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The prostrate system of the Gelidiales: diagnostic and taxonomic importance

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Abstract

Despite numerous recent studies on the Gelidiales, most taxa belonging to this order are still difficult to distinguish when in the vegetative or tetrasporic state. This paper describes in detail the morphological and ontogenetic features of the prostrate system of the order with the aim of validating its diagnostic and taxonomic significance. Observations were made on fresh, liquid preserved and cultured thalli. The morphology of the attachment system and the characteristics of rhizoid ontogeny have proven to be useful diagnostic and taxonomic characters. Species belonging to *Gelidium*, *Pterocladia* and *Pterocladiella* bear true attachment organs consisting of cells of both exogenous and endogenous origin. In the family Gelidiellaceae, in contrast, attachment to the substratum is effected by single independent exogenous rhizoids. The attachment rhizoids of the Gelidiales, both exogenous and endogenous, are of the same cell type, and are the so-called hyphae, historically considered typical of the family Gelidiaceae only. A new subdivision of the Gelidiales into three families is proposed here, with the amendment of both Gelidiellaceae and Gelidiaceae, and the Pterocladiaceae fam. nov.

Keywords: attachment; Gelidiales; Pterocladiaceae; rhizoids; rhizines; taxonomy.

Introduction

Diminutive species, as well as juvenile and dwarf plants of gelidialean macroalgae are difficult to identify, especially when vegetative. This can seriously flaw floristic and ecological works, especially because in some geographic areas entire populations of Gelidiales are known to propagate only vegetatively, or to be, at most, tetrasporic (Fan 1961, Dixon and Irvine 1977, Guiry and Womersley 1993). Tetrasporangial sorus characteristics alone do not permit either generic or specific assignment (Maggs and Guiry 1987, Guiry and Womersley 1992, Kraft and Abbott 1998).

The Gelidiales *sensu* Kylin (1923) consists of two families, Gelidiaceae and Gelidiellaceae. The family Gelidiaceae is characterized by typical unicellular thick-walled internal rhizoidal filaments (the so-called hyphae, rhizines, or endofibers) (Feldmann and Hamel 1934, 1936, Fan 1961, Lee and Kim 2003) and a triphasic isomorphic life history, whilst the family Gelidiellaceae (Fan 1961) is based on 1) the lack of hyphae and 2) the lack of sexual reproduction. Two distinct kinds of tetrasporangial sori, the *acerosa*-type and the *pannosa*-type, were described in the genus *Gelidiella* J. Feldmann *et* Hamel (Feldmann and Hamel 1934, Fan 1961). Very recently, the new genus *Parviphycus* Santelices (Gelidiellaceae) has been proposed to accommodate those species previously assigned to *Gelidiella* that bear "*pannosa*-type" tetrasporangial sori and show sub-apical cells undergoing a distichous pattern of division (Santelices 2004).

Gelidium J.V. Lamouroux and *Pterocladia* J. Agardh, two of the most widespread genera (which have been confused) of the Gelidiaceae, are separated only by basic features of cystocarps (cf. Santelices 1988, 1990). The genus *Pterocladiella* Santelices *et* Hommersand was later established to segregate from *Pterocladia* those species with distinct carposporophyte developmental characters (Santelices and Hommersand 1997).

However, the presence of internal rhizoidal filaments in some thalli or axes of the Gelidiaceae has been questioned, so it should not be taken for granted (Perrone 1994). In certain habitats, in fact, both small thalli and small species belonging to either *Gelidium* or *Pterocladiella* are known to assume a prostrate habit bearing uprights with a few, or, very often, without any internal rhizoids at all, such as *Pterocladiella melanoidea* (Schousboe *ex* Bornet) Santelices *et* Hommersand and *G. pusillum* (Stackhouse) Le Jolis on southeastern coasts of Italy (Perrone 1994) as well as *Pterocladiella minima* (Guiry *et* Womersley) Santelices *et* Hommersand in Australia (Guiry and Womersley 1992). In this latter form they can hardly be distinguished from species belonging to the family Gelidiellaceae. The apical growth pattern as well as an evident axial cell row throughout the erect axes, described as characteristic of *Parviphycus*, are also present in some genera of the family Gelidiaceae (Rico and Guiry 1997, pers. observ.). In addition, the absence of gametophytic thalli in the Gelidiellaceae can no longer be maintained, since Sreenivasa Rao (1974) observed meiotic divisions during tetraspore formation, and Kapraun et al. (1994) reported diploid and haploid nuclear DNA amounts in tetrasporophytes and presumptive gametophytes in *G. acerosa*. Furthermore, male gametophytes were described in *G. acerosa* (Santelices 1997a) and *Parviphycus tenuissimus* (J. Feldmann *et* Hamel) Santelices (as *G. tenuissima*) (Rico et al. 2002).

The *pannosa*-type tetrasporangial arrangement, attributed to *Parviphycus* (as *tenuissima*-type), can also be observed in other Gelidiaceae, such as *Pterocladiella melanoidea*, *Pterocladiella minima*, *Pterocladiella caloglossoides* (Howe) Santelices and *Capreolia implexa* Gui-

ry *et* Womersley as well as in young tetrasporangial sori of *Pterocladia lucida* (Brown *ex* Turner) J. Agardh, *Pterocladiella capillacea* (S.G. Gmelin) Santelices *et* Hommersand, *Pterocladiella bartlettii* (W.R. Taylor) Santelices, *Pterocladiella caespitosa* (Kylin) Santelices and some *Gelidium* species (Norris 1992b, Guiry and Womersley 1993, Adams 1994, Rico and Guiry 1997, Kraft and Abbott 1998, Santelices 1998, pers. observ.). Therefore, the generic assignment of vegetative or tetrasporic gelidioid thalli in a turf where creeping axes of clonal gelidioid algae are entangled and sometimes anastomosed is not possible (Perrone 1994).

Finding diagnostic vegetative characters has often been the goal of morphological research on the Gelidiales (Okamura 1934, Stewart 1976, Akatsuka 1981, 1986, Rodríguez and Santelices 1987, 1988). All the vegetative characters taken into consideration, however, have been more or less correctly criticized and evaluated as unreliable (Dixon 1958, Maggs and Guiry 1987, Norris 1992a, Felicini and Perrone 1994, Kraft and Abbott 1998).

The prostrate system of the Gelidiales has been considered interesting from both a diagnostic and a taxonomic point of view, since preliminary observations on some Mediterranean species of *Gelidiella*, *Parviphycus* (as *Gelidiella*), *Gelidium* and *Pterocladiella* (as *Pterocladia*) indicated that the attachment system features could be useful for distinguishing between the genera. While investigating the rhizoid ontogeny in some Mediterranean species of *Gelidiella*, de Gregorio and Perrone (1994) emphasized that only one kind of attachment rhizoid could be observed in the genus, i.e., single independent rhizoids. Until then, this kind of attachment system had been described only in *Parviphycus antipae* (Celan) Santelices (as *Gelidiella antipae* Celan); the few examples of "peg-like" holdfasts described in *Gelidiella acerosa* (Forsskål) J. Feldmann *et* Hamel, *Gelidiella lubrica* (Kützing) J. Feldmann *et* Hamel and *Parviphycus tenuissimus* (as *Gelidiella pannosa*) (Hatta and Prud'homme van Reine 1991, Norris 1992b) result from misinterpretation of the rhizoidal clump morphology.

