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Gelidiella calcicola sp. nov. (Rhodophyta) from the British Isles and Northern France

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Ireland

Gelidiella calcicola sp. nov. (Gelidiales, Gelidiaceae) is described from plants growing on loose-lying subtidal coralline algae and shells on southern, western and northern shores of the British Isles, and from Roscoff in Brittany, France. The species forms narrow, creeping axes attached at intervals by peg-like rhizoidal holdfasts. Irregularly pinnate branches arise at the points of attachment, arc downwards, and become attached and pinnately branched. No erect axes are formed; in all other described species of the genus *Gelidiella* at least some erect axes are formed from the creeping base. Internal rhizines, considered to be characteristic of all the genera of the Gelidiales except *Gelidiella*, are present in the medulla, but only at the attachment points. Surface cortical cells are large and usually arranged in chevron-like transverse rows. Tetrasporangia, formed only in the winter months, occur in lateral stichidia in chevron-like rows of 8-10 per row; they are spherical and apparently tetrahedrally or irregularly divided. Gametangial and carposporangial plants have not been found; these are known in only one species of the genus. Attempts to induce reproduction in vegetatively isolated plants in culture by subjecting them to a wide range of temperature and photoperiodic regimes in various enriched sea-water media strengths were unsuccessful. The new species is compared with *Gelidium pusillum* from the British Isles, and with the 21 previously described species of *Gelidiella*. The status of the family Gelidiellaceae is assessed and it is concluded that it should be merged with the Gelidiaceae. Some doubts are expressed as to the validity of the criteria used to delimit the genus *Gelidiella*.

Four members of the Gelidiaceae are currently included in the flora of the British Isles (Dixon & Irvine, 1977): *Gelidium latifolium* (Greville) Bornet & Thuret, *G. pusillum* (Stackhouse) Le Jolis, *G. sesquipedale* (Clemente) Thuret in Bornet & Thuret, and *Pterocladia capillacea* (S. G. Gmelin) Bornet & Thuret, all of which have internal rhizines and relatively small surface cortical cells (Dixon & Irvine, 1977). There are no reported British Isles representatives of *Gelidiella* J. Feldmann & Hamel (1934), a genus characterized by the absence of internal rhizines and formation of tetrasporangia in specialized stichidial blades. *G. pannosa* (J. Feldmann) J. Feldman &

Hamel is the only species of this predominantly tropical genus known from the NE Atlantic Ocean.

A small, creeping gelidialian alga found commonly on calcareous substrata in the British Isles and northern France has been assigned to *Gelidiella* on the basis of its tetrasporangial stichidia with tetrasporangia arranged in chevrons that develop acropetally, and the lack of rhizines except at attachment points. It differs from *G. pannosa* and all other *Gelidiella* species in the formation of prostrate axes only and is here described as a new species, *Gelidiella calcicola*. Features of the structure and reproduction of this species lead us to believe that the Gelidiaceae and Gelidiellaceae should be merged, and cast some doubt on the validity of the genus *Gelidiella* as currently circumscribed.

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MATERIALS AND METHODS

Specimens of *Gelidiella calcicola* sp. nov. were collected from the British Isles and northern France (Brittany) in the areas shown in Fig. 1 and at the localities listed in Table I.

Seasonality of field populations in Galway Bay, Ireland, was studied by sequential monthly collections between April 1981 and April 1982 at Carraroe, Co. Galway (53°14.5'N: 9°38.3'W) and off Carrickadda, Finavarra, Co. Clare (53°9.8'N: 9°6.8'W) where the plants grow on maerl [loosely coralline algae: *Phymatolithon calcareum* (Pallas) W. Adey & McKibbin and *Lithothamnion corallioides* P. & H. Crouan] and dead shells. Percentage cover was assessed after removal of the canopy layer by using a point quadrat (a travelling binocular microscope fitted with an eyepiece containing a cross-hair graticule) in a 20 × 10 cm grid of 200 points on the surface plants of a 300 cm³ maerl sample. Five replicate samples were examined on each sampling date. Samples were also examined for reproductive status of all component species. Means and 95% confidence limits for transformed [$\sqrt{(x+0.5)}$] percentage cover data are shown as histograms (Fig. 27). Bottom temperature was taken on each sampling date, and daylength was obtained from tables for Shannon Airport, about 60 km south of Galway.

Studies of anatomy and reproduction were carried out on fresh or 4% formalin-sea-water-preserved material. Sections were made with a freezing microtome or by hand-sectioning and were stained with 1% aqueous aniline blue, post-fixed in 1% HCl, and mounted in 80% Karo (commercial corn syrup). Slides and herbarium material have been deposited in the Phycological Herbarium, University College, Galway, Ireland (GALW). The holotype microscope slide is preserved in GALW and paratypes are deposited in: the Irish National Herbarium, Botanic Gardens, Glasnevin, Dublin (DBN), the British Museum (Natural History) (BM), the Smithsonian Institution, Washington, D.C. (US), and the Herbarium, Department of Botany, University of California, Berkeley, California (UC).

Isolation of tetraspores was attempted, but no viable tetraspores were released, and tetrasporangial plants were grown in culture from vegetative tips which were excised until the culture was unialgal. Other culture techniques were as described by Guiry & Cunningham (1984). Cultured plants were initially grown at 15°C, 16:8 h in 100% Provasoli's enriched seawater (PES; McLachlan, 1973), and replicates were later subjected to a wide range of temperature and photoperiod combinations of 100% and 10% PES and 50% von Stosch's

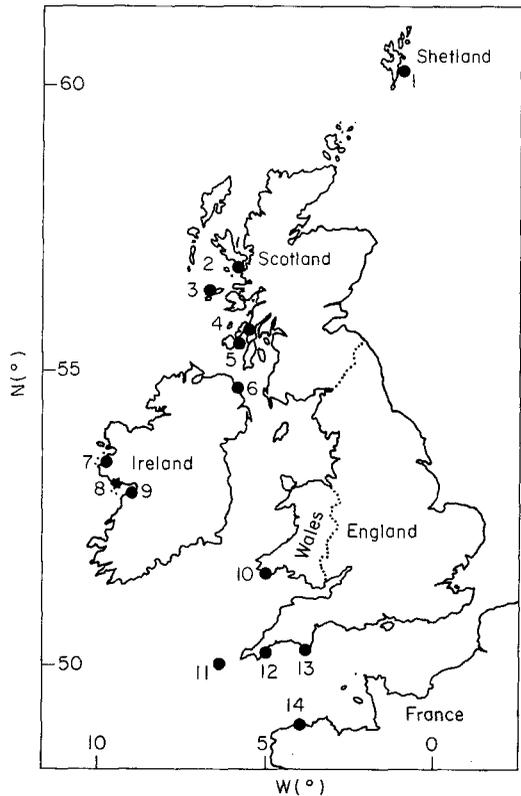


FIG. 1. Distribution of *Gelidiella calcicola* sp. nov., indicating the areas in which plants were collected. Full details are given in Table I; numbers refer to area numbers shown in parentheses in this table. Type locality is indicated by a star.

enriched seawater (VS; Guiry & Cunningham, 1984).

Unless given in the text, authority citations for species names are as listed in Parke & Dixon (1976).

OBSERVATIONS

External appearance

Plants form low-growing turf-like tufts as they creep (Fig. 3) on the surface of calcareous substrata, and may entirely conceal small pieces of shell or maerl. The narrow, compressed axes form peg-like rhizoidal attachment organs, composed of groups of unbranched rhizoids formed from medullary or cortical cells and rhizines originating from cortical cells, from the lower faces of the branches (Figs 4, 14). The axes branch laterally (Figs 2, 14) from the

TABLE I. Distribution and habitat of *Gelidiella calcicola* sp. nov. from specimens examined indicating area numbers shown in Fig. 1. Pc: growing on *Phymatolithon calcareum*; Lc: growing on *Lithothamnion corallioides*

