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Morphology and Systematics of *Holmsella pachyderma* (Pterocladiophilaceae, Gracilariales)

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The vegetative and reproductive development of *Holmsella pachyderma*, a parasite on *Gracilaria verrucosa* and *Gracilariopsis* sp. in Great Britain and Ireland, shows that it is incorrectly placed in the family Choreocolacaceae. Instead, *Holmsella* shares significant characters with members of the Gracilariaceae and with *Gelidiocolax* and *Pterocladiophila*, genera parasitic on Gelidiaceae. Similarities include the pattern of vegetative growth based on concavo–convex and transverse divisions of apical cells, the transverse cutting off of spermatangia which leads to chains in the parasitic species, the apparent absence of an auxiliary cell, and the presumed direct development of the gonimoblasts from a fertilized carpogonium, probably after fusion with unspecialized neighbouring gametophytic cells. Gonimoblasts of *Holmsella* consist of horizontal filaments fused at numerous points with gametophytic cells, and clusters of erect filaments bearing carposporangia in chains, interspersed among cortical filaments. We propose that *Holmsella* be placed in the Pterocladiophilaceae Fan et Papenfuss, along with *Gelidiocolax* and *Pterocladiophila*, and that the family be transferred to the order Gracilariales Fredericq et Hommersand.

Sturch (1926) created *Holmsella* based on *Choreocolax pachydermus* Reinsch (1875), a parasite of *Gracilaria verrucosa* (Hudson) Papenfuss (as *G. confervoides*). Reinsch based his description on specimen number 346 of Hohenacker's (1852–1862) *Algae Marinae Exsiccatae*. Irvine (1983) noted that number 346 in the Hohenacker's Exsiccatae at *BM* bears a label specifying the locality as Arromanches, Calvados (Normandy). Number 346 appears to have been a uniform gathering (Irvine, 1983). A loan request for possible type material of *Choreocolax pachydermus* Reinsch in the Reinsch herbarium at (*M*) failed to turn up an original specimen (Hertel, pers. comm).

In 1899 Sturch described the structure and reproduction of *Harveyella mirabilis*, then thought to be the only species in *Harveyella*. At the same time he called attention to a second species parasitic on *Gracilaria* which he had collected and which Mr E. M. Holmes considered to be identical with *Choreocolax pachydermus* Reinsch. Sturch proposed the provisional name, *Harveyella pachyderma*, which he attributed to Holmes and Batters. In 1924 Sturch illustrated the vegetative and reproductive development of *Choreocolax pachydermus* (as *Harveyella pachyderma*). Later, Sturch (1926) transferred *H. pachyderma* to a new genus, *Holmsella*, based on the nature of the carpogonial branch [two-celled in *Holmsella pachyderma*, vs. four-celled in *Harveyella mirabilis* (Reinsch) Schmitz and Reinke] and the presence in *Holmsella pachyderma* vs. the absence in *H. mirabilis* of an extensive post-fertilization fusion-cell network consisting of both carposporophytic and gametophytic tissues. Despite these differences in reproductive morphology, Sturch placed the parasitic genera *Choreocolax*, *Harveyella* and *Holmsella* together in a new family, the Choreocolacaceae Sturch (1926, as

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"Choreocolaceae"), in the Gigartinales. In 1937 Kylin transferred the Choreocolacaceae, but not including *Holmsella*, to the Cryptonemiales. Subsequently, Kylin (1956) considered *Holmsella* as *"Incertae sedis"* and advanced the idea that it might be related to *Gracilaria*. Kylin's taxonomic insight with regard to *Holmsella* has been largely ignored, as the genus is commonly interpreted as being an alloparasite in company with the other members of the Choreocolacaceae (Goff, 1982). Noble & Kraft (1983) suggested that *Holmsella* seems most appropriately placed in the Gigartinales (sensu strictu) along with, should the remaining genera prove similar, the family Choreocolacaceae.

Holmsella was monotypic and restricted to the north-east Atlantic until quite recently, when Noble & Kraft (1983) described a second species, *H. australis*, on *Gracilaria furcellata* Harvey from Flinders, Victoria, in south-eastern Australia.

Holmsella pachyderma was used as an experimental organism by Evans, Callow & Callow (1973) to demonstrate possible translocation of 14C-labelled compounds from host to parasite. They showed that the radioisotope was photosynthetically incorporated by the host into floridoside and subsequently translocated to the parasite where it was first converted into the soluble sugar mannitol and eventually into floridean starch.

Studies have been made on the ultrastructure of secondary pit–connections between *Holmsella pachyderma* and its host, *Gracilaria verrucosa* (Peyrière, 1981), and between *H. australis* and its host, *G. furcellata* (Wetherbee & Quirk, 1982). Wetherbee & Quirk (1982) documented structural details of the pit–plugs, which exhibit a distinctive flaring in the direction of assumed nutrient flow from host to parasite.

MATERIALS AND METHODS

Material of *Holmsella pachyderma* investigated includes female, male and tetrasporangial specimens on host *Gracilariopsis* sp. from Gwynned, N. Wales, collected by W. E. Jones, July 1987; and on host *Gracilaria verrucosa* from Blackhead, Co. Clare, Ireland, collected by J. Brodie, 12 June 1987. Material used in this study was fixed and preserved in 5% formalin/seawater. Transverse hand sections were stained with aceto-iron-haematoxylin-chloral hydrate (Wittmann, 1965) and mounted in a 1:1 Hoyer's mounting medium:-water, according to the procedure of Hommersand & Fredericq (1988). Herbarium abbreviations follow Holmgren, Keuken & Schofield (1981).