The same conclusions were reached by Shimada and Masuda (1999b) when reporting and describing *Gelidiella ligulata* E.Y. Dawson from Japan, because they observed the above kind of attachment in *Gelidiella acerosa*, the type species of the genus. *Parviphycus*, to which *Gelidiella adnata* E.Y. Dawson, *Gelidiella antipae* Celan, *Gelidiella tenuissima* J. Feldman *et* Hamel and *Gelidiella womersleyana* Kraft *et* I.A. Abbott have been transferred, also shares this character with *Gelidiella* (Santelices 2004).

In contrast, attachment organs distinct from the attachment system of the Gelidiellaceae have been described in some Gelidiaceae (Perrone 1994): the "peg-like type" in *Pterocladia* [*Pterocladia lucida* (Brown *ex* Turner) J. Agardh (Shimada et al. 1999)] and *Pterocladiella* [*Pterocladiella capillacea* (Felicini and Perrone 1986, 1994, Shimada et al. 1999), *Pterocladiella melanoidea* (de Gregorio et al. 1995), *Pterocladiella minima* (Guiry and Womersley 1992)], and the "brush-like type" in *Gelidium* [*Gelidium sesquipedale* (Clemente) Thuret (Seoane-Camba 1989)], eight Mediterranean species of *Gelidium* (Perrone 1994), most *Gelidium* species, such as *G. vagum* Okamura and *G. elegans* Kützing (Shimada et al. 1999), *G. samoense* (Santelices et al. 2004), *Acanthopeltis japonica* Okamura, *Ptilophora subcostata* (Okamura) Norris and *Capreolia implexa* (Shimada et al. 1999)]. Shimada et al. (1999) generated an SSU phylogeny in which three major species clades were resolved, (1) the *Gelidiella* clade, (2) the *Pterocladia*/*Pterocladiella* clade and (3) the *Gelidium*-complex clade. These clades were shown to correlate with each kind of attachment system, suggesting that the rhizoidal attachment ontogeny reflects a phylogenetic trend within the order Gelidiales.

This paper describes in detail the morphological and ontogenetic features of the prostrate system of the Gelidiales with the aim of validating their diagnostic and taxonomic significance.

Materials and methods

The following taxa were collected frequently from the Apulian coasts (Adriatic and Ionian Seas): *Parviphycus antipae*, *Gelidiella lubrica* (Kützing) J. Feldmann *et* Hamel, *Parviphycus tenuissimus*, *Gelidium spinosum* (S.G. Gmelin) Silva, *Gelidium pusillum*, *Gelidium spathulatum* (Kützing) Bornet, *Gelidium crinale* (Turner) Gaillon, *Pterocladiella capillacea* and *Pterocladiella melanoidea*. Fresh material was preserved in formalin-seawater, dried on herbarium sheets and also kept in stock cultures for 30–40 days under natural light and temperature conditions in order to observe the prostrate system growth and morphogenesis. Liquid-preserved material was also examined, as follows:

- *Gelidiella*/*Parviphycus: G. acerosa*, sterile and tetrasporic, 1994, Port Okha, India (sent by Dr. Vijayaraghavan); sterile and tetrasporic, 1995, Queensland, Australia (sent by Dr. M. Hommersand); sterile and tetrasporic, 1995, Taiwan (sent by Dr Mei Lin); *G. lubrica*, sterile and tetrasporic, Capo S. Alessio (Sicily), Italy; *Parviphycus antipae*, sterile and tetrasporic; *G. nigrescens* (Feldmann) Feldmann *et* Hamel, sterile, *G. ramellosa* (Kützing) Feldmann *et* Hamel, tetrasporic, *Parviphycus tenuissimus*, sterile and tetrasporic, all collected in 1993 at Is. Lachea (Sicily), Italy (sent by Drs M. Cormaci and G. Furnari); *G. ramellosa*, 1993, S. Paolo, Cheradi Islands, Taranto, Italy (sent by Dr E. Cecere).

- *Gelidium: G. sesquipedale* (Clemente) Thuret, São Rafael, Portugal (sent by Drs Rui Santos and I.M. Sousa Pinto); Playa de La Franca, Asturias, Spain (sent by Dr J.M. Rico); *G. spinosum*, sterile and tetrasporic; *G. spathulatum*, tetrasporic; *G. pusillum*, female, male and tetrasporic; *G. pulchellum* (Turner) Kützing, female, male and tetrasporic; *G. crinale*, sterile, all collected in 1993 at Is. Lachea (Sicily), Italy (sent by Drs M. Cormaci and G. Furnari); *G. bipectinatum* G. Furnari, sterile, 1988, Amendolara Sea mount, Ionian Sea, Italy (pers. collection).

- *Pterocladia/Pterocladiella: Pterocladia lucida,* tetrasporic, 1995, Coff Harbour, New South Wales, Australia (sent by Dr M. Hommersand); *P. capillacea*, tetrasporic, 1993, Is. Lachea (Sicily), Italy (sent by Drs M. Cormaci and G. Furnari); *P. capillacea*, 1995, Taiwan (sent by Dr Mei Lin).

Stolons and haptera were carefully detached from the natural substrata with 10% HCl, or excised from cultured thalli, observed intact under the light microscope Olympus BX–41 (Olympus, Melville, USA), also under polarized light, or sectioned as far as possible. Sections were obtained by hand or on a Leitz Kryomat microtome (Ernst Leitz Gmbh®, Wetzlar, Germany), and stained with 1% aniline blue and 0.5% HCl, or with toluidine blue O. Photographs were taken with a Nikon Coolpix 990 digital camera (Nikon, Tokyo, Japan). Morphometric parameters were taken by means of a micrometric ocular; data were analyzed on the basis of 50 observations on the same taxon.

Results

The erect fronds of all the specimens examined arose from a prostrate system of entangled stolons attached to the substratum by means of either independent rhizoidal filaments (Figure 1) or complex haptera (Figure 2). All specimens shared some features:

- In young thalli, stolons arose from the frond basal parts, as a rule. In mature and senescent plants, however, a considerable part of the prostrate system originated from the frond apices (main and lateral) growing into terete stoloniferous axes. The latter achieved all the features of the true stolons and were able to produce rhizoids, curving downwards and re-attaching the thallus to the substratum, as could be easily observed in cultured thalli. This phenomenon was more evident in species bearing compressed to flattened fronds than in species with terete uprights (Figures 3, 4).