Site and area (Fig. 1)	Substratum and habitat	Date and collector
Scotland		
Beosetter, N Bressay, Shetland (1) 60°10'N:1°7'W	Pc. Maerl bed at 10–20 m	Aug. 1983 Divers for D. Irvine
Tarskavaig, SW Skye (2) 57°2.2'N:5°56.7'W	Pc. Scattered maerl on clean sand at 16 m	23 Aug. 1980 F. A. Dipper
Red Rock, SE Coll (3) 56°34.8'N:6°37.1'W	Pc. Maerl bed on coarse sand at 16 m	19 Jun. 1981 CAM
Creachasdal Mor, NE Tiree (3) 56°32.2'N:6°42.4'W	Pc. Maerl scattered on sand plain at 12 m	15 Jun. 1981 Divers for F. A. Dipper
Gott Bay, E Tiree (3) 56°30.8'N:6°47.5'W	Pc. Maerl and sand ridges at 9 m	16 Jun. 1981 F. A. Dipper
Hynish Bay, SE Tiree (3) 56°28.6'N:6°51.7'W	Pc. Maerl and shell gravel ridges at 14 m	17 Jun. 1981 CAM
S. Danna Island, Loch Sween, Argyll (4) 55°56'N:5°40.8'W	Pc. and dead shells. Maerl in troughs between gravel waves at 7 m	2 Sept. 1985 S. Hiscock
Claig Castle, S Jura (5) 55°45'N:6°7.1'W	Pc and Lc. Stable maerl bed dominated by <i>Laminaria saccharina</i> , at 5 m	29 Jun. 1982 CAM
Ireland		
Ballygalley Head, Co. Antrim (6) 54°54.2'N:5°50.4'W	Pc. Scattered maerl on sand plain, 14 m	30 Jun. 1983 D. W. Connor
Ballynakill Harbour, Co. Mayo (7) 53°33'N:10°1.5'W	Lc. Maerl bed on stones, very wave- and current-sheltered, LWST	15 Apr. 1980 CAM
Coastguard Deep, Ballynakill (8) Harbour, Co. Mayo 53°34'N:10°2'W	Dead <i>Lithophyllum fasciculatum</i> maerl scattered on shell bottom, 8–10 m	18 Oct. 1980 B. E. Picton
Mweenish Island, Co. Galway (8) 53°18.9'N:9°51.9'W	Pc. Scattered maerl on sand under fish cages, with fungi and bacteria, 10 m	24 Jan. 1981 CAM
Flannery Bridge, Kilkieran Bay (8) Co. Galway 53°21.2'N:9°42.5'W	<i>Peyssonnelia harveyana</i> and <i>Phymatolithon polymorphum</i> and pebbles covered with crustose Corallinaceae in tidal rapids, 5 m	11 May 1980 CAM
Carraroe, Co. Galway (8) 53°14.5'N:9°38.3'W	Lc, Pc and dead shells. Clean, current-swept maerl bed on maerl debris, 3–5 m	Apr. 1981–Apr. 1982 (monthly) CAM
Finavarra, Co. Clare (9) 53°9.8'N:9°6.8'W	Lc, Pc, dead shells and limestone pebbles. Silty, fairly sheltered maerl bed on sand, 10 m	Apr. 1981–Apr. 1982 (monthly) CAM
Carrickadda, Finavarra (9) 53°9.0'N:9°6.8'W	Lc, Pc. Scattered maerl on sand, 0–3 m	16 Apr. 1980 CAM 10 Oct. 1985 J. Brodie
Muckinish Bay, Co. Clare (9) 53°6.9'N:9°51.9'W	Pc. Deep maerl banks formed by tidal rapids, LWST	20 Feb. 1980 CAM
Wales		
South Hook Pt, Milford Haven (10) Pembrokeshire 51°41.8'N:5°4.7'W	Lc, Pc. Maerl and sand waves, current exposed, 5 m	18 Jul. 1985 S. Hiscock
England		
Smith Sound, Scilly Isles (11) (between Annet and St Agnes) 49°53.5'N:6°21.5'W	<i>Peyssonnelia harveyana</i> and crustose Corallinaceae on pebbles. Current-exposed pebble bottom, dominated by <i>Stenogramme interrupta</i> , at 14 m	3 Jul. 1983 CAM
St Mawes Buoy, Fal Estuary (12) 50°9.1'N:5°3.3'W	Pc. Sparse, mostly dead, maerl on clean sand at 5 m	11 Jul. 1985 CAM
Middle Ground, Salcombe Harbour (13) Cornwall 50°14.3'N:3°45.3'W	Dead shell. On muddy sand, some current, 3 m	11 Sep. 1985 CAM
France		
Pighet maerl, Baie de Morlaix (14)	Lc, Pc. Maerl bed at 10 m	23 Sep. 1981 MDG
Guerhéon maerl, Baie de Morlaix (14)	Crustose Corallinaceae on dead shells, 8 m	Jul. 1985 A. Little

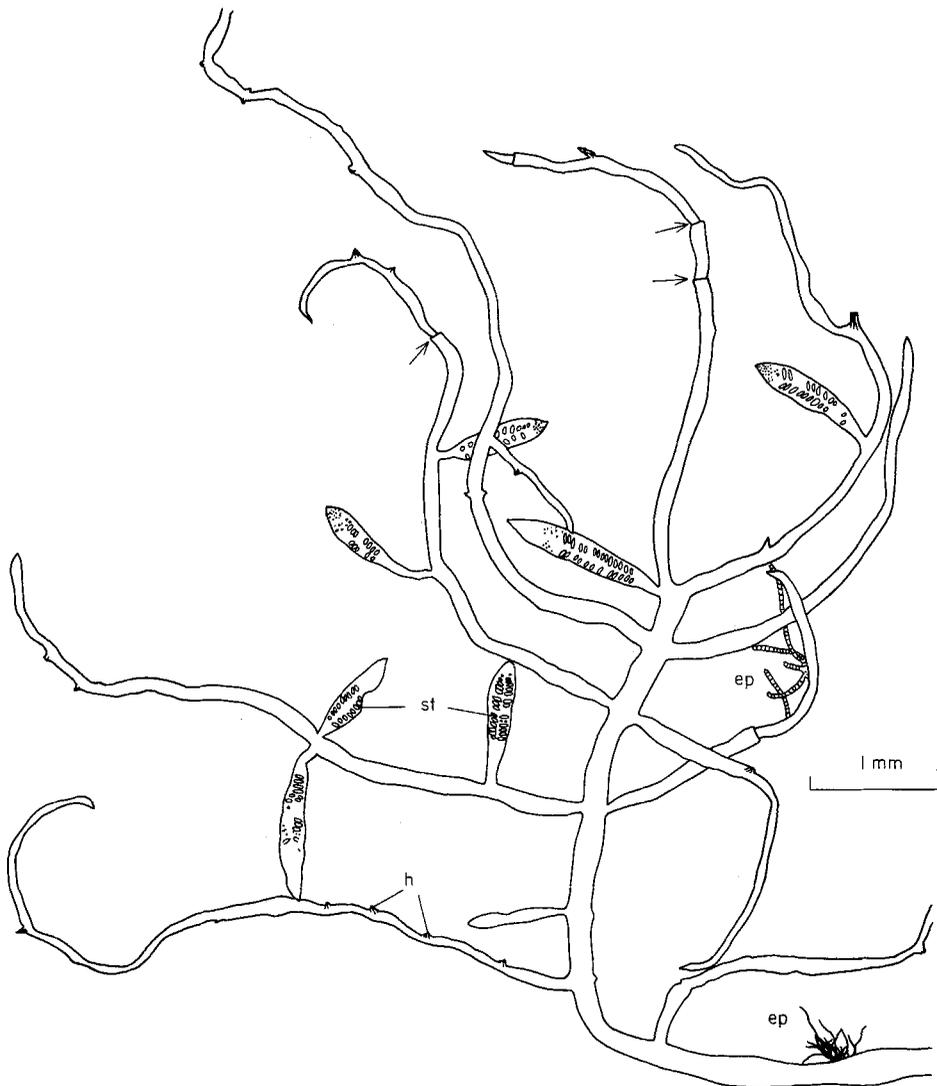
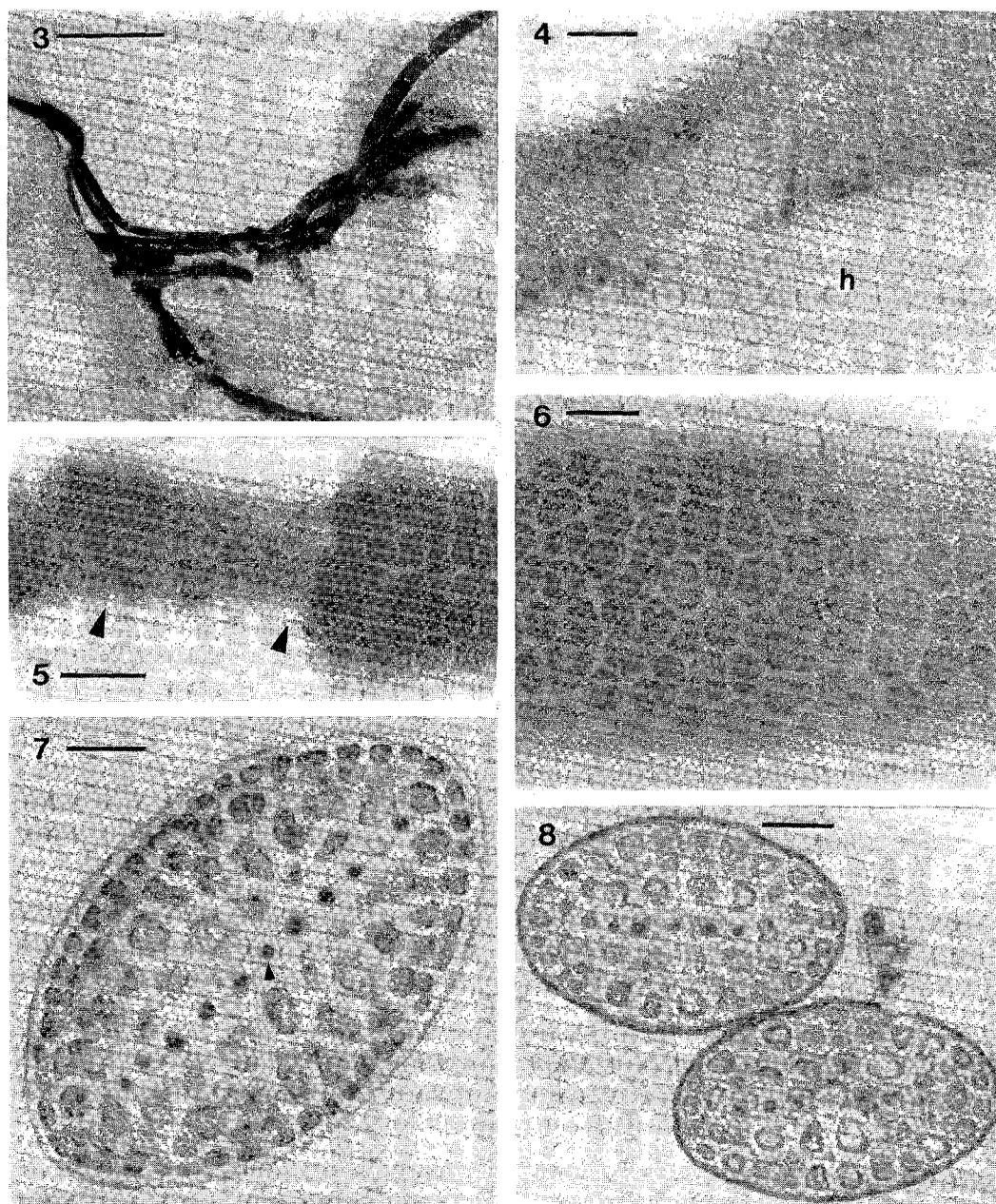


