a). Branches of two forms: large, ribbon-like, lanceolate to linear main axes of unlimited growth, proximally terete, diameter 450–600 µm, more distally progressively flattened, up to 6 mm in width, with new, ribbon-like undeterminate branches arising by 2–4 from truncated distal parts of the main erect axes and small, determinate, spatulate ramuli, up to 1.5 mm in length, which arise in longitudinally arranged rows from the surface of the flattened, indeterminate, erect thallus parts (fig. 11a). Apex of the indeterminate erect thallus parts blunt to emarginate, often truncated and proliferating, apical cells sunken and not very conspicuous (Fan, 1961, f. 1e). Cortical cells rounded to ovate in surface view, more or less arranged in tetrads, diameter 4–7 µm (fig. 11b). In cross section outer cortical cells rounded, diameter 4–8 µm, inner cortical cells as well as medulla cells round and inwardly grading to larger diameters, 5–12 µm (fig.

11e). Internal rhizines straight and congested in the medulla (fig. 11e). Tetrasporangia on small determinate ramuli, irregularly arranged and rounded in surface view, diameter 18–25 µm (fig. 11c). Cystocarps on small determinate ramuli, bilocular, with one ostiole on each surface (fig. 11d).

Distribution. World: only known from Indonesia. Indonesia: S coast of Java.

Discussion. The genus *Porphyroglossum* has been erected by Kützing (1847) with only one species. Later Schmitz (1894) added a second species, *P. japonicum* (= *Suhria japonica* Harvey). However, Akatsuka (1986b) inserted the latter species in his new genus *Onikusa*, leaving *Porphyroglossum* as a monotypic genus. The cell-rows of secondary order, as observed by Akatsuka (1983), have not been seen by us in our slides of Indonesian material. Whether this genus can be maintained is questionable and a close relationship with the genus *Gelidium* is apparent, as can be observed in table 4.

PTEROCLADIA

Pterocladia J. Agardh (1851) XI. — Type: *Pterocladia lucida* (Turner) J. Agardh. For description and discussion see Dixon & Irvine (1977a) 134 and Fan (1961).

11. Pterocladia caerulescens (Kützing) Santelices – Fig. 12

Gelidium caerulescens ('*coerulescens*') Kützing (1868) 19, t. 56, f. c, d. — *Pterocladia caerulescens* Santelices (1976) 173; (1977) 79; Cribb (1983) 34, t. 36, f. 3. — Type: *Vieillard 2103*, Wagap, New Caledonia (L 941,11-91).

Pterocladia tropica Dawson (1959) 40, f. 21 A–D, 22 B. — Type: *Dawson 19458*, Palmyra Atoll, Pacific Ocean [UC, not seen; see Santelices (1976)].

Gelidium irregulare Loomis (1960) 6. — Type: *Reed 965, Loomis 2974*, Peninsula, Pearl Loch, Hawaiian Islands (originally in AHFH, see Silva, 1978, now in LAM, not seen).

Gelidium corneum auct. non (Hudson) Lamouroux: Weber-van Bosse (1921) 225. — No type selected.

Small, erect, tufted, solitary plants, 6–30 mm high, consisting of short, cylindrical, prostrate axes (diam. 125–200 µm), attached to the substratum by peg-like haptera issued at short irregular intervals and branched erect thallus parts, proximally constricted and distally compressed, 100–175 × 300–900 µm (fig. 12a). Branching bipinnate or tripinnate, proximal laterals long and slender, distal laterals opposite or irregularly alternate, becoming shorter near the apex (fig. 12a). Apical parts of all axes and laterals blunt with a quite conspicuous, often somewhat extruding, apical cell (fig. 12b). In surface view cortical cells ovate, c. 2 × 6 µm, arranged in diagonal rows (fig. 12c). In cross section outer cortical cells quadrangular, anticlinally elongate, 6–11 × 4–5 µm; inner cortical cells in 2–3 layers, subquadrangular, inwards gradually larger, 7–11 × 7–14 µm; medulla cells ovate, more or less in rows, diameter 14–18 µm (fig. 12d). Internal rhizines straight and congested between the medulla cells. All Indonesian collections are sterile.