- Regardless of the prevailing shape and branching pattern of the erect thallus (terete, compressed or flattened, with pinnate, pectinate or sparse branches), both creeping axes and distal stolons were mostly terete or slightly compressed, with branches occurring as orthogonal or irregularly sparse lateral stolons and dorsal uprights (Figure 2). The number of internal rhizoidal filaments varied from none in *Gelidiella/Parviphycus*, to none, few or many in *Gelidium*, and none or few in *Pterocladiella* (Figures 5–7). Even though the stolon diameter could vary on the same thallus, the mean values were species specific. The mean diameter of stolons was always larger than that of the uprights in *Gelidiella* whilst the reverse occurred in *Gelidium* and *Pterocladiella* (Table 1).

- Both basal and distally formed stolons of the same taxon showed the same features. The outermost cortical cells were always larger than those of the erect fronds (Table 1). They were polygonal in shape with thicker cell walls and cuticle (Table 1; Figure 8a–c), contained few small chromatophores and were more often filled with starch granules (Figure 8a). In contrast, the outer cortex of the erect fronds usually consisted of small polygonal (especially in *Gelidiella/Parviphycus*), rounded (especially in *Gelidium*), or pyriform cells (especially in *Pterocladiella*) (Figure 9a–c).

- When stolons were well developed (3–4 mm long), they began to produce rhizoids 50–150 μm below the apices, regardless of contact with a substratum (easily observed in distal stolons formed in culture) (Figures 10–12). In wild thalli, distal stolons sometimes grew longer, unattached as tendrils, entangled in the next adjacent branches of the same or other individuals.

- The attachment rhizoid ontogeny was distinct in the different genera, as described below, but the rhizoidal cell characteristics were always the same. Rhizoidal cells are unicellular unbranched filaments. A young rhizoid is at maximum 8–10 μm wide in its apical region (Figure 13). The rhizoid cell wall appears bistratified (Figure 14), the inner part (approximately 1–1.5 μm thick) was lightly stained with aniline blue and unstained with toluidine blue O, the outer part (approximately 1.5–2 μm thick) stained with both dyes. Externally, the cell wall was coated with an indefinite mucilaginous sheath that was deeply stained with aniline blue (Figures 14, 15). When mature rhizoids were artificially extracted from the substratum and cleared of the substratum particles, they were observed to have lost the external sheath. They measured approximately 5–6 μm in diameter with a mean lumen diameter of 1 μm, and showed all the features of the internal rhizoidal filaments (or rhizines), their inner cell wall appearing refractive, as observed in polarized light (Figures 16, 19, 20, 29, 39).

The characteristics described below distinguish the prostrate system in the genera.

Gelidiella/Parviphycus

Very often the stolon apical zone appeared protected by a cap of regular or irregular thickness, which stained lightly with aniline blue (Figures 17, 18). The attachment regions could be very extensive (1–3 mm) or very small (30–40 μm) on the same stolon and consisted of a large number of independent colorless unicellular refractive rhizoids. Upright buds were almost always present opposite rhizoidal clumps on the dorsal side of the stolon (Figures 1, 20).

Each rhizoid was formed by the budding of an outermost cortical cell (Figure 21) which elongated into a filament as in the typical tip growth and remained in open connection with its mother cell (Figure 22). No internal refractive rhizoidal filaments were detected anywhere within the thallus of any of the specimens examined.

As in other gelidialean algae, most upright fronds often bore hairs in the form of unicellular colorless filaments arising from surface cells with an evident pit-connection between hair and mother cell (Figure 23). These filaments

could be misinterpreted as rhizoids, especially when morphological differences between uprights and prostrate axes are not carefully detected, and if distinct ontogenetic patterns are not taken into account.

Pterocladia*/*Pterocladiella

In both *Pterocladia lucida* and *P. capillacea* creeping axes were poorly developed compared to the erect thallus. In

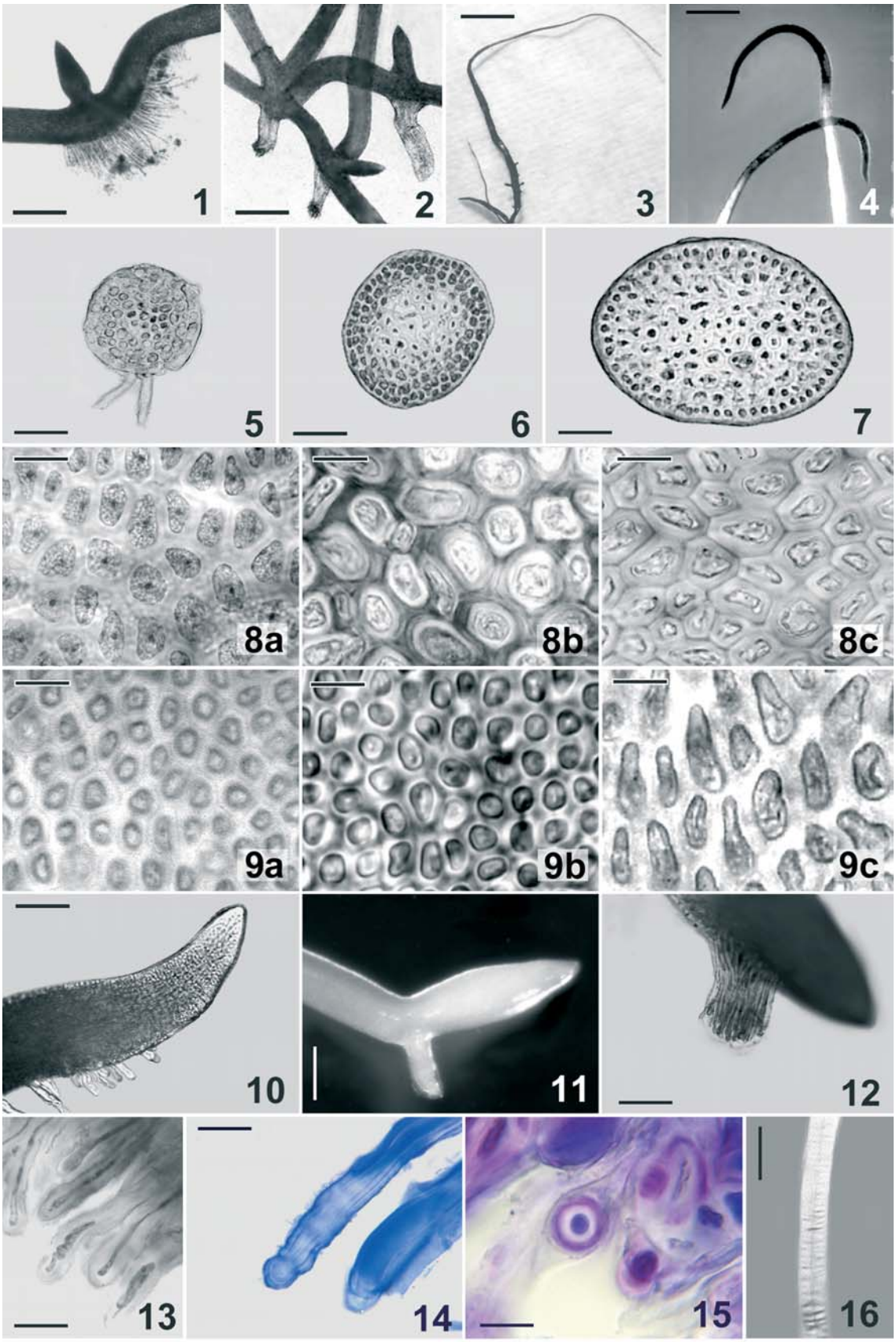

Table 1 Morphological parameters (mean values±SE, n=50) measured on uprights and stolons in both type species and Mediterranean representatives.