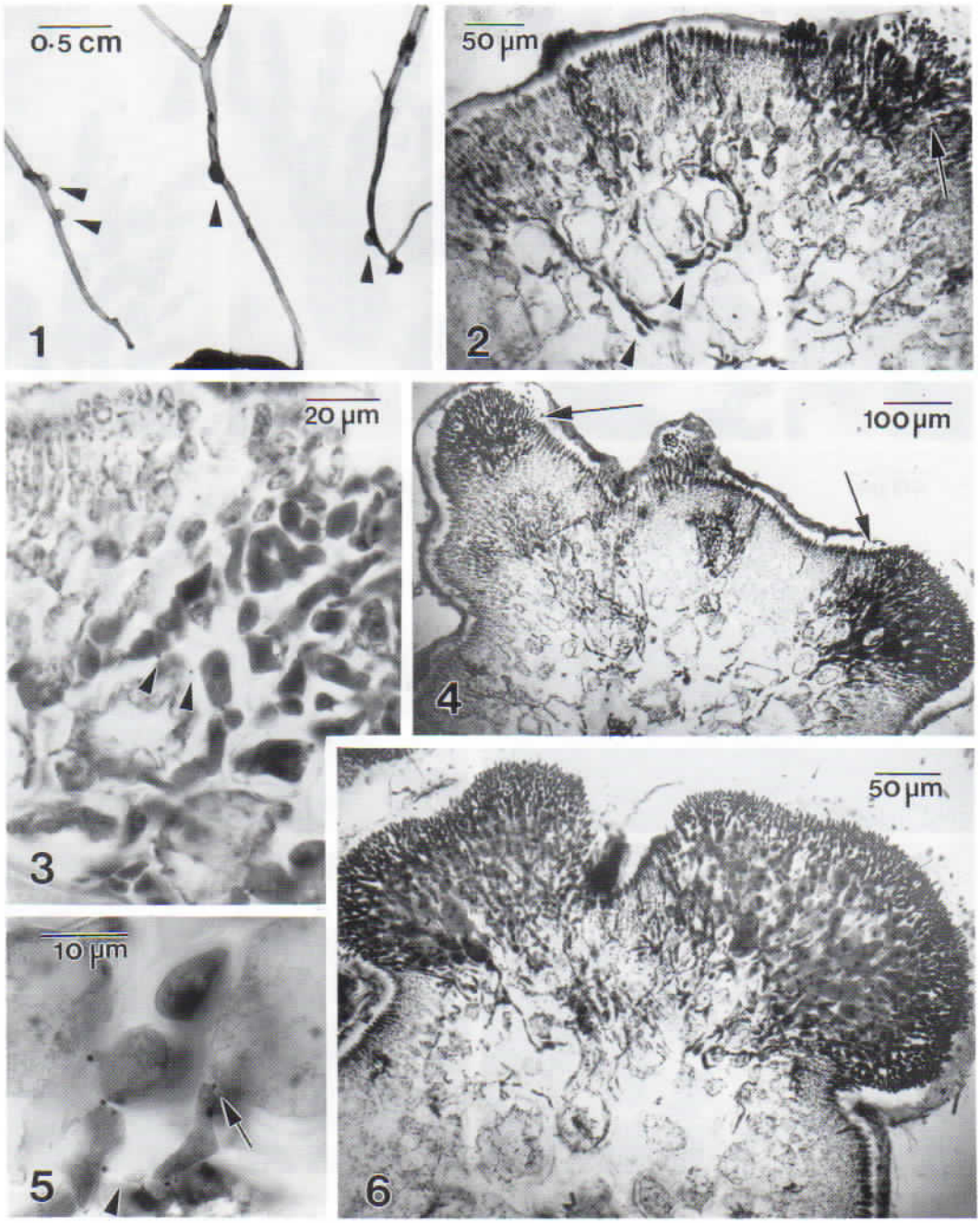
RESULTS

Vegetative organization

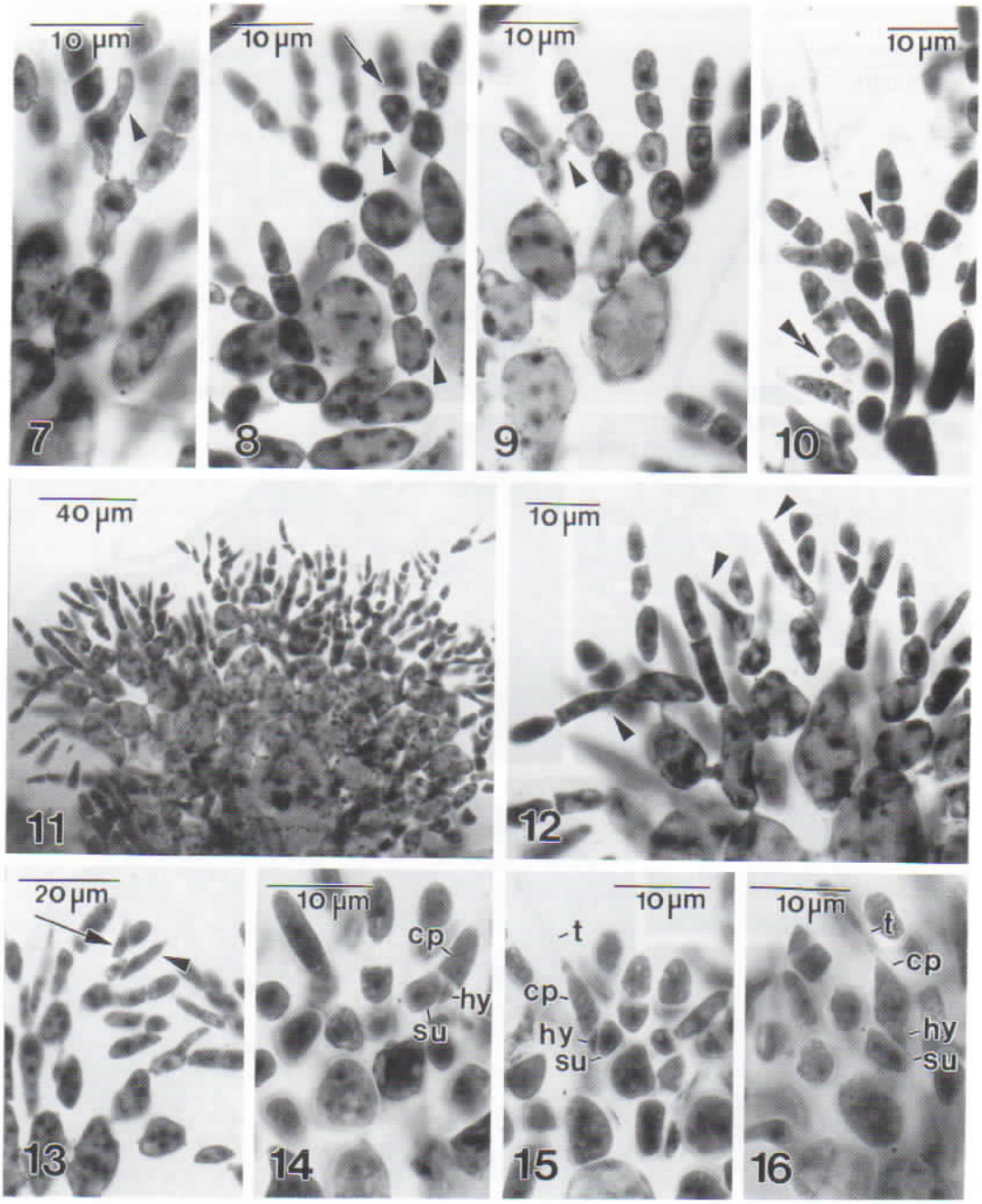
Holmsella pachyderma is a small, hemispherical, pigmented parasite (Fig. 1) that forms separate male, female and tetrasporophytic pustules on thalli of *Gracilaria verrucosa* and *Gracilariopsis* sp. in the southern and western British Isles. The thallus of the parasite is composed of an extensive system of rhizoidal filaments that grow intrusively between cortical and medullary cells of the host (Figs 2–4), and an erumpent reproductive pustule (Fig. 6).