Distribution. World: tropical parts of the Indo-Pacific Ocean (Hawaii Islands, New Caledonia, Indonesia, Ceylon). Indonesia: Noimini (Timor Island).

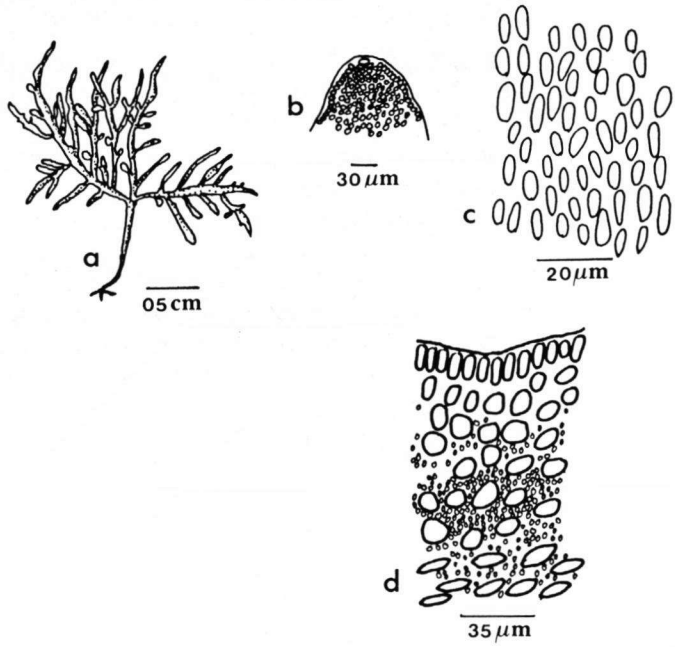

Fig. 12. *Pterocladia caerulescens*. a. Habit; b. apex with apical cell; c. cortical cells in surface view; d. cross section of an erect thallus part (a–d Noimini, Timor Island, L 941,27-272).

Discussion. Weber-van Bosse (1921), naming the Noimini specimens as *Gelidium corneum*, cited a figure by Børgesen (1916) as supposed to be identical. However, this Børgesen material has been included by Taylor (1943) in *Pterocladia capillacea* (Gmelin) Bornet & Thuret and *Gelidium americanum* (Taylor) Santelices (as *P. americana*). The type of *G. americanum* is Exsiccata *783* of the Phycotheca Boreali Americana in Taylor's personal herbarium. This specimen has been distributed as *G. caerulescens* Crouan, to which was added, with question mark, a reference to Kützing's description. The study by Santelices (1976) has made clear that these two entities are different taxa. In a sample from Ceylon of *P. caerulescens* we observed tetrasporangia. Santelices (1976) cited *P. rigida* Loomis as a synonym of *P. caerulescens* Kützing. Silva (1978) observed cystocarps with more than one ostiole on one side, calling for a reconsideration of the relationship between *P. rigida* and the other *Pterocladia* species.

12. Pterocladia caloglossoides (Howe) Dawson – Fig. 13

Gelidium caloglossoides Howe (1914) 96, t. 34, f. 1, t. 35; Weber-van Bosse (1921) 226. — *Pterocladia caloglossoides* Dawson (1953) 76; Santelices (1977) 78; Stewart & Norris (1981) 281; Cribb (1983) 34, t. 7, f. 2–5: Norris (1987) 39. — Type: *Coker 59*, Island of San Lorenzo, Peru [in NY, not seen, see Dawson (1953) and Stewart & Norris (1981)].

Pterocladia parva Dawson (1953) 77, t. 6, f. 2; (1954) 421, f. 33a–c. — T y p e: *Dawson 425*, San Filipe, Baja California, Mexico [LAM, not seen, see Stewart & Norris (1981)].