Taxa	Cross section w/t (μm±SE)		OCC (surface view) h/w (μm±SE)		OCC (cross section) cuticle thickness (μm±SE)	
	Upright	Stolon	Upright	Stolon	Upright	Stolon
Gelidiella acerosa	492±4.6/407±2.2	620±3.3/620±3.5	6.0±0.4/5.6±0.2	7.4±0.5/6.6±0.3	2.0±0.1	3.5±0.1
Gelidiella lubrica	160±2.7/65±1.5	257±4.3/235±2.9	7.2±0.3/7.4±0.3	7.8±0.2/10.4±0.3	1.5±0.1	2.0±0.2
Gelidium sesquipedale	1263±7.0/706±3.7	235±2.4/235±3.4	6.2±0.3/5.4±0.2	9.2±0.2/11.4±0.3	2.0±0.1	3.5±0.1
Gelidium spinosum	1070±10.2/235±4.1	257±1.6/214±1.4	5.6±0.2/6.8±0.2	6.8±0.2/8.4±03	1.5±0.1	4.0±0.2
Pterocladiella capillacea	1220±8.8/300±4.3	428±4.2/380±3.8	11.8±0.4/5.8±0.3	9.6±0.3/10.2±0.3	2.5±0.2	4.0±0.2
Pterocladiella melanoidea	385±2.7/128±1.6	150±1.9/118±2.1	12.8±0.4/7.0±0.3	12.0±0.4/3.0±0.4	2.0±0.1	4.0±0.2

w: width; t: thickness; h: height; OCC: outermost cortical cells.

P. melanoidea, in contrast, the prostrate system was more extensive than the erect thallus, especially in specimens of exposed turfs.

On the dorsal side of the stolons, flattened erect fronds always occurred opposite the haptera. A single dorsal upright was usually present in *Pterocladiella capillacea*, whilst in *P. melanoidea* 1–5 fronds could correspond to each hapteron (Figures 2, 36). The stolon diameter appeared to be distinct for the two Mediterranean species (Table 1). In the distal stolons, the formation of internal rhizoidal filaments gradually decreased and often stopped.

Pterocladia and *Pterocladiella* produced complex peg-like haptera and this production recurred at quite regular intervals (Figure 24).

The macroscopic appearance of a young unattached hapteron of *Pterocladiella capillacea* is a compact conical outgrowth 500–800 μm in length and 300–500 μm in diameter (Figure 25). Sometimes the rhizoidal bundles were twisted (Figure 26). In cross section, a bundle consisting of 200–300 rhizoidal filaments may be observed, enveloped by a thick strong hyaline sheath 5–10 μm in thickness, which stained dark with aniline blue (Figures 27, 28). In longitudinal sections of the stolons, some internal rhizoids may be observed directed from the opposite erect frond towards and penetrating the attachment organs (Figure 29).

Observations carried out on numerous haptera at various steps of their development in culture led us to the following interpretation of their ontogeny.

Each hapteron consists of bundles of parallel internal rhizoidal filaments originating from the inner cortical cells and orthogonally protruding between the surface cells of the stolons. There are typical floridean pit-connections between mother cells and rhizoids (Figure 30). The hapteron diameter enlarges in a centrifugal pattern through continuing formation of further rhizoidal filaments around them (Figures 31, 32), so that in the mature hapteron rhizoidal filaments become progressively shorter from the central zone to the periphery. Subsequently, the surface cells surrounding the hapteron area start to divide, producing multicellular pigmented filaments which form a corticated base (Figure 33). Each filament consists of a chain of rectangular cells (3–5 μm in diameter, up to 50 μm in length) (Figure 34), with some also growing between the rhizoidal filaments (Figure 35). Mature haptera showed longer cortical chains and then a more developed pigmented base.

Hapteron developmental morphology has been monitored only in laboratory cultures of *Pterocladiella capillacea*, but both the morphology and structure of *Pterocladia lucida* haptera support our interpretation.

This kind of hapteron attaches to the substratum, assuming various shapes, or penetrates it producing a