Spore attachment, germination and host penetration have never been described in *Holmsella* and were not seen in this study. An extensive endophytic system is produced, composed of inwardly directed rhizoidal filaments which ramify through the cortex and into the medulla (Figs 2, 4). Host cells do not divide in response to parasite penetration. Individual rhizoidal cells are multinucleate and initiate conjunctor cells that establish secondary pit–connections with vegetative host cells (Figs 3, 5). Secondary pit–connections are formed abundantly throughout development, apparently until rhizoidal branching ceases. Growth then reverses direction, with the filaments branching in fan-shaped arrays to form a vegetative pustule as they ascend to the host's surface (Fig. 4).

The erumpent, reproductive stage (Fig. 6) is associated with dissolution of the host cuticle. Apical cells of outwardly directed filaments divide by transverse or oblique divisions, while intercalary cells form lateral protrusions (Figs 7, 12) that initiate lateral



FIGS 1–6. *Holmsella pachyderma*. Fig. 1. Surface view of mature tetrasporangial pustules (arrowheads) growing on *Gracilariopsis* sp. (N. Wales). Fig. 2. Young vegetative pustule (arrow) on host *Gracilaria verrucosa*. Darkly staining multinucleate rhizoids penetrate host cortex intercellularly [arrowheads (Ireland)]. Fig. 3. Rhizoids contacting host tissue by means of secondary pit-connections [arrowheads (N. Wales)]. Fig. 4. Ramifying rhizoids in host tissue. Two young vegetative pustules (arrow) are entirely contained within host tissue (Ireland). Fig. 5. Detail of secondary pit-connection (arrow) between rhizoidal cell and medullary cell of host, and initiation of secondary pit-connection [arrowhead (N. Wales)]. Fig. 6. Two young erumpent pustules differentiating into female gametophytes (Ireland).



FIGS 7–16. *Holmsella pachyderma*. Fig. 7. Protrusion of intercalary cell (arrowhead) in an erumpent filament (Ireland). Fig. 8. Initiation of conjunctor cells (arrowheads) between vegetative cells. Protruded intercalary cell has septated (arrow) to produce a pseudodichotomy (Ireland). Fig. 9. Fusion of conjunctor cell (arrowhead) resulting in binucleate recipient cell and secondary pit-connection (Ireland). Fig. 10. Fusion of conjunctor cell (arrowhead) between a vegetative parent cell and an unfertilized carpogonium. Fig. 11. Vegetative pustule (Ireland). Fig. 12. Close-up of Fig. 11, showing protrusions of intercalary cells [arrowheads (Ireland)]. Fig. 13. Initiation of carpogonial branch (arrowhead) through septation of a lateral protrusion (arrow) of a former subapical cell (Ireland). Fig. 14. Uninucleate supporting cell (su) with 2-celled carpogonial branch consisting of hypogynous cell (hy) and terminal carpogonium [cp (N. Wales)]. Fig. 15. Same as in Fig. 14, with more elongate trichogyne [t (N. Wales)]. Fig. 16. Two-celled carpogonial branch, consisting of hypogynous cell (hy) and carpogonium (cp) with trichogyne (t), borne on binucleate supporting cell (su) that has cut off a lateral filament (N. Wales).

branches. Branching tends to be pseudodichotomous (Figs 9, 11, 12).

Potentially all but the two most distal cells of erumpent filaments cut off conjunctor cells (Fig. 8) that fuse with uninucleate cells of neighbouring filaments, forming binucleate recipient cells and secondary pit–connections (Fig. 9). Meanwhile, inner cells of the parasite pustule enlarge and continue to establish secondary pit–connections, thus becoming multinucleate (Figs 7–9, 11, 12). Such cells resemble medullary cells of the host tissue in shape and size.