Small, mat-forming, saxicolous plants, 3–10 mm high, consisting of terete prostrate axes (diam. 60–75 µm), attached to the substrate by peg-like haptera, issuing at regular intervals opposite to branched erect thallus parts, proximally terete, diameter 80–100 µm in cross section, and distally compressed throughout, 70 × 240–300 µm in cross section (fig. 13a, d, e). Branching pectinate, branches arise laterally from the margins of the erect compressed axes (fig. 13a). Apices of all erect parts conical, with a conspicuous, somewhat extruding apical cell (fig.13b). In surface view cortical cells round to ovate, diameter 5–10 µm, somewhat regularly arranged in longitudinal rows in older parts (fig. 13c). In cross section external cortical cells quadrangular, 4–10 × 4–8 µm; inner cortical cells in 2 or 3 layers, rounded to ovate, diameter 7–10 µm, irregularly arranged; medulla cells in 1–4 layers, rounded, diameter 7–10 µm (fig. 13d, e). Internal rhizines straight, grouped in the medulla (fig. 13d, e). Cystocarps solitary or in series of 2 or 3 on branches, ovate, 210–250 × 280–360 µm, unilocular, with one ostiole on one side (fig. 13a, arrows). No tetrasporangia observed.

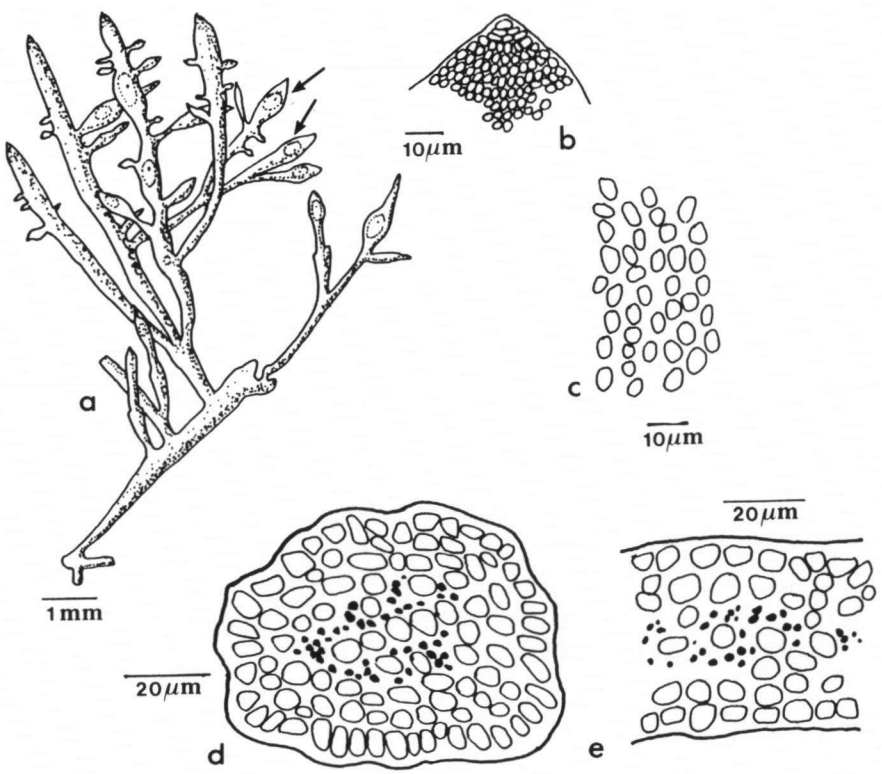

Fig. 13. *Pterocladia caloglossoides*. a. Habit, with cystocarps (arrows); b. apex in surface view; c. cortical cells in surface view; d & e. cross section of erect thallus, d. proximal terete part, e. distal compressed part (a–e Maumeri, Flores, L 941,27-306).

Distribution. World: tropical and warm temperate parts of the Indo-Pacific Ocean (Peru, Mexico, U.S.A., Hawaii, Great Barrier Reef, Philippines, Indonesia, Singapore, Vietnam, South Africa). Indonesia: Maumeri (Flores).

Discussion. The specimen from Maumeri had been named *Gelidium pusillum* var. *conchicola* by Weber-van Bosse (1921). We have compared it with specimens from the Rijksherbarium collection from Vietnam (*Dawson 11222*, as *Pterocladia parva*, L 961,231-134), Singapore (*Burkill 3365*, as *Gelidium prox.*, L 964,214-327), and San Juan Island, Washington, U.S.A. (*Norris 7242*, L 313845), and with published descriptions. Morphological variation in this species is rather large. Variations in height of the plants is from 2.4–3 mm (Norris, 1987; Cribb, 1983) to 25 mm (specimens from San Juan Island and Singapore). The pectinate branching, up to the third order in Indonesian specimens, can become pinnate or divaricate and up to the second order only (Norris, 1987; Cribb, 1983) or even palmate (specimens from Singapore and Vietnam). In the medulla 1–4 layers of cells occur in all specimens originating from Asian localities and in the type material, but Cribb (1983) observed up to 7 cell layers in his Great Barrier Reef specimens. In the San Juan Island specimens the number of internal rhizines is much higher than in specimens originating from Asian localities.