FIG. 2. Morphology of the HOLOTYPE plant of *Gelidiella calcicola* sp. nov.; showing pod-like tetrasporangial stichidia replacing lateral branches. Arrows indicate discontinuities in axis width resulting from regeneration. Abbreviations used in figures are as follows: ap: apical cell; ax: axial filament; c: cortical cell; cc: central cell; ep: epiphyte; h: holdfast; m: medullary cell; pc: pericentral cell; rh: rhizoidal filament; rn: rhizine; st: stichidium; sw: sporangial walls; t: tetrasporangium; tb: tetrasporangial bladelet; tc: tetrasporocyte or tetrasporangial initial.

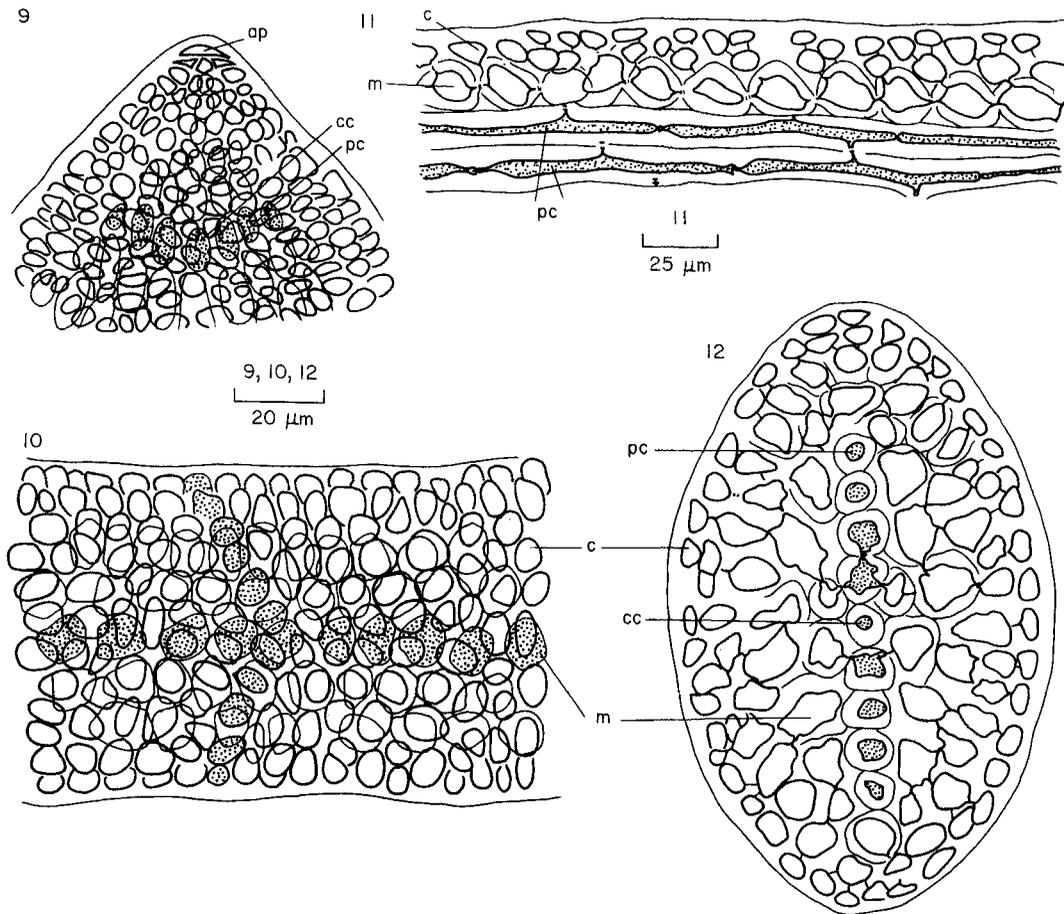
margins adjacent to the attachment points to form an irregularly pinnate branching pattern; a second or third pair of lateral branches is often formed subsequently in the axils of the original pairs. There are no true erect axes, since all branches are formed in the same, horizontal plane; they may grow upright at first, but they always curve downwards eventually, become prostrate

and form attachment organs. When the axes arc downwards they often re-attach to new pieces of shell and maerl, forming matted tangles of maerl and shell fragments linked by *Gelidiella* plants. These later separate resulting in a very effective form of vegetative reproduction.

The axes are compressed, 85–310 μm broad and 55–215 μm thick in transverse



FIGS 3–8. Morphology and anatomy of *Gelidiella calcicola* sp. nov. Abbreviations listed in legend for Fig. 2. Fig. 3. Habit of plant growing on *Phymatolithon calcareum* maerl, Finavarra, Co. Clare, Ireland, low intertidal, leg. J. Brodie, Sep. 1985. Scale bar = 1 mm. Fig. 4. Holdfast composed of pigmented and non-pigmented filaments, Carraroe, Co. Galway, Ireland, 19 Sep. 1985. Scale bar = 75 μ m. Fig. 5. Axis showing discontinuities in width (arrowed) from regeneration after damage. Carraroe, 19 Sep. 1985. Scale bar = 50 μ m. Fig. 6. Vegetative axis, showing rather irregular arrangement of cortical cells. Carraroe, 19 Sep. 1985. Scale bar = 15 μ m. Fig. 7. TS of large vegetative axis (grown in culture). Note central row consisting of deeply staining central cell (arrowed) and 10 pericentral cells. Scale bar = 30 μ m. Fig. 8. TS of axis with central row of five cells and short rows of medullary and cortical cells. Field material from Carraroe, 28 Jul. 1981. Scale bar = 30 μ m.