Female reproductive apparatus

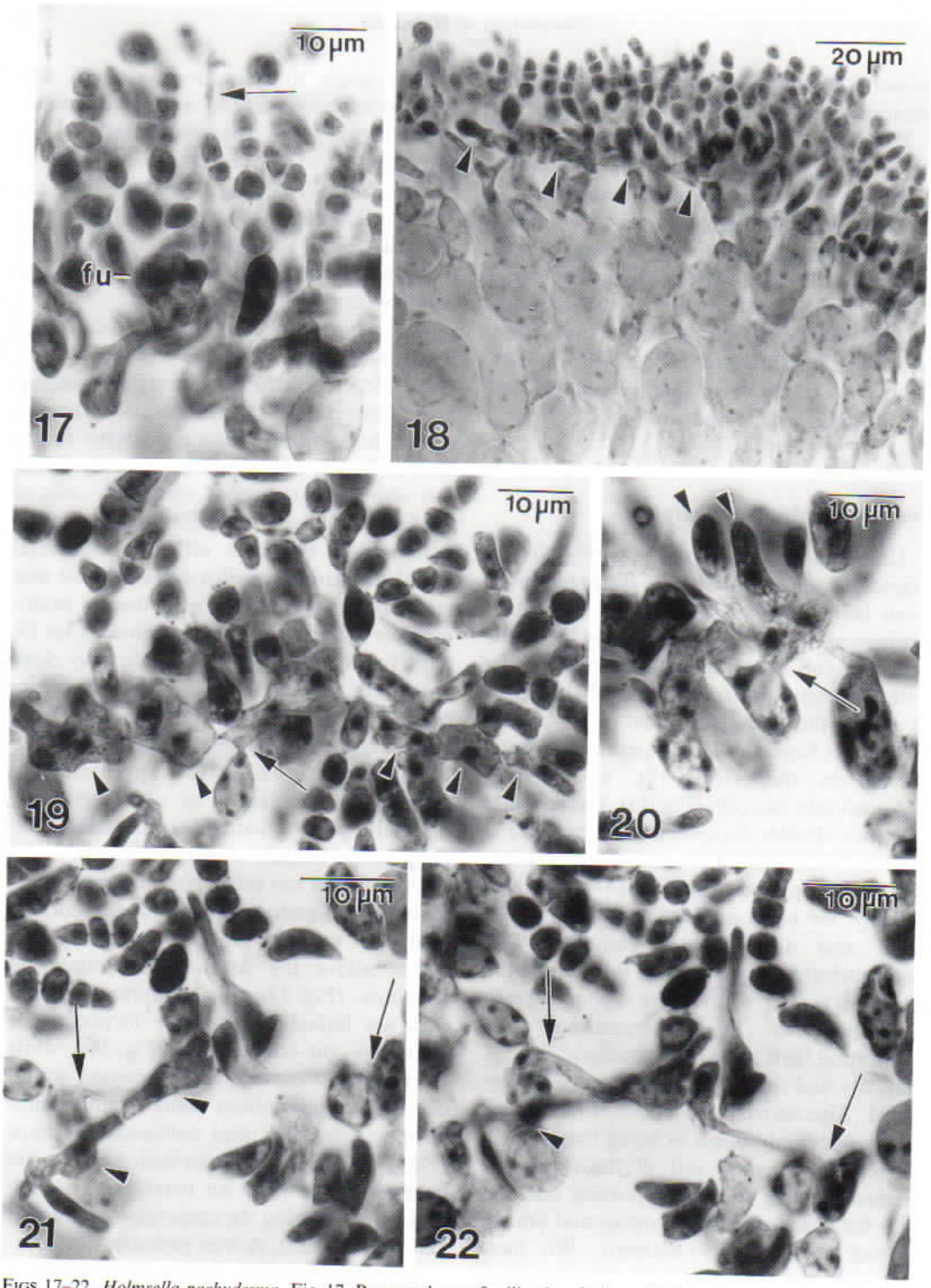
Unfertilized female pustules (Fig. 6) are pigmented and at first barely distinguishable from the uninfected host. Later they form prominent raised pustules that may be lobed. Initiation of a carpogonial branch begins with the lateral protrusion of a subapical cell in much the same way that a vegetative lateral is formed. This lateral, which is conical in shape (Fig. 13), first divides obliquely into two cells (Fig. 13). The terminal cell then divides transversely to produce a terminal carpogonium and a triangular-shaped hypogynous cell (Figs 14–15). Subsequently, the basal cell initiates a lateral filament and also becomes binucleate or multinucleate (Fig. 16). At this stage the basal cell is referred to as the supporting cell. According to this interpretation the supporting cell is an intercalary cell at maturity and the carpogonial branch is two-celled. Alternatively, it is possible to regard the carpogonial branch as being three-celled, with the intercalary cell of the vegetative filament serving as the supporting cell and with the basal cell of the carpogonial branch bearing a secondary filament. We have followed the convention of Sturch (1926) and Noble & Kraft (1983) in treating the carpogonial branch as a two-celled filament. Formation of conjunctor cells is so prevalent that occasionally one will even fuse with an unfertilized carpogonium (Fig. 10), which subsequently degenerates.

In a single instance, a fusion cell was situated in the vicinity of a remnant trichogyne (Fig. 17), but the relationship of the carpogonium to the fusion cell could not be determined. We strongly suspect that the fusion cell resulted from the fusion of vegetative cells onto the fertilized carpogonium, because auxiliary cells or connecting filaments were never detected.

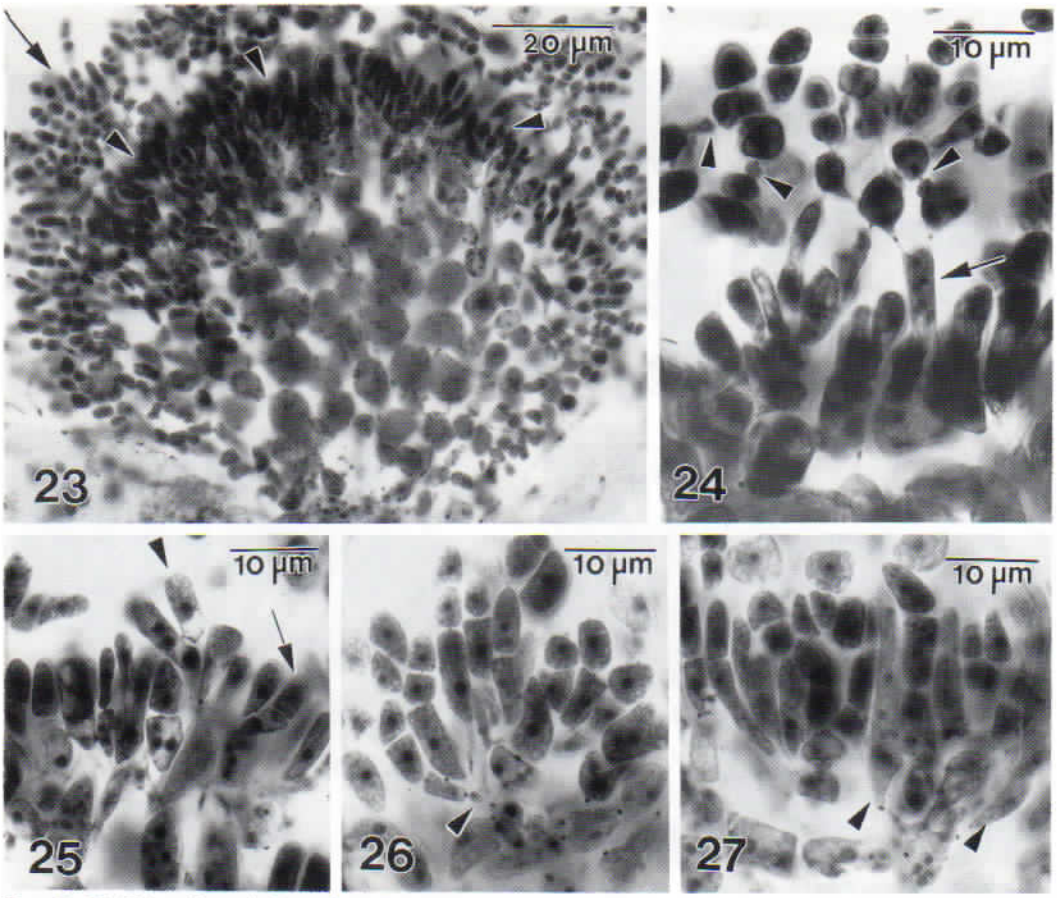
The gonimoblast consists of horizontal (periclinal) sterile filaments and erect (anticlinal) fertile filaments bearing carposporangia in chains. Gonimoblast filaments extend horizontally, forming a layer at the base of loosely branched files of cortical cells just above the expanded medullary cells of the female pustule (Fig. 18). Each horizontal gonimoblast cell cuts off one to several initials toward the thallus surface, while also initiating direct fusions with nearby multinucleate gametophytic cells below (Figs 19, 20). Horizontal gonimoblast cells may elongate over a considerable distance before contacting and fusing with the gametophytic cells (Figs 21, 22). These stretched gonimoblast cells may have the appearance of connecting filaments or "ooblastema", especially when situated near an unfertilized carpogonial branch.