WURDEMANNIA

Wurdemannia Harvey (1853) 245; Kylin (1956) 561; Taylor (1960) 361; Papenfuss (1966) 101. — Type: *Wurdemannia setacea* Harvey = *Wurdemannia miniata* (Duby) Feldmann & Hamel.

Pseudogelidium Schiffner (1933) 292. — Type given as *Pseudogelidium minutum* (Lamouroux) Schiffner (= *Wurdemannia miniata*).

Discussion. *Wurdemannia* is a monotypic genus of uncertain systematic position. For a discussion see Papenfuss (1966). According to that author this genus, for which Taylor (1960) erected a new family Wurdemanniaceae within the Gelidiales, may belong either to the Cryptonemiales or to the Gigartinales, the latter order perhaps being the more likely one.

13. Wurdemannia miniata (Sprengel) Feldmann & Hamel – Fig. 14

Fucus miniatus Draparnaud ex De Candolle (1815) 6, non O.F. Müller (1778) 7, t. 769, which is *Callophyllis laciniata* (Hudson) Kützing (Rhodophyceae). — *Sphaerococcus miniatus* Sprengel (1827) 340. — *Gelidium miniatus* Lamouroux (1813) 137, nom. nud.; Duby (1830) 953; Kützing (1849) 767; (1868) 20, t. 58, f. c–h. — *Wurdemannia miniata* Feldmann & Hamel (1934) 544; (1936) 260; Taylor (1960) 361; Papenfuss (1966) 101. — Lectotype: near Montpellier, Mediterranean France (in PC, not seen; see Feldmann & Hamel, 1934). For nomenclature see Silva, Meñez & Moe (1987).

Wurdemannia setacea Harvey (1853) 245; Kützing (1869) 9, t. 26, f. a–k; Børgesen (1916) 368. — Type: *Harvey 53*, Florida Keys, leg. Wurdemann, not seen, probably in TCD.

Mat-forming saxicolous plants, 10–40 mm high, consisting of terete prostrate axes (diam. 100–200 µm), attached to the substratum by peg-like or disk-like haptera, issued at irregular intervals opposite to branched, cylindrical, erect thallus parts, diameter 100–225 µm (fig. 14a). Branching irregular, occasionally somewhat dis-