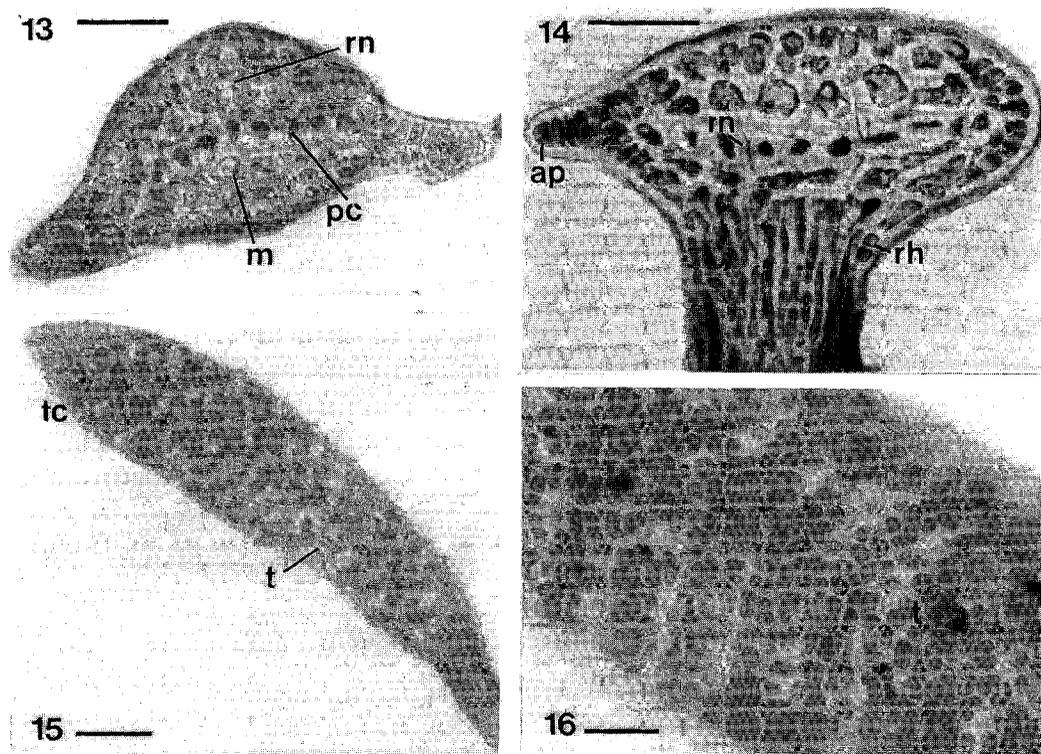
FIGS 9–12. Vegetative anatomy of *Gelidiella calcicola* sp. nov. Figs 9 and 10 are from field material (Carraroe, 4 Nov. 1981) and Figs 11 and 12 are of cultured material. Abbreviations listed in legend for Fig. 2. Fig. 9. Apex showing apical cell and division of its product cell into central (axial) and pericentral cells. One V-shaped central row is shaded for emphasis. Fig. 10. Cortical and medullary cells, with one V-shaped transverse row and one longitudinal row of hexagonal medullary cells shaded for emphasis. Fig. 11. Part of LS showing regularly arranged pericentral, medullary and cortical cells. Fig. 12. TS showing thick-walled central row of central and eight pericentral cells, medullary cells and short chains of cortical cells.

section, and there are usually marked discontinuities in width (Figs 2, 5) due to regeneration from truncated portions. Plants grown to at least 30 mm long; they are dark reddish brown, drying black.

Vegetative structure

Thalli are uniaxial, with a prominent, curved or domoid apical cell 8–13 μm wide \times 5–5.5 μm long. The first product cell of the apical cell divides to form a central cell and two pericentral cells (Fig. 9). The

subsequent pattern of cell divisions gives rise to chevron-like lines of (5)–7–11 central and pericentral cells and regular arrangements of cortical cells (Figs 6, 10), which are also aligned longitudinally (Fig. 10), but there is some variability in the arrangement of the cells and regular rows are not always present. The large, more or less hexagonal medullary cells are visible through the cortex and also show this chevron-like alignment (Fig. 10). Some isolated cortical cells are hyaline. In LS (Fig. 11) there is a regularly arranged central row of axially elongate,



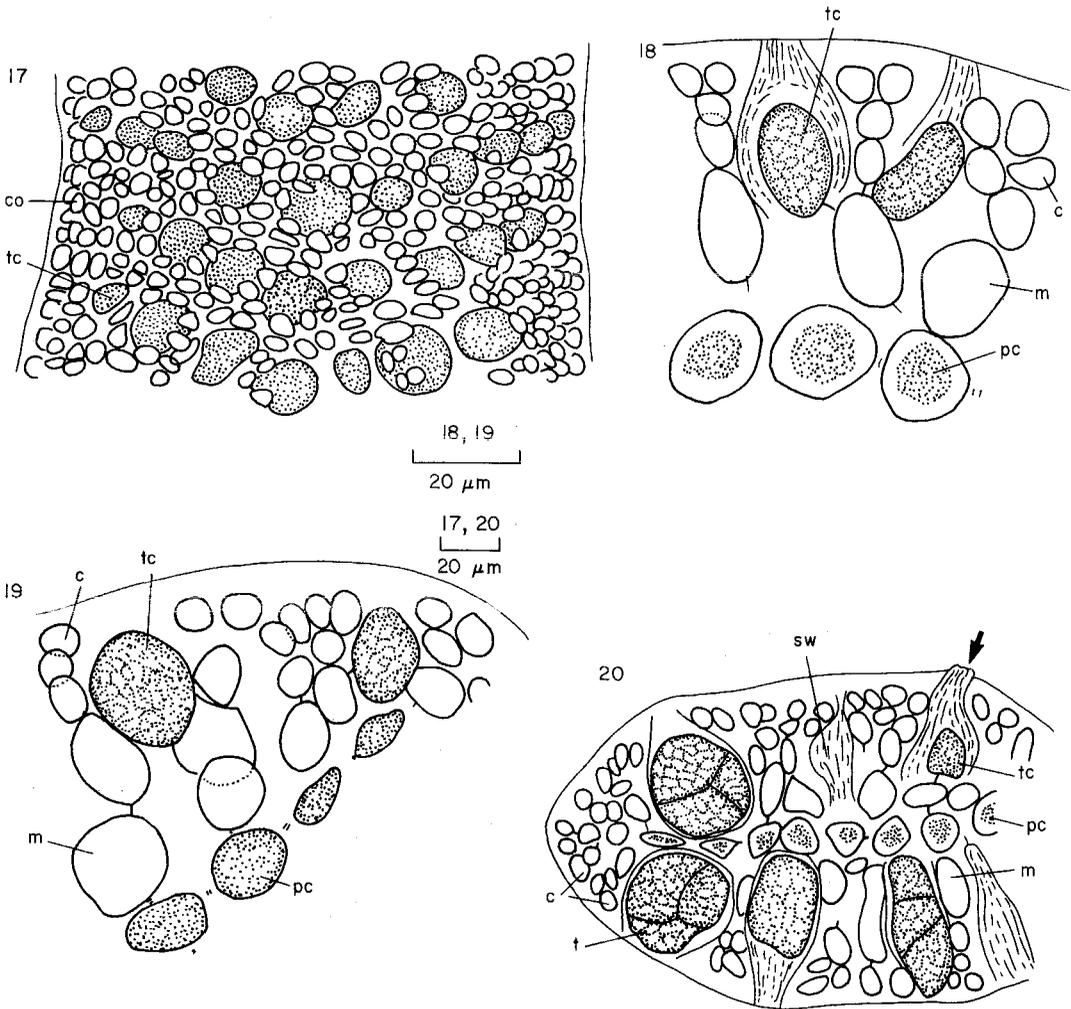
Figs 13–16. *Gelidiella calcicola* sp. nov. Abbreviations listed in legend for Fig. 2. Figs 13, 14. TS through holdfast region of axes (collected Carraroe, 28 Jul. 1981). Fig. 13. Development of paired lateral branches and thick-walled rhizines in the medulla parallel to the central row. Scale bar = 30 μ m. Fig. 14. Developing lateral branches and holdfast composed of multicellular pigmented filaments and non-septate hyaline (stained) rhizoidal filaments. Rhizines originate from cortical cells and traverse the medullary region towards the holdfast. Scale bar = 50 μ m. Fig. 15. Tetrasporangial stichidium of HOLOTYPE with V-shaped rows of tetrasporangia and positions of discharged tetraspores. Scale bar = 50 μ m. Fig. 16. Tetrasporangial stichidium of HOLOTYPE with chevrons developing and mature tetrasporangia. Scale bar = 30 μ m.

thick-walled (to 2.5 μ m thick) cells of 10–16 μ m diameter arranged in chevron-like rows; this arrangement is most obvious near the apices. The central cell is narrower (11.5–14 μ m wide and 95–115 μ m long) and cell contents are non-pigmented and stain deeply with aniline blue. The central row of thick-walled cells gives rise to a single layer of rounded medullary cells (9–)16–23 \times 27–40 μ m which form short chains of one to three cortical cells. The surface cortical cells are fairly widely spaced, 7–14(16) \times 7–11.5(16) μ m in optical section, and covered by a thick cuticle. In TS (Figs 7, 8, 12), the cells forming the row of (5–)7–11 central cells are distinguished by their thick walls and non-pigmented granular contents from the other starch-packed medullary cells

(Fig. 7). Thick-walled filaments (rhizines) are present in the medulla only in holdfast regions (Figs 13, 14), being formed by cortical cells and twining around the central cells and among the medullary cells. Holdfasts are composed of rhizoidal filaments and rhizines originating from medullary and cortical cells. Some filaments are pigmented and multicellular, others granular, hyaline, and non-septate, 3.5–4 μ m in diameter, four to six times longer than wide.

Reproduction

Tetrasporangia were found in a very small proportion of plants examined from only a few collections: at Carraroe, Co. Galway, Ireland, in November 1981 and January and



Figs 17–20. Tetrasporangia of *Gelidiella calcicola* sp. nov. Carraroe, Co. Galway, Ireland, 4 Nov. 1981. Fig. 17. Surface view of part of tetrasporangial stichidium with chevrons of developing tetrasporangia. Fig. 18. Developing tetrasporangial initials enclosed in thick, stratified walls. Fig. 19. Tetrasporangial initials showing terminal development in place of cortical cells. Fig. 20. TS of stichidium with mature spherical, tetrahedrally (?) divided tetrasporangia and one abnormal tetrasporangium with near-zonate divisions. Also shown are empty walls remaining after discharges of tetraspores. Arrow indicates tetrasporangial initial apparently regenerating inside old walls.