Once fusion has taken place between gonimoblast and gametophyte cells, the cortical filaments resume growth, extending the cortex above the developing gonimoblast filaments (Fig. 23). Neighbouring cortical cells are linked through the formation of secondary pit–connections (Fig. 24), while the innermost cortical cells immersed within developing gonimoblast tissue become multinucleate, elongate, and columnar in shape (Fig. 24). Elevated cortical cells are pigmented and form an overlying assimilatory layer covering the carposporophyte as it matures (Fig. 23). A true pericarp is absent.

Initials of upright gonimoblast filaments divide by oblique longitudinal septa, followed by transverse division of the subapical cells. Repeated divisions of this type form a branched gonimoblast (Fig. 25). Terminal gonimoblast cells continue to divide transversely, forming clustered files of



FIGS 17–22. *Holmsella pachyderma*. Fig. 17. Presumed post-fertilization fusion cell (fu). A trichogyne is out of the plane of focus (arrow), and its precise relationship to fusion cell could not be determined (Ireland). Fig. 18. Uninucleate gonimoblast cells (arrowheads) growing between cortical filaments before fusing with inner cortical cells (Ireland). Fig. 19. Both uninucleate and multinucleate gonimoblast cells (arrowheads), and direct fusion (arrow) of uninucleate gonimoblast cells with multinucleate vegetative cells (Ireland). Fig. 20. Horizontally extending gonimoblast cell fused to vegetative cell (arrow), the fusion product bearing upright gonimoblast cells [arrowheads (Ireland)]. Fig. 21. Elongate gonimoblast cell (arrowhead) partly fused to multinucleate vegetative cell [arrow (Ireland)]. Fig. 22. Same as in Fig. 21, but different focal plane (Ireland).



FIGS 23–27. *Holmsella pachyderma* from Ireland. Fig. 23. Cystocarpic pustule with horizontal zone of gonimoblast cells (arrowheads) and secondary assimilatory filaments (arrow). Fig. 24. Close-up of secondary assimilatory filaments, showing basal columnar cell (arrow) and secondary pit-connections (arrowheads). Fig. 25. Apical gonimoblast cell dividing by an obliquely longitudinal septum (arrowhead), followed by a transverse division of the subapical cell (arrow). Fig. 26. Chains of developing gonimoblast cells bearing carposporangia distally, and initiation of conjunctor cell (arrowhead) basally. Fig. 27. Chains of gonimoblast cells bearing carposporangia distally are clustered between columnar cells (arrowheads).

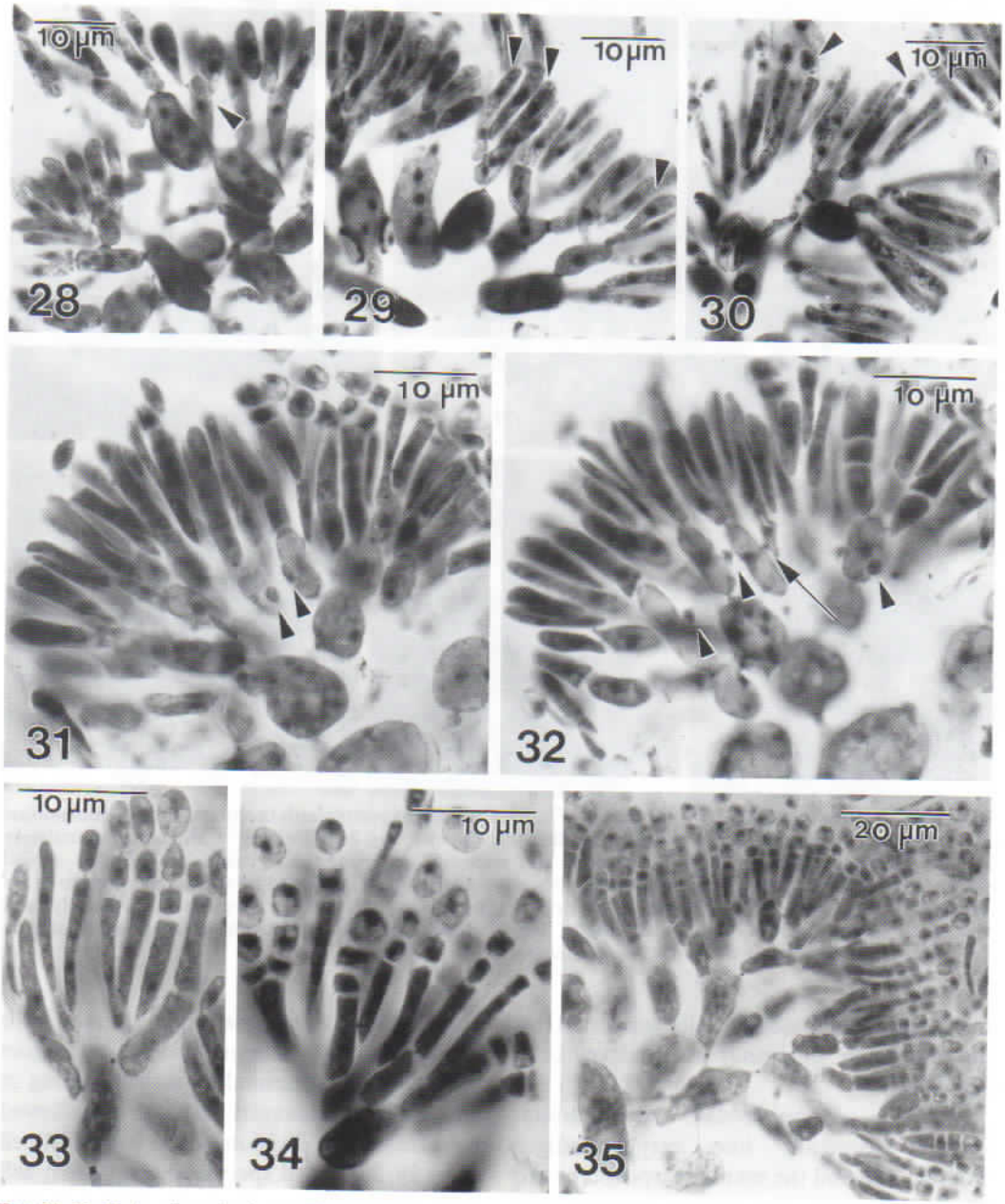
uninucleate gonimoblast cells separated by multinucleate, columnar vegetative cells (Fig. 27).