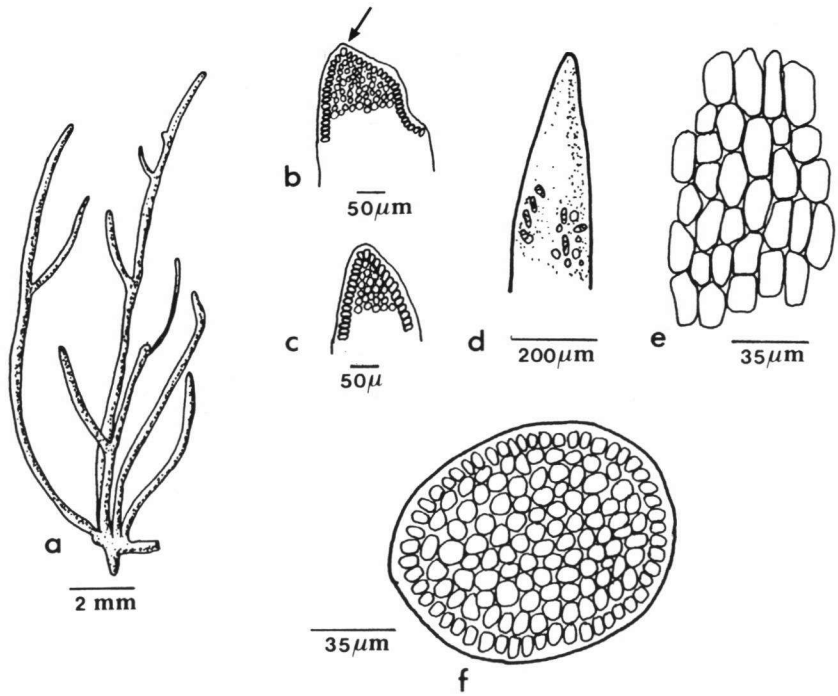

Fig. 14. *Wurdemannia miniata*. a. Habit; b–d. apices of erect thallus parts, in b a damaged specimen with fresh growth and an apical cell (arrow), in d with zonate tetrasporangia; e. surface view of cortical cells; f. cross section of an erect thallus part (a, c, f Komodo Island, *SN-II, 10784*; b Taka Bone Rate = Tiger Islands, *SN-II, 11341*; d, e Taka Bone Rate = Tiger Islands, *SN-II, 11346*).

tichous (fig. 14a). All erect parts apically attenuate to blunt, usually without a conspicuous apical cell (fig. 14b–d). Cortical cells in surface view angular, longitudinally elongate, 8–20 × 4–10 μm, somewhat regularly arranged in longitudinal rows (fig. 14e). In cross section outer cortical cells subquadrangular (7–21 × 7–11 μm); inner cortical cells and medulla cells rounded, diameter 8–17 μm (fig. 14f). No internal rhizines present. Tetrasporangia peripheral in unswollen branches, irregularly arranged, ovate in surface view (c. 34 × 16 μm) and zonately divided (fig. 14d). Cystocarps not known.

Distribution. World: in tropical and warm temperate waters all over the world. Records in literature may concern *Ceratodictyon* (= *Gelidiopsis*) *intricatum*. Indonesia: Ambon, Komodo, Taka Bone Rate (Tiger Islands).

Discussion. It is rather difficult to distinguish sterile specimens of this species from members of the *Ceratodictyon* group, more especially *C. intricatum*. The habit of both species is very similar, but in anatomy these taxa differ in the composition of the medulla. In *Wurdemannia* the internal cortical cells as well as the medulla cells are rounded in cross section and all are of more or less the same size. However, in *Ceratodictyon* the inner cortical cells are, in cross section, usually in

wardly grading to larger diameters and the medulla cells show a tendency to be smaller than the innermost cortical cells. Furthermore, in surface view cortical cells in *Wurdemannia* are angular and quite large, while in *Ceratodictyon* they are mostly rounded or ovate and much smaller. The best character to separate these two taxa is the manner of division of the tetrasporangia, however. In *Wurdemannia* tetrasporangia are zonate, in *Ceratodictyon* they are cruciate. Records of sterile specimens of which only the habit but not the internal structure is shown have not been cited by us in the references. Original specimens have to be studied in detail before they can be considered to belong to *Wurdemannia* or to *Ceratodictyon*.Erect thallus parts that have been damaged, for instance by grazing, may show an apical cell when they start growth to repair the damage (fig. 14b, arrow).

ACKNOWLEDGEMENTS

The first author thanks the director of the Rijksherbarium, Leiden, Prof. Dr. C. Kalkman, for providing room and facilities during his research. We both thank Dr. H.P.Nooteboom (L) for providing the Latin diagnoses.

REFERENCES

AGARDH, C.A. 1822. Species Algarum 1 (2). Lund.

AGARDH, J.G. 1851. Species Genera et Ordines Algarum 2 (1). Lund.

AKATSUKA, I. 1981. Comparative morphology of the outermost cortical cells in the Gelidiaceae (Rhodophyta) of Japan. Nova Hedwigia 35: 453–463.

— 1982. Preliminary observations and literature analysis of morphological variability in some Japanese species of Gelidium (Gelidiacae, Rhodophyta) and an evaluation of criteria used in their discrimination. Nova Hedwigia 36: 759–774.

— 1983. The morphological relationship between Gelidium japonicum (Harvey) Okamura and Gelidium pristoides (Turner) Kützing. Nova Hedwigia 37: 197–207.