March 1982, and at Finavarra, Co. Clare, Ireland in February 1982 (Fig. 27), suggesting that the species is winter fertile. They are formed in determinate branches which develop into flattened pod-like stichidia about 500–800 (1200) μm long and 170–190 μm broad (Figs 2, 15). Stichidia are found in the same position as ordinary branches, being formed singly or in opposite pairs but not terminally on the main axes. A

few plants were found in which the stichidial axes had continued vegetative growth. The tetrasporangia are formed in a regular pattern of chevrons (Figs 15–17), with 8–10 sporangia in each transverse row when mature. All stichidia examined had discharged spores from the posterior rows, leaving gaps amongst the cortical cells. Mature tetrasporangia are borne in the middle of the stichidium and immature

sporangia in the apical rows. The tetrasporangia develop terminally from cortical cells (Figs 18, 19), displacing other cortical cells, and divide in a tetrahedral-like or irregular manner. When mature they are more or less spherical, 25–38 µm in diameter (Fig. 20) and surrounded by a thick stratified wall. Early stages of cleavage were not observed and the exact nature of the sequence of formation of tetraspores is unknown. Some sporangia appeared to have regenerated within old tetrasporangial walls (Fig. 20).

Gelidiella calcicola sp. nov.

Diagnosis. Plantae repentes quidem 30 mm longae, ex axibus angustis compressis compositis, ad intervalla rhizoidis structuris ad instar paxillorum affixis, caespes densus super substratatis calcareis formantes. Frondes uniaxialis, cum cellulis centralis seriales septenorum vel undenorum dispositis. Plantae gametangia necnon carposporophytica desunt. Tetrasporangia in structuribus similibus leguminum non nisi in ramis brevis lateralis facti, seriales octonorum versus denos ad instar chevronorum ordinati, tetrahedratim vel irregularitim divisi, sphaerici, 25–38 µm diam.

Holotypus: Planta tetrasporophytica (Figs 2, 15, 16) prope locum dictum "Carraroe", prope Galviam, Hibernia, 5 m sub paginam maris, C. A. Maggs lecta, 4 Nov. 1981 (GALW); paratypi, prope locum dictum "Carraroe", 4 m sub paginam maris, J. Brodie lecta, 19 Sep. 1985, GALW, DBN, BM, US, UC.

Culture studies

Cultures were started from vegetative tips of thalli bearing tetrasporangial stichidia collected at Carraroe, Co. Galway, on 4 November 1981. Stock cultures were maintained at 15°C, 16:8 h and grew well, forming the characteristic branching pattern, but plants did not attach to glass. When sufficient stocks had been accumulated, replicates were subjected to all possible combinations of transfer between 20°C, 16:8 h; 15°C, 16:8 h; 15°C, 8:16 h; 10°C, 16:8 h; 10°C, 8:16 h; 5°C, 8:16 h, in 100% and 10% PES and 50% VS, but no

reproduction was obtained, although plants survived at all regimes. Irradiance levels did not, however, exceed 30 µmol m⁻² s⁻¹ (see Discussion). Thalli grown at 20°C, 16:8 h, developed almost terete axes but reverted to compressed axes when transferred back to 15°C, 16:8 h. At 10°C, 16:8 h, numerous hyaline hairs, not observed in field-collected plants, were formed near the apices.

Distribution and Ecology

Plants of *Gelidiella calcicola* were found on southern, western and northern coasts of the British Isles and in northern France (Fig. 1, Table I) growing from extreme low water to c. 15 m depth on mobile substrata, principally on loose-lying coralline algae (maerl). The species grows on both live and dead maerl, crustose corallines on pebbles and stones, dead shell, occasionally on calcareous pebbles, and often overgrows crustose maerl epiphytes such as *Peyssonnelia* spp.

The epifloral species characteristically collected with *Gelidiella calcicola* included: *Spermothamnion repens*, the *Trilliella*-phase of *Bonnemaisonia hamifera*, *Polysiphonia urceolata*, *Cryptopleura ramosa* and *Plocamium cartilagineum*. Plants of *Gelidiella* themselves supported a variety of epiphytes, such as *Melobesia membranacea*, *Furcellaria lumbricalis* sporelings, and *Audouinella* spp.

Sequential collections of maerl made in 1981–1982 at the two sites in Galway Bay showed that plants are present throughout the year, and exhibit little seasonality in cover abundance (Fig. 27). At Finavarra, a significant drop in recorded abundance in August–September and high variance in July were due to overgrowth by other small species of the turf layer (e.g. *Gracilaria verrucosa*, *Cryptopleura ramosa*, the *Falkenbergia*-phase of *Asparagopsis armata*) which obscured the *Gelidiella*. Cover was generally lower and very variable throughout the year at Carraroe, probably as a result of the patchiness of the maerl, which is continually shifted and sorted by water movement, but at both sites in Galway Bay, and at many

other sites throughout the British Isles and northern France, the species is one of the cover-dominants in the "herb" layer of maerl beds.

Gelidiella calcicola is one of the most typical components of the maerl epiflora, being found even in very impoverished maerl beds. In a maerl bed near Carna, Co. Galway, for example, which was below fish-rearing cages and thus heavily contaminated by faeces and decaying food, it was the only surviving algal species. However, *G. calcicola* was surprisingly rare on one maerl bed studied, at Falmouth on the south-west coast of England (Table I). This maerl bed supports a diverse epiflora (Farnham & Bishop, 1985) but only a few *G. calcicola* plants were observed, and only in the peripheral areas of the maerl bed.

Reproductive plants were rarely observed during the study period, but reproduction showed a marked seasonal periodicity, tetrasporangia being present only in winter collections (Fig. 27), from early November sporadically until March at Carraroe, and only in February at Finavarra. No gametangial or cystocarpic plants were found at any time.

DISCUSSION

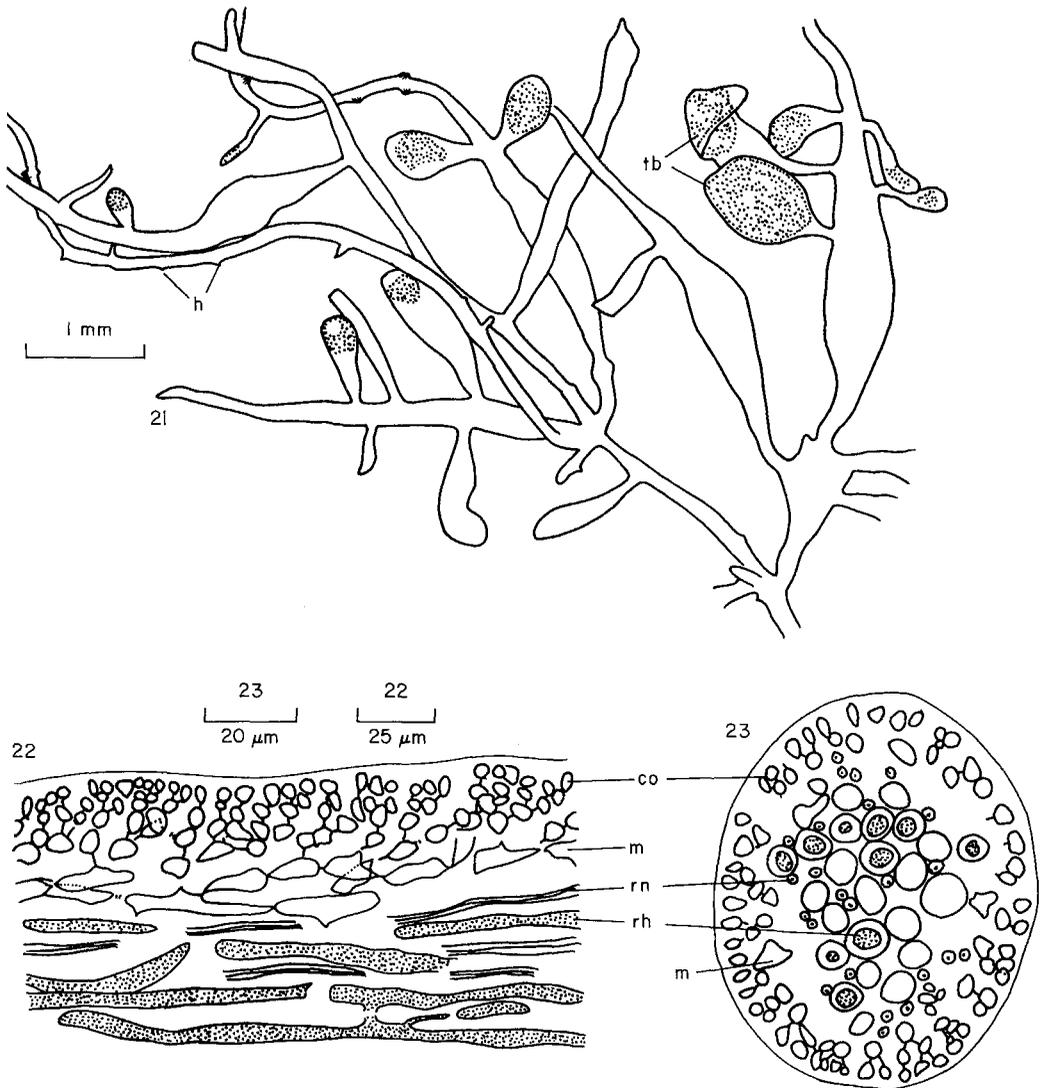
Comparison with *Gelidium pusillum*

Of the species of Gelidiales known from the British Isles and northern France, *Gelidiella calcicola* is most similar to *Gelidium pusillum*, which forms axes of 0.3–1 mm diameter (Dixon & Irvine, 1977). However, in contrast to the regular branching pattern and relatively invariant axis width of the maerl epiphyte, narrow plants of *Gelidium pusillum* (Fig. 21) consist of terete to flattened axes which form an irregular arrangement of branches of variable width. A comparison of the internal anatomy and reproduction shows that *Gelidiella calcicola* differs in several other respects from *Gelidium pusillum*. The regular chevron-like rows of relatively large [7–14 (16) × 7–11.5 (16) μm] cortical cells of *Gelidiella*