Each file of gonimoblast cells is transformed basipetally into carposporangia (Figs 26, 27), and the mature carpospores are expelled through the spaces between the overlying assimilatory filaments.

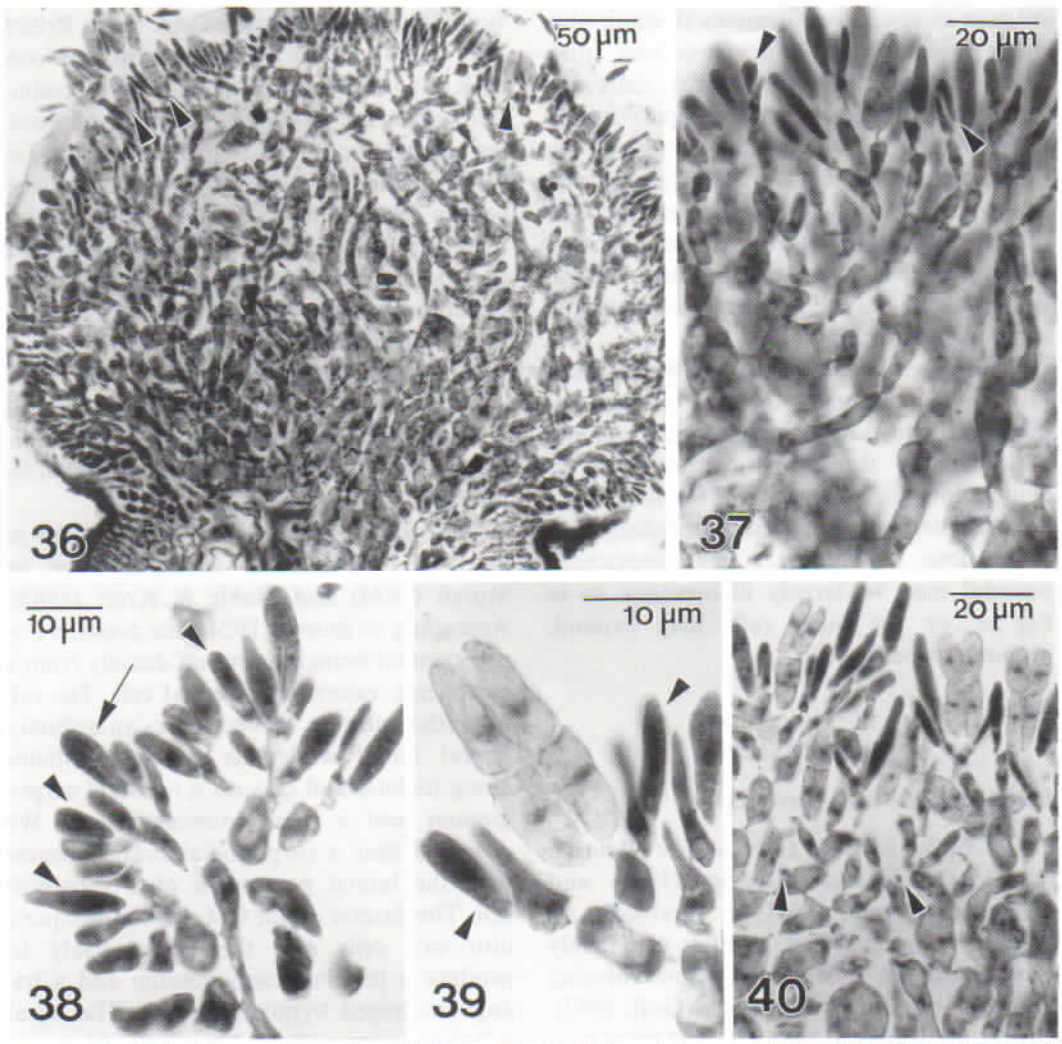
Male reproductive apparatus

Spermatangia are produced across the entire surface of a spermatangial pustule (Fig. 35), which, in contrast to female and tetrasporangial pustules, is unpigmented.

Initiation of spermatangial parent cells begins when an outer cortical cell undergoes an oblique longitudinal division resulting in a pair of spermatangial parent cells, followed by a transverse division of the subapical cell (Figs 28–30). Each spermatangial parent cell may divide further, forming branched filaments that resemble a candelabrum containing upwards of a dozen spermatangial parent cells. Branching is usually completed before the first spermatangia are cut off (Fig. 30) and is therefore monopodial. Secondary pit–connections are formed abundantly between subcortical cells bearing the spermatangial parent cells before initiation



FIGS 28–35. *Holmsella pachyderma*. Fig. 28. Cortical cell (arrowhead) bearing potential pair of spermatangial parent cells (Ireland). Fig. 29. Oblique longitudinal division in an outer cortical cell resulting in a pair of spermatangial parent cells [arrowheads (Ireland)]. Fig. 30. Spermatangia (arrowheads) cut off distally by transverse division from spermatangial parent cells (Ireland). Figs 31, 32. Two focal planes showing formation of conjunctor cells (arrowheads) and secondary pit-connections (arrow) between subcortical cells bearing spermatangial parent cells (Ireland). Fig. 33. Spermatangia cut off distally by transverse division from spermatangial parent cell (Ireland). Fig. 34. Chains of developing spermatangia cut off in succession from contents of spermatangial parent cells (Ireland). Fig. 35. Transverse section through spermatangial pustule (N. Wales).