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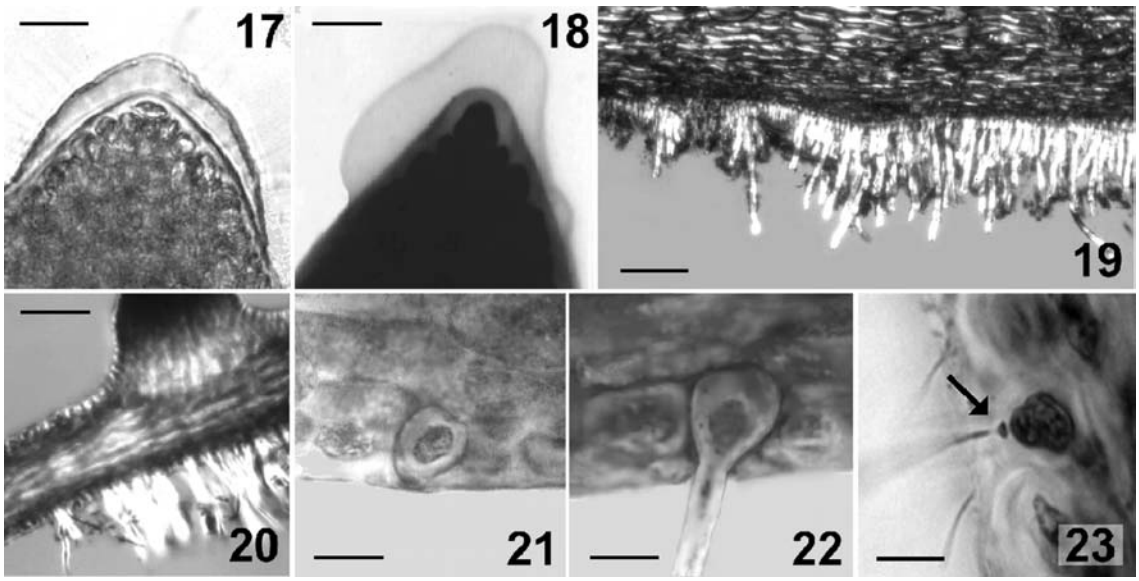
Figures 1–16 Characteristics of the prostrate system of the Gelidiales.
(1) *Gelidiella lubrica* (cultured). Stolon producing a large number of independent attachment rhizoids. A young upright subsequently arising opposite the rhizoidal region (aniline blue staining). Bar=350 μm. (2) *Pterocladiella melanoidea* (wild). Prostrate system consisting of stolons which bear uprights opposite peg-like haptera. Bar=250 μm. (3) *Pterocladiella capillacea* (wild). Distal stolon from plagiotropic differentiation of a compressed upright apex. Bar=10 μm. (4) *Gelidium pusillum* (wild). Distal stolon from plagiotropic differentiation of an upright apex. Note the lack of internal rhizoidal filaments (polarized light). Bar=200 μm. (5–7) Cross-section of mature stolons (wild). Internal rhizoidal filaments are completely absent (aniline blue staining). (5) *Parviphycus tenuissimus*. Bar=80 μm. (6) *Gelidium spathulatum*. Bar=200 μm. (7) *Pterocladiella capillacea*. Bar=100 μm. (8) Stolon outer cortex (surface views; aniline blue staining): (a) *Gelidiella acerosa* (liquid preserved); (b) *Gelidium sesquipedale* (liquid preserved); (c) *Pterocladiella capillacea* (wild). Bars=10 μm. (9) Upright outer cortex (surface views; aniline blue staining): (a) *Gelidiella acerosa* (liquid preserved); (b) *Gelidium sesquipedale* (liquid preserved); (c) *Pterocladiella capillacea* (wild). Bars=10 μm. (10–12) Stolons subapically producing attachment rhizoids or haptera. (10) *Gelidiella acerosa* (liquid preserved). Independent rhizoids. Bar=350 μm. (11) *Pterocladiella capillacea* (wild). Peg-like hapteron. Bar=400 μm. (12) *Gelidium crinale* (wild). Young brush-like hapteron. Bar=50 μm. (13) *Gelidiella lubrica* (cultured). Attachment rhizoids. Bar=10 μm. (14) *Gelidium crinale* (wild). Attachment rhizoids. Note the bi-stratified cell wall and the external mucilage (aniline blue staining). Bar=10 μm. (15) *Pterocladiella capillacea* (cultured). Transection of an attachment rhizoid (toluidine blue O staining). Bar=7 μm. (16) *Gelidiella acerosa* (liquid preserved). Mature rhizoidal filament exhibiting the refractive quality of an internal rhizoidal filament (polarized light). Bar=10 μm.



Figures 17–23 The prostrate system of the Gelidiellaceae.
(17) *Gelidiella acerosa* (liquid preserved). Thick cap protecting the stolon apex (phase contrast). Bar=100 μm. (18) *Gelidiella nigrescens* (liquid preserved). Stolon apex cap (aniline blue staining). Bar=40 μm. (19) *Gelidiella acerosa* (liquid preserved). Stolon attachment zone, with independent refractive rhizoids (polarized light). Bar=100 μm. (20) *Parviphycus tenuissimus* (wild). Stolon rhizoidal clump opposite an upright bud (polarized light). Bar=60 μm. (21–22) *Gelidiella lubrica* (cultured). Budding of a stolon surface cell that is growing into a filamentous rhizoid. Bars=5 μm. (23) *Gelidiella lubrica* (cultured). Longitudinal section of upright thallus. Hair and its mother cell are separated by a pit-connection (arrow). Bar=20 μm.

hole (Felicini 1992). In wild specimens, haptera spontaneously or mechanically detached or extracted from the substratum reveal that the most frequent breakage occurs between the corticated base and the rhizoidal bundle. In contrast, when haptera were carefully removed with acid treatment, they retained their rhizoidal bundles, showing that the hyaline sheath was irregularly broken or more often lacking, so that the naked rhizoid tips became evident (Figures 36, 37).

Gelidium

The prostrate system of the *Gelidium* species consisted of short robust stolons attached to the substratum by means of large and stout brush-like haptera. Sometimes the uprights corresponded to the haptera on the dorsal side.

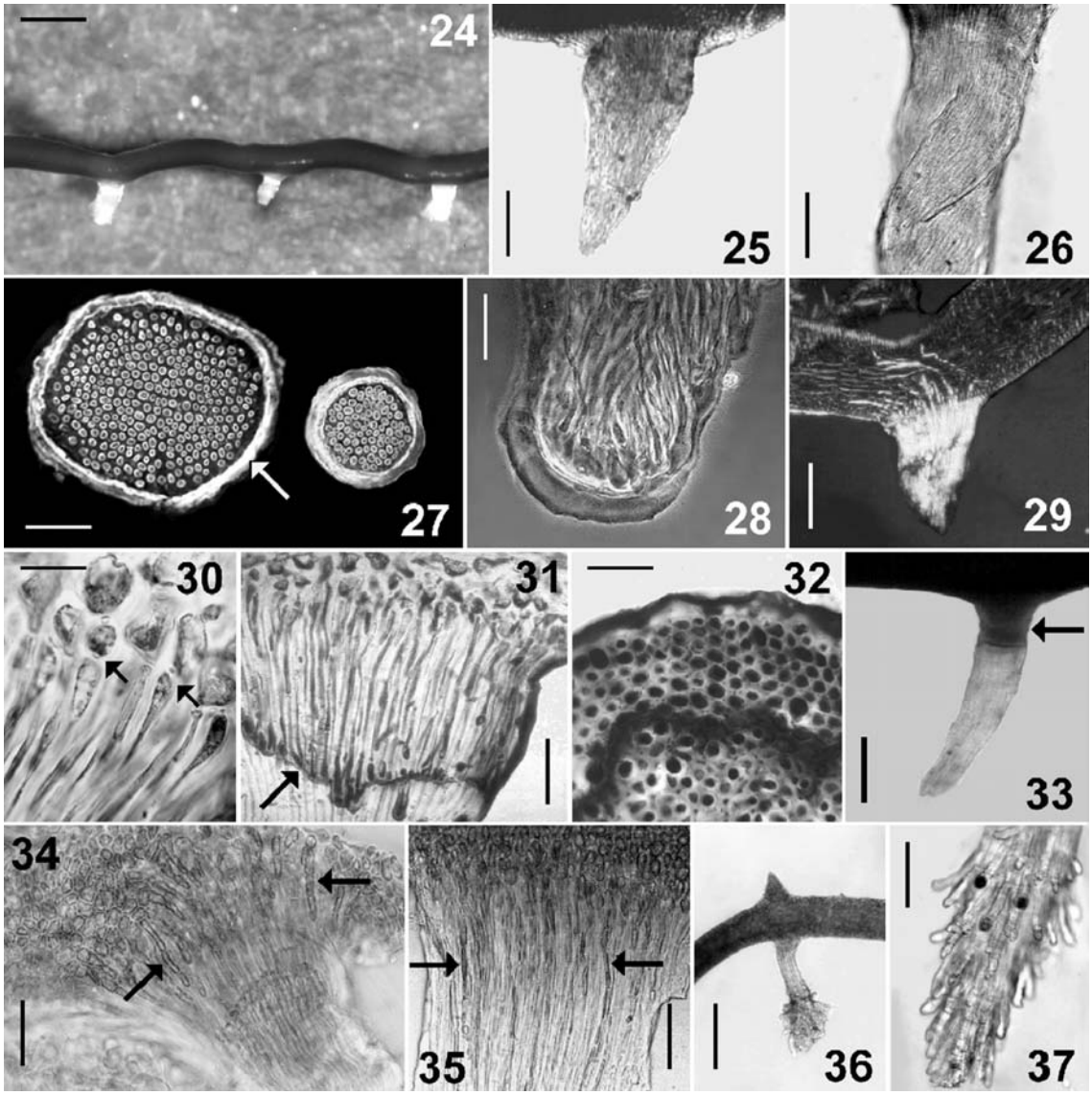
The ontogeny of the rhizoidal organs has proven to be analogous to that in *Pterocladiella*, as observed in cultured thalli. In young distally formed stolons, internal rhizoids sometimes decreased in number, but in diminutive species they sometimes stopped forming (*Gelidium pusillum* and *G. crinale*) (Figures 4, 6). In old stolons some hyphae may be observed coming from the opposite erect fronds, as in *Pterocladiella*.