calcicola contrast strongly with the random arrangement of small [3.5–5 (7) × 3.5–5 μm] cortical cells in *Gelidium pusillum* (Fig. 24). In LS of *Gelidiella calcicola* (Fig. 11), the regular positioning of the central elongate, rounded medullary and large cortical cells is in clear contrast to a similar section of *Gelidium pusillum* (Fig. 22) in which the medullary filaments vary greatly in length and width, and are interspersed with rhizines. In *Gelidiella calcicola* there is a sharp boundary between the central filaments and cortical cells, whereas in *Gelidium pusillum* there is a transition zone composed of irregularly elongate medullary cells. The cortical filaments are one to three cells long in *Gelidiella calcicola* and four to six cells long in *Gelidium pusillum*. In TS, *Gelidium pusillum* (Fig. 23) consists of a medullary region of little-pigmented cells and scattered thick-walled rhizines, with few pit connections being visible due to the greater length of the cells relative to those of *Gelidiella calcicola*. The production of tetrasporangia in uniformly shaped stichidia in *Gelidiella calcicola* differs markedly from their formation in *Gelidium pusillum* on small to large oval bladelets, in which they are arranged randomly, with mature and developing tetrasporangia in close proximity (Figs 25, 26). Tetrasporangia in *Gelidium pusillum* measure 20 × 40 × 20–30 μm and are cruciately, irregularly, or tetrahedrally divided (Dixon & Irvine, 1977).

Taxonomic position

J. Cabioch (1964, pp. 130–134) made a detailed morphological study of creeping *Gelidium*-like plants occurring on maerl at Roscoff and provisionally assigned them to the genus *Gelidiella*. Reproductive organs were not observed, so that the plants could not be identified with any certainty and the occurrence of rhizines near the holdfasts put their attribution to *Gelidiella* in some doubt, although J. Cabioch (1969) later referred to them as "*Gelidiella* sp.". These plants are identical to those recently collected by us in

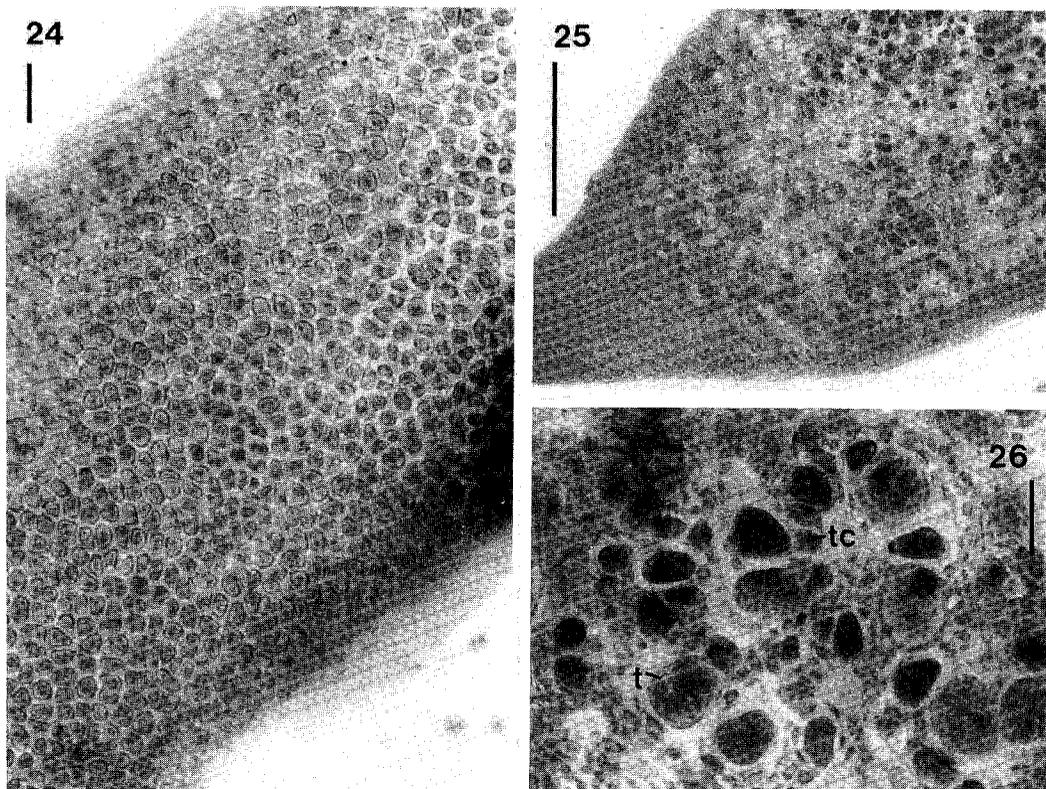


FIGS 21–23. *Gelidium pusillum*. Intertidal at Lambay Island, Co. Dublin, Ireland, 30 Aug. 1982. Abbreviations listed in legend for Fig. 2. Fig. 21. Morphology of plant bearing rounded tetrasporangial bladelets. Note the variation in axis width. Fig. 22. LS showing irregular, relatively long, thin-walled rhizoidal medullary filaments with few pit connections and interspersed with rhizines. Fig. 23. TS showing medulla composed of rhizoidal filaments, many of which are represented by walls, and rhizines.

the British Isles and northern France (Table I), and correspond to the genus *Gelidiella* in the often regular arrangement of the cortical cells. The opportunity of examining tetrasporangia in the plants from the west of Ireland has shown the formation of apparently tetrahedrally divided tetrasporangia in regularly arranged chevrons in stichidia, confirming this identification.

Comparison of *Gelidiella calcicola* with other *Gelidiella* species

Members of the genus *Gelidiella* are mostly tropical and subtropical in distribution (Kyllin, 1956; Kraft, 1981), but six species are known from the Mediterranean (Table II). The only species known from the relatively cold waters in the eastern Atlantic



FIGS 24–26. *Gelidium pusillum*. Intertidal at Lambay Island, Co. Dublin, Ireland, 30 Aug. 1982. Abbreviations listed in legend for Fig. 2. Fig. 24. Irregular arrangement of small cortical cells in surface view. Scale bar = 20 μm . Fig. 25. Tetrasporangial bladelet with tetrasporangia at all stages of development. Scale bar = 250 μm . Fig. 26. Surface view of mature and developing tetrasporangia in irregular arrangement. Scale bar = 30 μm .

is *G. pannosa* (Feldmann & Hamel, 1936; Donze, 1968; Boudouresque, 1969, 1970; Ardré, 1970), which is found sporadically from the French Côte Basque south to Morocco (Dangeard, 1949) and Sénégal (Dangeard, 1951). Plants of *G. pannosa* from Biarritz were described by Feldmann & Hamel (1936) and a Mediterranean population has been studied in detail by Boudouresque (1969). The species forms minute tufts of little-branched erect axes about 50 μm in diameter and 3–4 mm long from a creeping base (Feldmann & Hamel, 1936, fig. 11A, B; Boudouresque, 1969, fig. 1). Tetrasporangial stichidia are about 100 μm in diameter, and bear rows of one to four tetrasporangia in Mediterranean plants (Boudouresque, 1969, 1970). *G. calcicola* thus differs in vegetative and reproductive morphology from *G. pannosa*.