FIGS 36–40. *Holmsella pachyderma* from N. Wales. Fig. 36. Mature tetrasporangial pustule with tetrasporangia (arrowheads). Fig. 37. Obliquely longitudinal divisions by concavo–convex septa of apical cells (arrowheads) from filaments of tetrasporangial pustule. Fig. 38. Tetrasporangial initials (arrowheads) and tetrasporangium (arrow). Cells not being transformed into tetrasporangia divide by transverse divisions. Fig. 39. Cruciately divided tetrasporangium and developing tetrasporangial initials (arrowheads). Fig. 40. Mature tetrasporangia scattered over surface of tetrasporangial pustule. Medullary cells form abundant conjunctor cells (arrowheads), leading to formation of secondary pit-connections.

of the spermatangia (Figs 31, 32). A single spermatangium is first cut off distally by transverse division from a spermatangial parent cell (Figs 30, 33). Continued division of the basal spermatangial parent cell rapidly builds up a chain of up to four spermatangia, which mature basipetally (Figs 33–34). The spermatangial parent cells become progressively shorter as a result of the basal initiation of spermatangia. Initially the spermatangia are connected by primary pit–connections which disappear as distal spermatia mature and are released.

Tetrasporangia

Tetrasporangia are cruciately divided and scattered over the entire surface of the pigmented tetrasporangial pustule (Figs 36, 40). Fertile filaments branch in the same

manner as vegetative filaments through obliquely longitudinal concavo–convex divisions, except that the apical cells are transformed into tetrasporangial initials (Figs 37–39). The subapical bearing cell has the potential to septate and form a new branch, with each apical cell of the new filament potentially becoming a tetrasporangial initial (Fig. 39). Tetrasporangial initiation in *Holmsella* is therefore associated with sympodial branching.

Each vegetative cell of a tetrasporangium-bearing filament below the most distal subapical cell quickly enlarges and becomes multinucleate through the formation of conjunctor cells that connect with neighbouring cells to establish secondary pit-connections (Fig. 40). Tetrasporangial pustules may be largely filamentous as in Fig. 36, or the inner cells may expand, becoming isodiametric.

DISCUSSION

Plant structure and reproduction

Holmsella is like *Choreocolax* Reinsch (1875), *Gelidiocolax* Gardner (1927) and *Gardneriella* Kylin (1941) in producing an endophytic system that ramifies extensively throughout the host tissue before forming erumpent reproductive pustules (Goff, 1982). Cortical layers of both female and tetrasporangial thalli are pigmented, whereas spermatangial pustules are entirely colourless. Vegetative growth is based on a combination of concavo–convex and transverse divisions of apical cells, much as in members of the Gracilariaceae (Fredericq & Hommersand 1989*a*,*b*). The chief difference is that subterminal cells commonly protrude laterally before cutting off the initial of a lateral branch.

In agreement with Noble & Kraft (1983), and in contrast to Evans, Callow & Callow (1973), we find that subcortical and medullary cells are multinucleate and secondary pit–connections are abundant between cells of the parasite within a pustule and also between parasite and host cells in both *Holmsella pachyderma* from the British Isles and *H. australis* from Australia. Noble & Kraft (1983) observed that all reproductive organs are produced in emergent colourless pustules covered by isolated groups of photosynthetically active host outer cortical cells in *H. australis*. In constrast, we find that only the male pustules are colourless and that both female pustules containing carposporophytes and tetrasporophytic pustules are pigmented in *H. pachyderma*. Internal cells of the female pustule are narrow and elongate in *H. australis*, whereas they are enlarged and isodiametric in *H. pachyderma*. Other species differences are documented by Noble & Kraft (1983).

The carpogonial branch is two-celled at maturity in *Holmsella*, as documented by Sturch (1924) and Noble & Kraft (1983). According to Sturch (1924), the procarp (= carpogonial branch) is cut off distally from a peripheral, externally oriented cell. The cell beneath continues to function as an ordinary lateral initial while the procarp distends along its base and cuts off a terminal carpogonium and a small intercalary cell. We observed that a carpogonial branch begins with the lateral protrusion of a subapical cell. This lateral initial first divides obliquely into two cells and then transversely to produce a terminal carpogonium and a triangular-shaped hypogynous cell. The basal cell then forms a lateral branch. In this interpretation the carpogonial branch apparatus is initially three-celled, and only later appears two-celled.

Sturch (1924) regarded *Holmsella* as having an auxiliary cell, which he interpreted as a terminal cortical cell. The diploid nucleus was said to be transferred to the auxiliary cell by means of a short tube ("ooblastema") departing from the carpogonium, after which the auxiliary cell divided into a lower foot cell and an upper cell. The upper cell was said to contain the dividing diploid nuclei and to initiate wandering gonimoblast cells that subsequently fused with gametophytic cells. Noble & Kraft (1983) could not detect an auxiliary cell in either *Holmsella pachyderma* or *H. australica* and

interpreted the cells seen by Sturch (1924) as being possibly the basal cells of carpogonial branches from which the carpogonium had broken away. They illustrated a putative connecting filament emanating from the lower part of a carpogonium in a single instance, but found no evidence of zygote transfer. No identifiable auxiliary cells or connecting filaments were detected in the material we examined.

Both Sturch (1924) and Noble & Kraft (1983) observed that the spermatangia in *H. pachyderma* were produced in short chains. In addition, Noble & Kraft (1983) reported that the spermatangial parent cells exhibited sympodial growth, each lateral giving rise to overtopping spermatangial filaments. Growth of the spermatangial parent cells was monopodial in our material, however, with spermatangial parent cells cutting off spermatangia almost immediately after branching was completed. Spermatangia are produced in straight chains by repeated transverse divisions of the spermatangial parent cell at the base of each chain, hence growth is intercalary.

Noble & Kraft (1983) observed that branching of the tetrasporangial filaments in *H. pachyderma* was sympodial, as is confirmed by our studies.

Taxonomic relationships of *Holmsella*

The family Choreocolacaceae is founded upon *Choreocolax polysiphonieae* Reinsch (1875), a parasite of *Polysiphonia* (*Vertebrata*) *lanosa* (L.) Tandy in the North Atlantic Ocean. Representatives of this species from Pacific North America have been transferred to *Leachiella* Kugrens (1982). As recently as 1986 the Choreocolacaceae was circumscribed to include *Gelidiocolax*, *Harveyella* and *Holmsella*, in addition to *Choreocolax*, (South & Tittley, 1986). *Choreocolax* (Sturch, 1926), *Leachiella* (Kugrens, 1982) and *Harveyella* (Goff & Cole, 1975) can all be interpreted as having a four-celled carpogonial branch borne on a supporting cell that either cuts off an auxiliary cell or serves directly as the auxiliary cell itself. All are parasites of taxa belonging to the order Ceramiales and may be related fundamentally to that order. *Holmsella*, in contrast, has a two-celled carpogonial branch and appears to lack auxiliary cells. In this respect it is similar to *Gelidiocolax* Gardner (1927) and *Pterocladiophila* Fan & Papenfuss (1959). If this interpretation is correct, none of these three latter genera belongs in the Choreocolacaceae.