— 1986a. Pterocladiastrum, a new genus segregated from Pterocladia (Gelidiales, Rhodophyta). Botanica mar. 29: 51–58.

— 1986b. Surface cell morphology and its relationship to other generic characters in non-parasitic Gelidiaceae (Rhodophyta). Botanica mar. 29: 59–68.

BLOMQUIST, H., & L.R. ALMODOVAR. 1961. The occurrence of Gelidiella tenuissima Feldmann et Hamel in Puerto Rico. Nova Hedwigia 3: 67–68.

BØRGESEN, F. 1916. The marine algae of the Danish West Indies 3 (2). Dansk Bot. Ark. 3: 81–144.

— 1919. The marine algae of the Danish West Indies 3 (5). Dansk Bot. Ark. 3: 305–368.

— 1932. A revision of Forsskål's algae ... Dansk Bot. Ark. 8 (2): 1–14.

— 1934. Some Indian Rhodophyceae, especially from the shores of the presidency of Bombay. IV. Kew Bull. 1934: 1–30.

— 1935. A list of marine algae from Bombay. K. danske Vidensk. Selsk. Skr. (Biol.) 12 (2): 1–64.

— 1938. Contributions to a South Indian marine algal flora. 3. J. Indian Bot. Soc. 17: 205–242.

— 1943. Some marine algae from Mauritius. III. Rhodophyceae (2). K. danske Vidensk. Selsk. Skr. (Biol.) 19 (1): 1–85.

BORNET, E. 1892. Les algues de P.K.A. Schousboe ... Mém. Soc. natn. Sci. nat. math. Cherbourg 28: 165–376.

— & G. THURET. 1876. Notes algologiques (1). Paris.

BORY DE ST. VINCENT, J.B.G.M. 1825. Dictionnaire classique d'histoire naturelle, ... 7 (Four. - G). Paris.

BOUDOURESQUE, C.-F. 1969. Gelidiella tenuissima (Thuret) Feldmann et Hamel en Mediterranée occidentale. Tethys 1: 783–792.