Rhizoidal filaments are never produced by the outermost cortical cells. A group of 10–50 internal rhizoidal filaments, recently cut off from the inner cortical cells below the tip, protruded from the inside of the thallus, breaking the cuticle. In the early stage of its formation, the hapteron was a small conical body in which rhizoids weakly adhered to each other (Figure 12) and later on the rhizoids continued to lengthen independently and diverge (Figures 38, 39). The shape of the mature hapteron recalls that of a worn brush. The surrounding outermost cortical cells (those in the close proximity of the pierced area) also divided profusely, so that the large base of the hapteron was well corticated and pigmented. Rhizoidal filaments adhered to or penetrated the substratum singly (Seoane-Camba 1989).

In wild plants, haptera spontaneously or mechanically detached from the substratum showed the same breakage zone as *Pterocladiella*, and the single rhizoids were hardly ever recovered even when the substratum was carefully dissolved. In this state, they cannot be distinguished from those of *Pterocladia* and *Pterocladiella*.

Discussion

Most Florideophyceae have a prostrate system that plays a basic role in establishing and perennating populations. In many instances, red seaweeds also form prostrate axes from the distal parts of uprights, a phenomenon termed “secondary heterotrichy” by Dixon (1973). In *Schottera nicaeensis* Guiry *et* Hollenberg (Gigartinales), the production of distal stolons from senescent blades in summer plants has proven to be a planned event in the life cycle of this phyllophoracean alga (Felicini and Perrone 1972, Perrone and Felicini 1988). This production can be induced in young winter plants by factors stimulating precocious senescence, such as nitrogen starvation (Perrone and Felicini 1974), licorine (an inhibitor of the ascorbic acid synthesis) (Perrone and Garuccio 1983) and long-day photo-regimes (Perrone and Felicini 1993). In *Pterocladiella capillacea,* plagiotropic differentiation of the thallus occurs in response to unfavorable ecological conditions (Dixon 1958). In laboratory cultures, change of

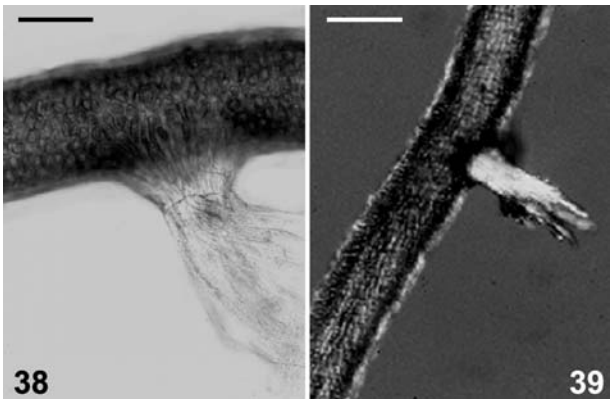


Figures 24–37 The prostrate system of the Pterocladiaceae.
(24) *Pterocladiella capillacea* (cultured). Stolon bearing peg-like haptera at quite regular intervals. Bar=1 mm. (25–26) *Pterocladiella capillacea* (cultured). Conical and spiralled peg-like haptera. Bars=170 μm. (27) *Pterocladiella capillacea* (cultured). Transections of a peg-like hapteron: proximal (left) and apical (right) sections. Arrow indicates the thick sheath. Bar=50 μm. (28) *Pterocladiella capillacea* (cultured). Longitudinal section of peg-like hapteron apex. Bar=50 μm. (29) *Pterocladiella capillacea* (wild). Longitudinal section of a stolon at the level of a hapteron (polarized light). Bar=250 μm. (30) *Pterocladiella capillacea* (wild). Longitudinal radial section of the peg-like hapteron basal part. Note the origin of rhizoidal filaments from the inner cortical cells and pit-connections between rhizoids and their mother cells (arrows) (aniline blue staining). Bar=20 μm. (31) *Pterocladiella capillacea* (wild). Longitudinal tangential section of the hapteron basal part. A second external bundle of rhizoidal filaments can be observed (arrow) (aniline blue staining). Bar=50 μm. (32) *Pterocladiella capillacea* (wild). Transection of the hapteron basal part showing both the external and primary bundles of rhizoids separated by the primary sheath (aniline blue staining). Bar=30 μm. (33) *Pterocladiella melanoidea* (wild). Mature hapteron exhibiting the pigmented basal cortication (arrow). Bar=100 μm. (34) *Pterocladiella capillacea* (wild). Initial cortication of the basal part of the hapteron in surface view. Arrows indicate multicellular cortical filaments. Bar=50 μm. (35) *Pterocladiella capillacea* (wild). Longitudinal section of the hapteron showing multicellular cortical filaments (arrows) growing between the rhizoidal ones. Bar=50 μm. (36) *Pterocladiella melanoidea* (wild). Hapteron extracted from the dissolved substratum; in the apical part the sheath is lost, and rhizoids appear free. Bar=200 μm. (37) *Pterocladiella capillacea* (wild). Hapteron extracted from the dissolved substratum; the sheath is completely lacking and rhizoidal apices are evident. Bar=300 μm.

upright axes into stolon axes is induced by low irradiance (Felicini 1970, Felicini and Perrone 1994), and photodependence is regulated by temperatures higher than 18°C (Felicini et al. 2002).