Of the Mediterranean species treated by Feldmann & Hamel (1934, 1936), *Gelidiella calcicola* most closely resembles Tunisian specimens of *G. ramellosa* (Kützing) J. Feldmann & Hamel. They illustrated plants of this species (Feldmann & Hamel, 1936, fig. 8) as pinnately branched erect axes of 80–150 μm diameter arising from a creeping basal part. The stichidia were formed from lateral branches of the erect axes, and were often in a pinnate arrangement. *G. ramellosa* differs from *G. calcicola* by the production of erect axes and the formation of stichidia about 100 μm in diameter with tetrasporangia 20–25 \times 30–38 μm in rows of only four to five. In Tunisia and Mediterranean France (Boudouresque, 1967), *G. ramellosa* grows as a turf on shaded rocks exposed for the greater part of the tidal cycle. There is some doubt as to whether the Tunisian

TABLE II. Species of *Gelidiella* described to date, showing tetrasporangial characters and geographical distribution

Species of <i>Gelidiella</i>	Arrangement of tetrasporangia	Number in rows when viewed from above	Size of tetrasporangia (μm)	Distribution
<i>acerosa</i> (Forsskål) Feldmann & Hamel, 1934	Irregular	—	17–24 × 34–52	Widespread in tropical and subtropical seas; Mediterranean
Type species				
<i>adnata</i> Dawson, 1954	Chevrons	4	25	Vietnam
<i>antipai</i> Célán, 1938*	Paired	2	30–60	Black Sea, Mediterranean, Pacific Mexico
<i>bornetii</i> (Weber van Bosse) Feldmann & Hamel, 1934	Chevrons	nd	nd	Malaya, Cochinchina, India
<i>calcutola</i> Maggs & Guiry sp. nov.	Chevrons	8–10	25–38	British Isles, Brittany (N France)
<i>feldmannii</i> Beardseith, 1941	Chevrons	8–12	nd	Tristan da Cunha
<i>hancockii</i> Dawson, 1944†	Irregular	—	nd	Pacific Mexico
<i>indica</i> Sreevasa Rao, 1971	Irregular	—	16.5–23	India
<i>ligulata</i> Dawson, 1953	Irregular	—	nd	Pacific Mexico, Solomon Is.
<i>lubrica</i> (Kützling) Feldmann & Hamel, 1934	Straight rows	4–6	25–30	Mediterranean, Solomon Is.
<i>machristiana</i> Dawson, 1957	Unknown	—	—	Pacific Costa Rica
<i>myrioclada</i> (Børgesen) Feldmann & Hamel, 1934	Chevrons	3–6	27–38	India, Tanzania, Vietnam
<i>nigrescens</i> (Feldmann) Feldmann & Hamel, 1934	Unknown	—	—	Mediterranean
<i>pannosa</i> (Feldmann) Feldmann & Hamel, 1934‡	Chevrons	1–6	12–40	E & W Atlantic, W Mediterranean, Thailand, Vietnam, Puerto Rico
<i>ramellosa</i> (Feldmann) Feldmann & Hamel, 1934§	Chevrons	4–6	30–38 × 20–25	Indonesia, Marshall Is.
<i>refugiensis</i> Dawson, 1944	Unknown	—	—	Australia, Japan, ?Mediterranean
<i>rigidiuscula</i> (Feldmann) Feldmann & Hamel, 1934	Unknown	—	—	Pacific Mexico
<i>sanctarum</i> Feldmann & Hamel, 1934	Chevrons	4–6	30–40	Sri Lanka
<i>setacea</i> (Feldmann) Feldmann & Hamel, 1934	Unknown	—	—	Morocco, Guadeloupe
<i>taylorii</i> Joly, 1957	Irregular	—	nd	Guadeloupe, French Guiana
<i>tinjerensis</i> Seoane-Camba, 1977	Chevrons	(2–)4–10	nd	Brazil
<i>trinitatis</i> W. R. Taylor, 1943	Chevrons	nd	c. 30	Canary Is.
			nd	Trinidad, Cuba, Costa Rica, Brazil

nd: No data available.

*Includes *Gelidiella stichidiospora* Dawson (1953) according to Boudouresque (1972).†Includes *G. mexicana* Dawson (1944) *pro parte* (see Dawson, 1953, p. 83).

‡Boudouresque (1969) lists morphological differences between Mediterranean and Atlantic plants of this species and it seems likely that two different entities are represented. See also Fan (1961, p. 340, adnot.) regarding nomenclature.

§Originally described from Australia (Kützling, 1843), and Mediterranean specimens may not represent the same biological species.

||See text of present paper.

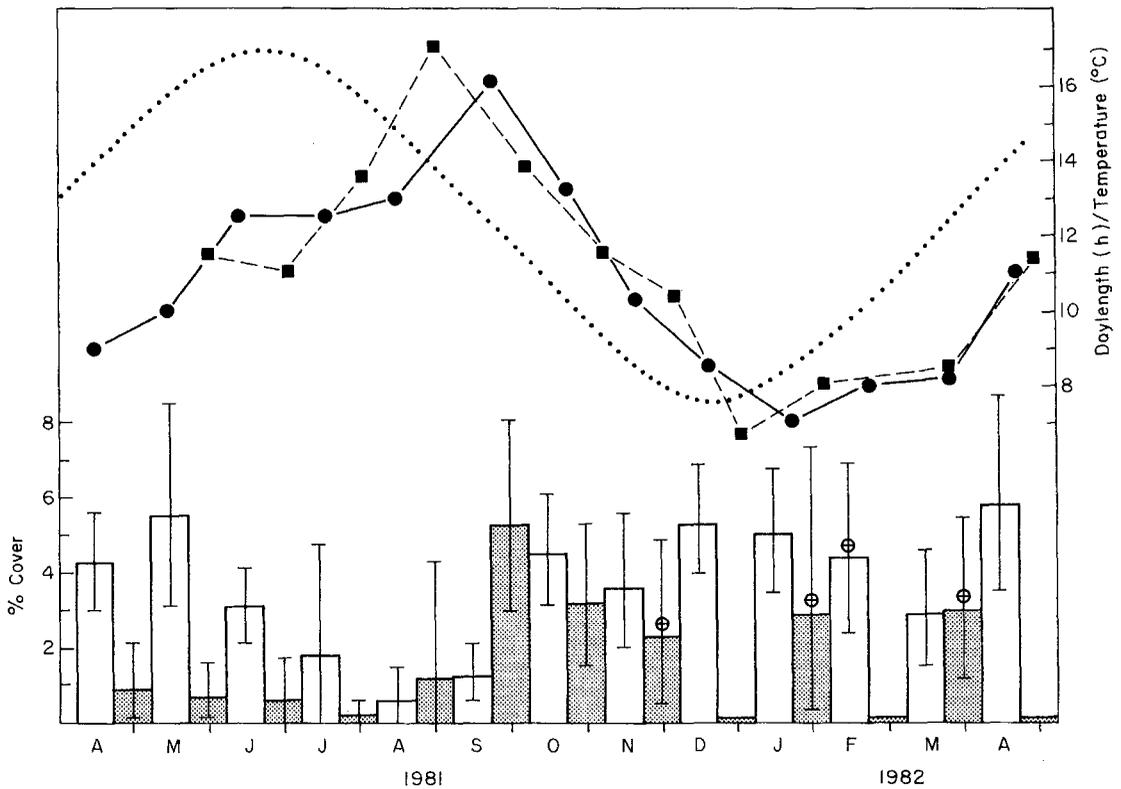


FIG. 27. Phenology of *Gelidiella calcicola* sp. nov. at two sites in Galway Bay, Ireland, during 1981–1982. Histograms represent percentage cover in five replicate samples from Finavarra, Co. Clare (unshaded) and Carraroe, Co. Galway (shaded); ⊕ denotes presence of tetrasporangial plants (..... daylength; ●—● bottom temperature, Finavarra; ■—■ bottom temperature, Carraroe).

specimens described by Feldmann & Hamel (1936) are identical to the type material of *Acrocarpus ramellosus* Kützinger (1843, p. 405) from Australia (the basionym); Ardré (1970) reported that plants from Portugal previously assigned to *G. ramellosa* (Ginsberg-Ardre, 1963) had been redetermined as *G. pannosa* and that type material of *Acrocarpus ramellosus* from the east coast of Australia examined by her consisted of axes of up to 250 µm in diameter.

Gelidiella stichidiospora Dawson (1953) from the Gulf of California was described as forming a velvet-like turf on the shells of living abalone (*Haliotis*); this alga differs from *G. calcicola* in the formation of conspicuous erect axes and in the production of tetrasporangia in two regular ranks rather than 8–10 as found in *G. calcicola*.

Boudouresque (1972) suggested that *G. stichidiospora* Dawson was conspecific with the previously described *G. antipae* Celan (1938, as "*Gelidiella antipae*") from the Black Sea.

In most species of *Gelidiella* for which tetrasporangia are known (Table II) they are arranged in rows of (1)–2–6; the only two species other than *G. calcicola* for which rows of more than six are known are *G. feldmannii* Baardseth (1941) from Tristan da Cunha, where they are formed in rows of 8–12, and *G. tinerfensis* Seoane-Camba from the Canary Is., in which they occur in rows of (2)–4–10. *G. feldmannii* differs from *G. calcicola* in the formation of erect, flattened or terete fronds from terete, creeping axes, the cortical cells are not in regularly arranged rows, and tetrasporangial

sori form on the main axes as well as on the lateral branches. *G. tinerefsensis* differs from *G. calcicola* in that it forms erect as well as creeping branches and tetrasporangia are frequently formed in branched stichidia. *G. calcicola* is unique amongst the species of the genus in its formation of prostrate axes of indeterminate growth with no erect fronds.