CANDOLLE, A.P. DE. 1815. Flore française ... Vol. 6. Paris.
CRIBB, A.B. 1983. Marine algae of the Southern Great Barrier Reef. Australian Coral Reef Soc. Handb. 2. Brisbane.
DAWSON, E.Y. 1944. The marine algae of the Gulf of California. Allan Hancock Found. Publ. 3: 189–453.
— 1953. Marine red algae of Pacific Mexico. 1. Allan Hancock Found. Publ. 17: 1–171.
— 1954. Marine plants in the vicinity of Nha Thrang, Viet Nam. Pacific Sci. 8: 373–469.
— 1957a. An annotated list of marine algae from Eniwetok Atoll, Marshall Islands. Pacif. Sci. 11: 92–132.
— 1957b. Marine algae from the Pacific Costa Rican gulfs. Los Angeles County Mus. Contr. Sci. 15: 1–28.
— 1959. Changes in Palmyra Atoll and its vegetation through the activities of man, 1913–1958. Pacif. Natural. 1 (2): 2–51.
DIXON, P.S., & L.M. IRVINE. 1977a. Seaweeds of the British Isles. 1 (1). London.
— & — 1977b. Miscellaneous notes on algal taxonomy and nomenclature IV. Bot. Notiser 130: 137–141.
DUBY, J.E. (ed.). 1830. A.P. de Candolle, Botanicon gallicum ... Ed. 2, Vol. 2. Paris.
EGEROD, L. 1971. Some marine algae from Thailand. Phycologia 10: 121–142.
EISSES, J. 1953. Seaweeds in the Indonesian trade. Indonesian J. Natur. Sci. 109: 41–56.
FAN, K.C. 1961. Morphological studies of the Gelidiales. Univ. Calif. Publs. Bot. 32: 315–368.
FELDMANN, J. 1931a. Remarques sur les genres Gelidium Lamour., Gelidiopsis Schmitz et Echinocaulon (Kütz.) emend. Rec. Trav. Cryptogamiques dédiés à Louis Mangin, pp. 151–166. Paris.
— 1931b. Note sur quelques algues marines de Tunésie. Notes Stat. Océanogr. Salammbô 24: 1–20.
— & G. HAMEL. 1934. Observations sur quelques Gélidiacées. Revue gén. Bot. 46: 528–549.
— & — 1936. Floridées de France. VII. Gélidiales. Revue algol. 9: 209–264.
FORSSKÅL, P. 1775. Flora aegyptiaco-arabica: Post mortem auctoris edidit Carster Niebuhr. Copenhagen.
GREVILLE, R.K. 1830. Algae brittanicae ... Edinburgh.
GRUNOW, A. 1874. Algae der Fidschi-, Tonga-, und Samoa-Inseln, gesammelt von Dr. A. Graeffe. J. Mus. Godeffroy 3: 23–50.
HARVEY, W.H. 1853. Nereis boreali-americana. Part II. Rhodospermae. Washington.
HOWE, M.A. 1914. Marine Algae of Peru. Mem. Torrey Bot. Club 15: 1–185.
KÜTZING, F.T. 1843. Phycologia generalis ... Leipzig.
— 1847. Diagnosen einiger neuen ausländischen Algenspecies, welche sich in der Sammlung des Herrn Kammerdirectors Klenze in Laubach befinden. Flora 30: 773–776.
— 1849. Species algarum. Leipzig.
— 1868. Tabulae phycologicae ... 18. Nordhausen.
— 1869. Tabulae phycologicae ... 19. Nordhausen.
KYLIN, H. 1956. Die Gattungen der Rhodophyceen. Lund.
LAMOUROUX, J.V.F. 1805. Dissertations sur plusieurs espèces de Fucus. Agen.
— 1813. Essai sur les genres de la famille des thalassiophytes non articulées. Ann. Mus. Nat. Hist. Natur. 20: 21–47, 115–139, 267–293.
LAWSON, G.W., & D.M. JOHN. 1982. The marine algae and coastal environment of tropical west Africa. Vaduz.
LE JOLIS, A. 1863. Liste des algues marines de Cherbourg. Mém. Soc. Imp. Sci. nat. Cherbourg 10: 1–168.
LOOMIS, N.H. 1949. New species of Gelidium and Pterocladia with notes on the structure of the thalli in these genera. Allan Hancock Found.Publ. Occasional Pap. 6: 1–29.
— 1960. New species of Gelidium and Pterocladia from the Pacific Coast of the United States and the Hawaiian Islands. Allan Hancock Found. Publ. Occasional Pap. 24: 1–35.
MAGGS, C.A., & M.D. GUIRY. 1987. Gelidiella calcicola sp. nov. (Rhodophyta) from the British Isles and Northern France. Br. Phycol. J. 22: 417–434.