All the species of Gelidiales examined during this work bore stolons from distal parts of the erect fronds. Distal stolons showed morphological and cytological features distinct from those of the parent uprights, but resembling those of the parent basal stolons. Distal stolons were morphologically similar in all the genera studied.

The morphology of the attachment system and the characteristics of rhizoid ontogeny have proven to be useful diagnostic and taxonomic characters for distinguishing vegetative thalli of species belonging to the Gelidiales. Our observations have confirmed that a distinct kind of attachment to the substratum is present in



Figures 38–39 The prostrate system of the Gelidiaceae. (38) *Gelidium pusillum* (wild). Brush-like hapteron with initial basal cortication. Bar=100 μm. (39) *Gelidium sesquipedale* (liquid preserved). Young brush-like hapteron showing mature refractive rhizoidal filaments (polarized light). Bar=230 μm.

the Gelidiellaceae (effected by single independent rhizoids formed by the stolon surface cells growing into filaments).

In contrast, genera belonging to the family Gelidiaceae form complex haptera (de Gregorio and Perrone 1994, Perrone 1994, Shimada et al. 1999). In the literature, the attachment organs of species belonging to the Gelidiales have been named in so many different ways that there is often confusion: 1) "holdfast", has almost always been used to refer to the entire attachment system, such as stolons plus haptera, but sometimes to refer to only the hapteron; 2) "rhizoidal branches", a definition also used for the stolons, and perhaps botanically erroneous, because of misinterpretation of hapteron basal cortication; 3) "fascicles of rhizoids"; 4) "rhizoidal clumps", and so on. Here, we prefer to consider the prostrate system as consisting of stolons bearing either independent rhizoids or haptera, with haptera acting as the attachment organs.

Since the red macroalgal thallus is thus differentiated into more than just upright and prostrate parts, we believe it necessary for macroalgal morphological descriptions to use standardized botanical terminology as far as possible, thus avoiding mistakes and misleading interpretations.

The haptera of the Gelidiaceae are true organs, because they consist of cells of different origin, shape, cytological features, development and function. The attachment rhizoids are internal rhizoidal filaments with an endogenous origin from the inner cortical cells and, therefore, typical pit-connections form between rhizoids and their mother cells. The hapteron basal cortication has a secondary exogenous origin from the surface cells.

The same ontogeny had been described in the haptera of *Solieria filiformis* (Kützing) Gabrielson (Solieriaceae) (Perrone and Cecere 1994). The members of Solieriaceae characteristically bear internal multicellular branched rhizoidal filaments, originating from the inner cortical and medullary cells. When forming attachment rhizoids, thalli behave in various ways according to both the presence and nature of the substratum. When the attachment is initiated from intact apices, they behave like the Gelidiaceae, producing a cell type towards the outside identical to those having a supporting function inside the thallus. Stolons form the attachment rhizoids below the apices. A group of rhizoidal filaments protrudes from the thallus, breaking through the cuticle and growing independently if a suitable substratum is not within reach, otherwise they coalesce and attach to the substratum. Usually, a subsequent cortication also forms from the outermost cortical cells, so that the resulting hapteron could be misinterpreted as a cortical disk (Perrone and Cecere 1997).

In species belonging to *Gelidium*, *Acanthopeltis*, *Capreolia* and *Ptilophora*, the rhizoidal filaments in the haptera grow independently, being joined together basally by the cortication, like a bouquet, in only the most mature haptera. On the contrary, in the haptera of *Pterocladia* and *Pterocladiella*, rhizoidal filaments always coalesce from the origin and are bound together by a thick mucilaginous sheath, assuming a peg-like shape (Perrone 1994, Shimada et al. 1999). Therefore, the hapteron morphology can be considered a diagnostic character at genus level in the Gelidiaceae.

The present research has also demonstrated that both the exogenous and endogenous rhizoidal filaments of the Gelidiales, despite their distinct origin, have the same cellular characteristics which correspond to those of the so-called rhizines. Histological staining reveals that the rhizoid cell wall consists of two clearly distinct parts: 1) the inner that is cellulosic and 2) the outer that contains sulphated galactans and proteins. The rhizoidal apex secretion, which forms the external amorphous mucilage, is also sulphated galactan with a greater protein component.

In peg-like haptera of the *Pterocladia*/*Pterocladiella* group, this mucilage is very abundant and strong so that rhizoidal filaments not only coalesce, but also grow embedded in a thick sheath. Cell wall composition and structure agree with previous observations on the tissues of *Gelidium pacificum* Okamura (Akatsuka and Iwamoto 1979). The mature rhizoid cell wall corresponds to that of the rhizines, historically considered typical of the Gelidiaceae family alone, in both refractivity and bistratification (Felicini and Perrone 1986).

Therefore, the Gelidiellaceae also bear rhizine-like cells, even if they are only outside the thallus, with an attachment function. These results are in agreement with Norris' hypothesis (1992a) that internal rhizoidal filaments may have evolved from rhizoidal attachment cells.

The absence of rhizoidal filaments inside the thallus, on the other hand, is consistent in the Gelidiellaceae, but since this absence has sometimes been observed in other diminutive species of Gelidiaceae, such as *Gelidium pusillum*, *Pterocladiella melanoidea* (Perrone 1994) and *Pterocladiella minima* (Guiry and Womersley 1992), it should not be considered as a distinctive character of the Gelidiellaceae. Finally, the presence of rhizine-like filaments in *Gelidiella* and *Parviphycus* shows better the relatedness of these genera to the Gelidiaceae. The exogenous ontogeny of the attachment rhizoidal filaments has proven to be characteristic of the Gelidiellaceae, also supporting the circumscription of this often questioned family (Maggs and Guiry 1987).

Molecular analyses of taxa within the Gelidiales have identified four major lineages equivalent to *Gelidiella*, *Pte-*

rocladia and *Pterocladiella* as sister taxa, and a fourth large clade including species of *Acanthopeltis*, *Gelidium*, *Ptilophora*, *Porphyroglossum* and *Capreolia* (Freshwater et al. 1995, Bailey and Freshwater 1997, Freshwater and Bailey 1998, Shimada et al. 1999). These lineages are also defined by morphological characters such as rhizoidal filament ontogeny, hapteron morphology and carposporophyte development.

From a taxonomic point of view, a division of the Gelidiales into three families, with an amendment of both Gelidiellaceae and Gelidiaceae, and the establishment of the Pterocladiaceae fam. nov. are proposed here based on the results of the present and other recent studies and considerations.

Gelidiellaceae Fan (1961) emend. Perrone, Felicini *et* Bottalico

Thalli consisting of prostrate and erect axes growing uniaxially; often the main stolon represents the main axis; uprights terete to flattened, sparsely or pinnately branched; thallus devoid of internal thick-walled refractive unicellular rhizoidal filaments; segments of apical cells distichously or decussately dividing; attachment system consisting of independent unicellular thick-walled refractive rhizoidal filaments originating from the surface cells growing into filaments which remain in open connection with their mother cells.