The similarities between *Gelidiocolax*, *Pterocladiophila* and *Holmsella* are striking. Spermatangia are produced in straight chains and are linked by primary pit–connections, being cut off as intercalary cells by transverse divisions of an elongate spermatangial parent cell in *Gelidiocolax* and *Pterocladiophila* (Fan & Papenfuss, 1959; J. & G. Feldmann, 1963; Ganesan, 1970: Abélard & Cabioch, 1983; Stegenga & Vroman, 1986), just as in *Holmsella*. Carpogonial branches appear to be initiated as two-celled laterals on a supporting cell that bears a vegetative filament, to judge from the figures in Fan & Papenfuss (1959) and Yoneshigue & Oliveira (1984). The developmental sequence may well be the same as that described here for *Holmsella*. Early postfertilization stages have not been seen in *Gelidiocolax* or *Pterocladiophila* but a small fusion cell has been recorded at the base of the gonimoblast in *Gelidiocolax pustulata* (Yoneshigue & Oliveira, 1984) and *Pterocladiophila hemisphaerica* (Stegenga & Vroman, 1986). There are no reports of connecting filaments or auxiliary cells. Gonimoblasts lie in chambers, sometimes called conceptacles, surrounded by host tissue in all species of *Gelidiocolax* and *Pterocladiophila* that have been studied. Carposporangia are produced in clustered chains in a manner reminiscent of that seen in *Gracilaria verrucosa* (Fredericq & Hommersand, 1989*a*).

Tetrasporangia are cruciately divided and borne terminally in a naked, erumpent pustule in *Gelidiocolax* (Fan & Papenfuss, 1959; J. & G. Feldmann, 1963; Ganesan, 1970; Seoane-Camba, 1982; Yoneshigue & Oliveira, 1984). Some of the published figures of *Gelidiocolax* suggest that sympodial branching may occur in later stages of

tetrasporophyte development, as in *Holmsella*. Development of the tetrasporangial filaments is evidently sympodial in *Pterocladiophila*, and the tetrasporangia are zonately divided by two successive divisions (Fan & Papenfuss, 1959; Stegenga & Vroman, 1986).

An endophytic system is produced that ramifies within the host in *Gelidiocolax* and *Pterocladiophila*. J. & G. Feldmann (1963) and Abélard & Cabioch (1983) both state specifically that rhizoids of the parasite were never seen to form secondary pit-connections with host cells. On the other hand, the figures of Fan & Papenfuss (1959) and Stegenga & Vroman (1986) suggest the possible presence of secondary pit-connections in the species they studied, and Seoane-Camba (1982) clearly demonstrates that they are present in *Gelidiocolax deformans*. Illustrations of early stages in the formation of erumpent reproductive pustules show that development involves a combination of concavo–convex and transverse divisions in *Gelidiocolax* (J. & G. Feldmann, 1963; Yoneshigue and Oliveira, 1984) similar to that seen in *Holmsella* and in the apices of *Gracilaria* (Fredericq & Hommersand, 1989*a*) and *Gracilariopsis* (Fredericq & Hommersand, 1989*b*).

Even though the earliest stages of gonimoblast formation are still unknown, all the evidence suggests that *Holmsella*, *Gelidiocolax* and *Pterocladiophila* lack auxiliary cells and that gonimoblasts develop directly from the fertilized carpogonium or a carpogonial fusion cell. The chief distinguishing character of *Holmsella* is the presence of two phases of gonimoblast development in which the gonimoblast first grows horizontally within the cortex of the pustule parallel to the surface and fuses secondarily with neighbouring and underlying gametophytic cells, followed by the initiation of erect filaments that bear the carposporangia. Gonimoblasts of *Gelidiocolax* and *Pterocladiophila* are erect and develop within chambers surrounded by host tissue. They are relatively simple in construction, with only the innermost gonimoblast cells fusing or forming secondary pit-connections.

Pterocladiophila is distinguished from *Gelidiocolax* in that both male and tetrasporangial pustules develop in chambers surrounded by host tissue, much as in the female pustules of both. In addition, the tetrasporangia are zonately rather than cruciately divided.

We think it justified to place all three genera in the same family, the Pterocladiophilaceae Fan and Papenfuss. Fan & Papenfuss (1959) originally placed great importance on the presence of zonately (rather than cruciately) divided tetrasporangia in creating a new family for *Pterocladiophila*. Division of the tetrasporangial initial is successive in the zonate tetrasporangia of *Pterocladiophila* (rather than simultaneous as in the Corallinales) as it is in the cruciate tetrasporangia of *Holmsella* and *Gelidiocolax*. Both cruciate and zonate tetrasporangia are recorded in five other families of Florideophycidae (Guiry, 1985). Accordingly, we feel that this distinction should be de-emphasized.

Fan & Papenfuss (1959) and J. & G. Feldmann (1963) have emphasized that *Gelidiocolax* and *Pterocladiophila* are morphologically unlike members of the Gelidiales, the two genera being universally regarded as alloparasites. Although vegetative development of the three genera is quite unlike anything seen in the Gelidiales, the pattern of concavo–convex divisions of apical and cortical cells is identical to that seen in members of the Gracilariales (Fredericq & Hommersand, 1989*a*, *b*). Particular features of spermatangial initiation and gonimoblast development are also reminiscent of those seen in the Gracilariales.

Gracilariophila Setchell et Wilson, in Wilson (1910) was interpreted by Fredericq, Hommersand & Norris (1989) as a recently evolved adelphoparasite of *Gracilariopsis*. We regard *Holmsella* as having originated as an adelphoparasite of an ancestor of the Gracilariales, and we see *Gelidiocolax* and *Pterocladiophila* as being alloparasites of the Gelidiales related to *Holmsella*.

For the present, we propose that *Holmsella*, *Gelidiocolax* and *Pterocladiophila* belong to the Pterocladiophilaceae, a family which we place in the Gracilariales.

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