MÜLLER, O.F. 1778. Icones plantarum. Florae Danicae ... 5 (13). Copenhagen.
NORRIS, R.E. 1987. Pterocladia (Gelidiaceae, Rhodophyceae), a genus previously unknown in South Africa, as it occurs in Natal. S. Afr. J. Bot. 53: 39–43.
OKAMURA, K. 1929–1932. Icones of Japanese algae 6. Tokyo.
PAPENFUSS, G.F. 1966. Notes on algal nomenclature V. Phykos 5: 95–105.
PICCONE, A. 1884. Contribuzioni all'algologia Eritrea. Nuovo Giorn. Bot. Ital. 16: 281–332.
RAO, P.S. 1970. Systematics of Indian Gelidiales. Phykos 9: 63–78.
— & M.K. TRIVEDI. 1980. Reproduction in Gelidiella. In: T.K. Desikachary & V.N. Raja Rao (eds.), Taxonomy of algae: 255–260. Madras.
RODRIGUEZ, D., & B. SANTELICES. 1987. Patterns of apical structure in the genera Gelidium and Pterocladia (Gelidiaceae, Rhodophyta). Hydrobiologia 151/152: 199–203.
— & — 1988. Separation of Gelidium and Pterocladis on vegetative characters. In: I.A. Abbott (ed.), Taxonomy of economic seaweeds II. Calif. Sea Grant Coll. Progr., Rep. No. T-CSGCP-018: 115–125.
SANTELICES, B. 1976. Taxonomic and nomenclatural notes on some Gelidiales (Rhodophyta). Phycologia 15: 165–173.
— 1977. A taxonomic review of Hawaiian Gelidiales (Rhodophyta). Pacif. Sci. 31: 61–84.
— 1988. Taxonomic studies on Chinese Gelidiales (Rhodophyta). In: I.A. Abbott (ed.), Taxonomy of economic seaweeds II. Calif. Sea Grant Coll. Progr., Rep. No. T-CSGCP-018: 91–107.
SCHIFFNER, V. 1933. Meeresalgen aus Süd-Dalmatien, gesammelt von Franz Berger. Öst. bot. Z. 82: 283–308.
SCHMITZ, F. 1894. Neue japanische Florideen von K. Okamura. Hedwigia 33: 190–201.
SETCHELL, W.A., & N.L. GARDNER. 1930. Marine algae of the Revellagigedo Islands Expedition in 1925. Proc. Calif. Acad. Sci. 19: 109–215.
SILVA, P.C. 1978. Type specimens of Gelidiaceae (Rhodophyceae) described by Nina H. Loomis. Phycologia 17: 257–261.
— , E.G. MEÑEZ & R.L. MOE. 1987. Catalog of the benthic marine algae of the Philippines. Smithsonian Contr. Mar. Sci. 27: 1–179.
SOEGIARTO, A. 1978. Indonesian seaweed resources: their utilization and management. Proc. Int. Seaweed Symp. 9: 463–471.
SPACH, E. 1841. Histoire naturelle des végetaux. Vol. 10. Paris.
SPRENGEL, K. 1827. Caroli Linnaei ... Systema vegetabilium, ed. 16, vol. 4. Göttingen.
STACKHOUSE, J. 1795. Nereis britannica, ... Bath.
STEWART, J.G., & J.N. NORRIS. 1981. Gelidiaceae (Rhodophyta) from the Northern Gulf of California, Mexico. Phycologia 20: 273–284.
TANAKA, J., & M. CHIHARA. 1988. Macroalgae in Indonesian mangrove forests. Bull. Natn. Sci. Mus., Tokyo, Ser. B, 14: 93–106.
TAYLOR, W.R. 1943. Marine algae from Haiti collected by H.H. Bartlett in 1941. Pap. Mich. Acad. Sci. 28: 143–163.
— 1945. Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands. Allan Hancock Found. Publ. 12: 1–582.
— 1960. Marine algae of the Eastern tropical and subtropical coasts of the Americas. Ann Arbor.
TURNER, D. 1819. Fuci, Sive Plantarum Fucarum Generi ... Vol. 4. London.
TURRA, A. 1780. Flora italicae prodromus. Vicenza.
VAHL, M. 1802. Endeel Kryptogamiske planter fra St. Croix. Skr. Naturhist-Selsk. 5: 29–47.
WEBER-VAN BOSSE, A. 1904. Note sur deux algues de l'Archipel Malaisien. Rec. Trav. Bot. Néerl. 1: 96–105.
— 1921. Liste des algues du Siboga, 2. Siboga-Expeditie 54, b: 187–310.
— 1926. Algues de l'expédition danoise aux îles Kei. Vidensk. Medd. Dansk. Naturh. Foren. 81: 57–155.
— 1928. Liste des algues du Siboga, 4. Siboga-Expeditie 54, d: 393–533.
WIGHT, R. 1839. Illustrations of Indian Botany ... I. Madras.

WOMERSLEY, H.B.S., & A. BAILEY. 1970. Marine algae of the Solomon Islands. Philos. Trans. R. Soc. London (Biol.) 259: 257–352.

ZANEVELD, J.S. 1955. Economic marine algae of tropical South and East Asia and their utilization. Indo-Pacif. Fisheries Counc. Spec. Publ. 3: 1–55.

— 1959. The utilization of marine algae in tropical South and East Asia. Economic Bot. 13: 89–131.

ZHANG JUNFU (C.F. CHANG) & XIA ENZHAN. 1988. Chinese species of Gelidium Lamouroux and other Gelidiales (Rhodophyta), with key, list, and distribution of the common species. In: I.A. Abbott (ed.), Taxonomy of economic seaweeds II. Calif. Sea Grant Coll. Progr., Rep. No. T-CSGCP-018: 109–113.