Female reproductive system unknown; spermatangial sori raised or forming colorless patches in apices of main axes and/or lateral branchlets; tetrasporangial sori in conical or compressed apical regions of main axes and laterals; tetrasporangia arranged irregularly or in parallel transverse or chevron-like rows; tetrasporangia tetrahedrally or decussately divided.

Type genus *Gelidiella* J. Feldmann *et* G. Hamel (1934: 529).

Gelidiaceae Kützing (1843: 390 and 405, "Gelidieae") emend. Perrone, Felicini *et* Bottalico

Thalli consisting of prostrate and erect axes growing uniaxially; uprights terete to flattened, sparsely or pinnately branched; none to many internal thick-walled refractive unicellular rhizoidal filaments originating from the inner cortical cells and growing basipetally, obliquely or transversally through the thallus; prostrate system consisting of terete to compressed stolons irregularly branched; attachment system effected by complex brush-like haptera consisting of both internal thick-walled refractive rhizoidal filaments, growing independent and protruding between the surface cells, and pigmented multicellular uniseriate filaments originating from the surface cells; rhizoidal filaments singly adhering to, or more often penetrating the substratum; upright fronds sometimes arising opposite the haptera.

Triphasic or more rarely biphasic life history; gametophytes dioecious or sometimes monoecious; raised bilocular cystocarps; carposporangia developing on both planes of the cystocarp; male spermatangial sori in superficial colorless patches. Tetrasporangia in apical sori with or without sterile margins, cruciate or tetrahedrally divided; young sori usually with an ordered tetrasporangium arrangement in parallel rows; mature tetrasporangia either disorderly or in parallel rows.

Type genus *Gelidium* J.V. Lamouroux (1813: 128).

Pterocladiaceae fam. nov. Felicini *et* Perrone

Thallus prostratis teretibus axibus et compressis erectis frondibus compositus; fronda saepe pinnata cum lateralibus ramis irregulariter alternis vel disticis; uniaxialis structura ex una apicali cellula genita; nullae vel multae internae fibrae rhizoidales, unius cellulae compositae, ex cortice interno generatae, deorsum descendentes, percurrentes axes erectos prostratosque; axes prostrates conicis hapteribus affixi qui penetrant in calcaria substrata; hapteron pluribus endogeneratis rhizoidalibus fibris compositum, perlucente sed firma vagina involutum, adulta aetate cum externa corticali ac pigmentata base esogeneratis pluribus filis cellulorum composita; axes erecti plerumque surgentes oppositi hapteribus.

Cyclus vitae Polysiphonia similis; plantae sexuales dioicae vel monoicae; cystocarpum eminente, uniloculare interdum biloculare, adherente ad unum latus pavimenti cystocarpi; carposporangia in uno vel omnibus latis placentae generata. Tetrasporangia in soribus apicalibus vel in ramulis, sine ordine collocata vel in lineas paribus intervallis inter se distantes.

Thalli consisting of prostrate and erect axes growing uniaxially; uprights compressed to flattened, sparsely or pinnately branched; none to many internal thick-walled refractive unicellular rhizoidal filaments originating from the inner cortical cells and growing basipetally through the thallus; prostrate system consisting of terete to compressed stolons irregularly branched; attachment system effected by complex peg-like haptera consisting of internal thick-walled refractive rhizoidal filaments coalescing in a thick sheath and protruding between the surface cells, as well as pigmented multicellular uniseriate filaments originating from the surface cells around the hapteron base and forming a basal cortication; this kind of hapteron can adhere to the substratum, assuming various shapes, or penetrate it as a whole producing a circular hole; upright fronds always opposite the haptera.

Triphasic isomorphic life history; sexual plants dioecious or monoecious; unilocular raised cystocarps; carposporangia developing on either one or all sides of the cystocarp central plane. Tetrasporangia in apical sori, arranged irregularly or in chevron-like rows.

Type genus *Pterocladia* J. Agardh (1851: xi), designated here.

Order Gelidiales: key to families

1 Thallus completely lacking internal thick-walled refractive unicellular rhizoidal filaments; attachment system consisting of independent thick-walled refractive rhizoidal filaments originating from only the outermost cortical cells and remaining in open connection with their mother cells; rhizoidal filaments

singly adhering to, or more often penetrating the substratum ……Gelidiellaceae

1 Thallus usually provided with internal unicellular thick-walled refractive rhizoidal filaments; these can be lacking in either diminutive species or stunted thalli. Attachment to the substratum effected by complex haptera……2

1 Brush-like haptera consisting of both internal thick-walled refractive unicellular rhizoidal filaments originating from the inner cortical cells, protruding between the surface cells and growing independently, and pigmented multi-cellular uniseriate filaments originating from the surface cells and forming a basal cortication; rhizoidal filaments singly adhering to, or more often penetrating the substratum……Gelidiaceae

2 Peg-like haptera consisting of both internal thick-walled refractive unicellular rhizoidal filaments originating from the inner cortical cells, protruding between the surface cells and growing coalescent in a thick sheath, as well as pigmented multi-cellular uniseriate filaments originating from the surface cells and forming a basal cortication; hapteron adhering to or penetrating the substratum as a whole ……Pterocladiaceae

Terminology to be used in morphological descriptions of the prostrate system of the Gelidiales

Prostrate system System of stolons with plagiotropic growth pattern that functions in attachment to the substratum and ensures perennation of the species.

Stolons Secondary adventitious branches, arising from the stipe or distally from any part of the thallus; also deriving from a frond apex growing into axes with basipetal growth. Distinctive features: usually terete with irregular branching, they never bear sexual organs, they produce rhizoids (Gelidiellaceae) or haptera (Gelidiaceae and Pterocladiaceae).

Internal rhizoidal filaments Long filamentous colorless thick-walled cells produced secondarily by inner cortical and medullary cells, one per cell, pit connected to their mother cell, with basipetal growth, not forming secondary pit connections with the neighboring cells. Their cell wall has a predominantly cellulosic composition and thus becomes highly refractive in polarized light when mature. In the haptera, they play the role of attachment rhizoids. Distinctive for Gelidiaceae and Pterocladiaceae. In the past, known as hyphae, rhizines or endofibers.

Rhizoids Filamentous cells produced outwards as extensions of stolon surface cells with which they remain in open connection (like root hairs). At maturity, they have the same appearance and characteristics as the internal rhizoidal filaments. Distinctive for the Gelidiellaceae.

Haptera Attachment organs produced by stolons of the Gelidiaceae and Pterocladiaceae. They consist of internal rhizoidal filaments protruding outwards and growing independently (Gelidiaceae) or embedded in a thick sheath (Pterocladiaceae). Proximally, the haptera are secondarily corticated by multicellular pigmented filaments of cortical origin. When mature, the haptera have a distinct brush-like shape in the Gelidiaceae, and a peg-like shape in the Pterocladiaceae.

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