Comparison of *Gelidiella* with other genera

Gelidiella was proposed by Feldmann & Hamel (1934, p. 529) as a new name for the genus *Echinocaulon* Kützing (1843, p. 405) *nom. illeg.* The latter is a later homonym of *Echinocaulon* Spach (1841, p. 521), a genus of flowering plants now considered synonymous with *Polygonum* Linnaeus (Polygonaceae). As *Gelidiella* Feldmann & Hamel was a substitute name for *Echinocaulon* Kützing they share the same type. The lectotype species of *Echinocaulon* is *E. rigidum* Kützing and the type species of *Gelidiella* is automatically *Gelidiella rigida* (Kützing) Feldmann & Hamel. Feldmann & Hamel (1934) were of the opinion that *Gelidiella acerosa* (Forsskål) Feldmann & Hamel [based on *Fucus acerosus* Forsskål (1775, p. 109) from the Red Sea] was a taxonomic synonym of *Gelidiella rigida*. They characterized the genus mainly by the lack of internal rhizines (thick-walled medullary filaments, called "hyphae" by some authors), which are found in all other genera of the Gelidiales (Fan, 1961). The other features of the genus are: relatively large cortical cells in regular longitudinal rows (in some species only), creeping basal parts, and the formation of tetrasporangia in stichidia (specialized fertile branches).

According to Feldmann & Hamel (1934), stichidia in *Gelidiella* are of two types: conical with cruciately or irregularly divided tetrasporangia in the *G. acerosa* group of species, or flattened with regular transverse rows of tetrahedrally divided tetrasporangia in the *G. pannosa* group. Feldmann & Hamel (1934) pointed out that in the stichidia of *Gelidiella* species the sporangia

are arranged such that all the tetrasporangia in a given row are at about the same stage of development, with the younger rows near the apices. This contrasts with the random arrangement of mature and developing tetrasporangia in most *Gelidium* species.

The mode of cleavage of the tetrasporangia of *Gelidiella calcicola* is perplexing. Sporangia with two cleavage products were not seen so that the division sequence does not seem to be successive. Most of the sporangia with regular cleavages are spherical, with spores of an equal size. Nevertheless, the arrangement does not appear to correspond with the type of tetrahedral arrangement otherwise found only in the Rhodymeniales and Ceramiales. Some confusion regarding the precise mode of division of tetrasporangia is evident in the literature on the Gelidiales, authors referring to cruciate, tetrahedral and irregular tetrasporangia, often in the same species. A similar mode of division seems to occur in some species of Bonnemaisoniaceae.

Although we have not obtained tetraspore release or reproduction in vegetatively isolated plants in culture, Feldmann (1938) germinated the tetraspores of *Gelidiella pannosa* (as *G. tenuissima*) and Chihara & Kamura (1963) grew the tetraspores of *G. acerosa* from southern Japan. In both studies it was found that the germination pattern was like that of *Gelidium* species (see Chemin, 1937; Inoh, 1947) but the authors were unable to complete the life histories. Macler & West (1987) have found that *Gelidium coulteri* W. Harvey will only reproduce in culture when grown initially at an irradiance of $< 50 \mu\text{mol m}^{-2} \text{s}^{-1}$ and then transferred to $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ or when starved in unenriched sea-water at $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 2–3 weeks and then fortified with full-strength enriched sea-water media. An irradiance of $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ is nearly five times the maximum used during our culture studies of *Gelidiella calcicola* and it may be that sudden increases in irradiance levels, both in culture and in the wild, when combined with short days and low temperatures stimulate reproduc-

tion. Further studies are clearly necessary.

The function of the occasional colourless cells found in the cortex of *Gelidiella calcicola* remains in doubt. Boudouresque (1969, 1970) referred to similar cells in *G. pannosa* as secretory cells but they may also represent hyaline hair initial cells (see Akatsuka, 1986). Such cells do not appear to have been observed in other species of Gelidiales (Fan, 1961; Akatsuka, 1970), but may have been overlooked. Hyaline hairs, which have occasionally been described for other species of *Gelidiella* [Feldmann & Hamel (1934) in *G. lubrica*; Akatsuka (1970) in *G. acerosa*; Boudouresque (1970, 1972) in *G. pannosa* and *G. antipai*, respectively], were found only in cultured plants of *G. calcicola*, and we agree with Boudouresque (1972) that the presence or absence of hairs in species of *Gelidiella* is not of much taxonomic significance. Akatsuka (1970, 1978) described hyaline hairs in several species of *Gelidium*, *Pterocladia* and *Gelidiella* from Japan and found that the "mother cells" or initials were frequently seen without hair formation being apparent. Dromgoole & Booth (1985) have recently described the development of hairs in the New Zealand species *Gelidium caulacanthum* J. Agardh.

Reassessment of Gelidiellaceae and *Gelidiella*

Fan (1961) described the family Gelidiellaceae with the single genus *Gelidiella* as encompassing those entities which have both erect and prostrate axes, the major features distinguishing the family from other Gelidialian algae being (1) the absence of rhizines (hyphae) in the medulla, (2) the lack of gametangia and carposporophytes, and (3) the presence of stichidia. The validity of each of these characters will now be discussed.

In *Gelidium melanoideum* Bornet from the Mediterranean very few rhizines are formed and then occur only in the old fronds; the tetrasporangia are disposed in distinct chevron-like rows (Feldmann & Hamel, 1936, fig. 16) in sori formed on the main

axis. This species is referred to the genus *Gelidium* largely, it seems, because some rhizines are present and tetrasporangial stichidia are not formed. The occurrence of rhizines at points of attachment of *Gelidiella calcicola* provides a further link between the two genera. Although rhizines have not been observed in any other *Gelidiella* species, further studies, particularly of transverse sections through holdfasts, may reveal their presence in other members of the genus.

Sreenivasa Rao & Trivedi (1986) have recently given a preliminary account of the structure of the cystocarps of an undescribed species of *Gelidiella* from Diu Is., off the Saurashtra coast of India. Plants of the same species forming tetrasporangia in stichidia were also found. This account represents the first report of cystocarps in the genus and their structure was found to be similar to that of the cystocarps of *Gelidium*.

Stichidia are considered to be modified branches of a thallus that become broader than the main axis in the formation of reproductive structures. The term is particularly favoured when the structures are spindle-shaped. In many species of *Gelidium*, including *G. pusillum* (Fig. 21), tetrasporangia are formed in lateral branches that become broader than the main axis; the tetrasporangial sorus may or may not entirely cover such branches. There is no reason why these should not be regarded as stichidia. In some species of *Gelidiella* (e.g. *G. feldmannii* Baardseth, 1941, fig. 25A) tetrasporangial sori may be formed on the main axis and these may be continuous with sori formed on the lateral branches. In *Gelidiella tinerefensis* (Seoane-Camba, 1977), the shape of the tetrasporangial stichidia is very variable and they are frequently extensively branched.

It thus appears that none of the characters used by Fan (1961) to distinguish the Gelidiellaceae from the Gelidiaceae stand up to critical examination.

CONCLUSIONS

Gelidiella calcicola is very successful as a creeping species on subtidal loose-lying

corallines, accompanying dead shells and small stones. J. Cabioch (1969) considered that it plays an important rôle in stabilizing maerl beds. It is generally common in the British Isles and probably northern France wherever shallow-water, unattached subtidal coralline beds occur. The formation of maerl beds takes place principally in areas of relatively good water quality and which experience some tidal currents (L. Cabioch, 1967). That it has not been described previously is primarily due to its low creeping habit, its occurrence largely in the subtidal zone, its winter reproduction and the scarcity of fertile plants. It is likely that a combination of sudden increases in irradiance levels, short daylengths, and low temperatures is responsible for the induction of tetrasporogenesis in this species. Since evidence could not be obtained in culture regarding the rate of development of stichidia, it is impossible to draw any firm conclusions about the relative importance of these environmental factors. However, the reproductive phenology of *Gelidiella calcicola* is similar to that of the *Rhododiscus*-phase of *Atractophora hypnoides*, in which short-day photoperiodic induction of tetrasporangia is enhanced by low temperatures (Maggs & Guiry, 1987).

Examination of subtidal maerl populations in Spain, Portugal and elsewhere in the eastern Atlantic and western Mediterranean may reveal further populations of this distinctive species. As *G. calcicola* is capable of surviving at 5°C in culture, it is also likely to occur in Norway.

Since Fan's (1961) distinctions between the Gelidiaceae and Gelidiellaceae cannot be sustained, we therefore propose that these two families should be merged. Additionally, distinguishing between the genera *Gelidium* and *Gelidiella* is now difficult. Species of these two genera will have to be reassessed; we would like to suggest that such a reorganization could be carried out on the basis of the presence or absence of tetrasporangia formed acropetally in chevron-like series. Unfortunately, such an arrange-

ment is not found in the type species, *Gelidiella rigida* (= *G. acerosa*).

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