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Morphological observations on the adelphoparasite *Gracilariophila oryzoides* (Gracilariales, Rhodophyta)

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Gracilariophila oryzoides belongs to the Gracilariaceae based on features of early reproductive development and is interpreted as a recently evolved adelphoparasite of *Gracilariopsis lemaneiformis*. Based on reproductive morphology the parasite closely resembles its host; the cystocarp lacks tubular nutritive cells that fuse with cells of the pericarp, gonimoblast filaments are organized into comparatively straight chains, and gonimoblast conjunctor cells fuse with cells in the floor of the cystocarp. Lack of a specialized nutritive tissue in the cystocarp is discussed with regard to the parasitic lifestyle. Spermatangia are cut off singly by transverse division from spermatangial parent cells produced from surface cortical cells. Penetration and connection between parasite cells and vegetative host cells, and subsequent growth into a pustule are documented.

Key Index Words: Adelphoparasite—Gracilariaceae—Gracilariophila—*parasitism—red algae—reproductive morphology—systematics.*

Historical Perspective

SETCHELL and WILSON in WILSON (1910 p. 81) described *Gracilariophila* as a small parasitic red alga from San Francisco, California, thought to infest both *Gracilariopsis lemaneiformis* (BORY) DAWSON, ACLETO et FOLDVIK (as *Gracilaria multipartita*) and *Gracilaria papenfussii* ABBOTT (as *G. confervoides*). They recognized one species, *Gracilariophila oryzoides*, which they characterized by the presence of penetrating rhizoids, lack of pigmentation, and antheridia scattered over the entire spermatangial thallus. Whereas the holotype specimen is apparently lost in the Herbarium of the University of California at Berkeley (*UC*), an isotype specimen collected by GARDNER from Fort Point, San Francisco, is housed in *US* (*US* 851G).

Though not assigning *Gracilariophila* to any existing family, WILSON (1910) noted a close taxonomic relationship with *Gracilaria* GREV., then placed in the suborder Sphaerococcoideae. *Gracilariophila* was ignored in subsequent classification schemes, until SMITH (1944 p. 268) placed it in the Gracilariaceae, a taxonomic opinion accepted by DAWSON (1949).

Gracilariophila was the first parasitic red algal genus reported growing on members of Gracilariaceae, the second being *Holmsella* STURCH (1926 p. 603) [type species: *H. pachyderma* (REINSCH) STURCH (1926 p. 604) on *Gracilaria verrucosa* (HUDSON) PAPENFUSS (as *G. confervoides*)], and the third *Gracilariocolax* WEBER VAN BOSSE (1928 p. 393) [type species: *G. henriettiae* W.v.B. from Malaysia on *Gracilaria radicans* HAUCK]. Originally placed in the Gigartinaceae, FELDMANN and FELDMANN (1958) transferred *Gracilariocolax* to the Gracilariaceae, although it is currently placed under *Incertae sedis* (see FARR et al. 1979 p. 741).

Gracilariophila oryzoides is reported from Smith Island, Washington, to Bahia Rosario,

Baja California del Norte, Mexico (ABBOTT and HOLLENBERG 1976). In addition to *G. oryzoides*, five other species of *Gracilariophila* have been described. SETCHELL (1923 p. 393) described *G. gardneri* on *Gracilaria textorii* var. *cunninghamii* (FARLOW ex J. AGARDH) DAWSON [as *G. cunninghamii* J. AG.] collected near Santa Monica, California, based on its larger size and more strongly projecting cystocarps. WEBER VAN BOSSE (1928) erected four new species and one new variety from the Malay Archipelago, while not ruling out the possibility that the various habits could represent different developmental stages. She recognized two clusters of species based on manner of host penetration: the Californian species by means of rhizoids, and the Malaysian species by establishment of pit-connections with host cells, and placed the four Malaysian species in her section *Arhiza*, a reference to the lack of rhizoids. Subsequently, CHANG and XIA (1978) identified three of WEBER VAN BOSSE's species in China, and found that *Gracilariophila infidelis* (W.v.B.) W.v.B. and *G. deformans* W.v.B. both possess deep spermatangial conceptacles.

FELDMANN and FELDMANN (1958) recognized two major groups of florideophycean parasites, adelphoparasites and alloparasites. They placed *Gracilariophila* among the adelphoparasites, a group in which the parasite and host are closely related taxonomically.

Discussing his new genus *Congracilaria*, YAMAMOTO (1986:287) suggested that four genera of Gracilariacean adelphoparasites may ultimately be distinguished based on mode of penetration and spermatangial configuration: 1) *Gracilariophila* SETCHELL et WILSON, possessing rhizoids and superficial spermatangia, 2) *Gracilariophila* sensu WEBER VAN BOSSE (1928), lacking rhizoids and with superficial spermatangia, 3) *Gracilariophila* sensu CHANG and XIA (1978), in which rhizoid presence has still to be investigated, but with spermatangia in conceptacles and 4) *Congracilaria* YAMAMOTO, lacking rhizoids and with spermatangia in conceptacles. Although WEBER VAN BOSSE (1928) did illustrate deep spermatangial conceptacles in *Gracilariocolax*, YAMAMOTO (1986) did not hint at the possible congenerity of *Congracilaria* and *Gracilariocolax*.

Materials and Methods

Material used in this study was fixed and preserved in 5% formalin/seawater. Transverse hand sections were stained with aceto-iron-hematoxylin chloral-hydrate (WITTMAN 1965) and mounted in 1:1 Hoyer's mounting medium:water according to the procedure of HOMMERSAND and FREDERICQ (1988). Material of *Gracilariophila oryzoides* investigated includes female and male specimens on *Gracilariopsis lemaneiformis* from Pebble Beach, Monterey, California, 20. vii. 74, M. H. Hommersand, and in the drift, south of Hotel Coronado, Coronado, San Diego Co., California, 26. ix. 69, and tetrasporophytes from Execution Rock, Bamfield, Vancouver, British Columbia, Canada, 4. vi. 85, M. H. Hommersand. All specimens are deposited at *NCU*.

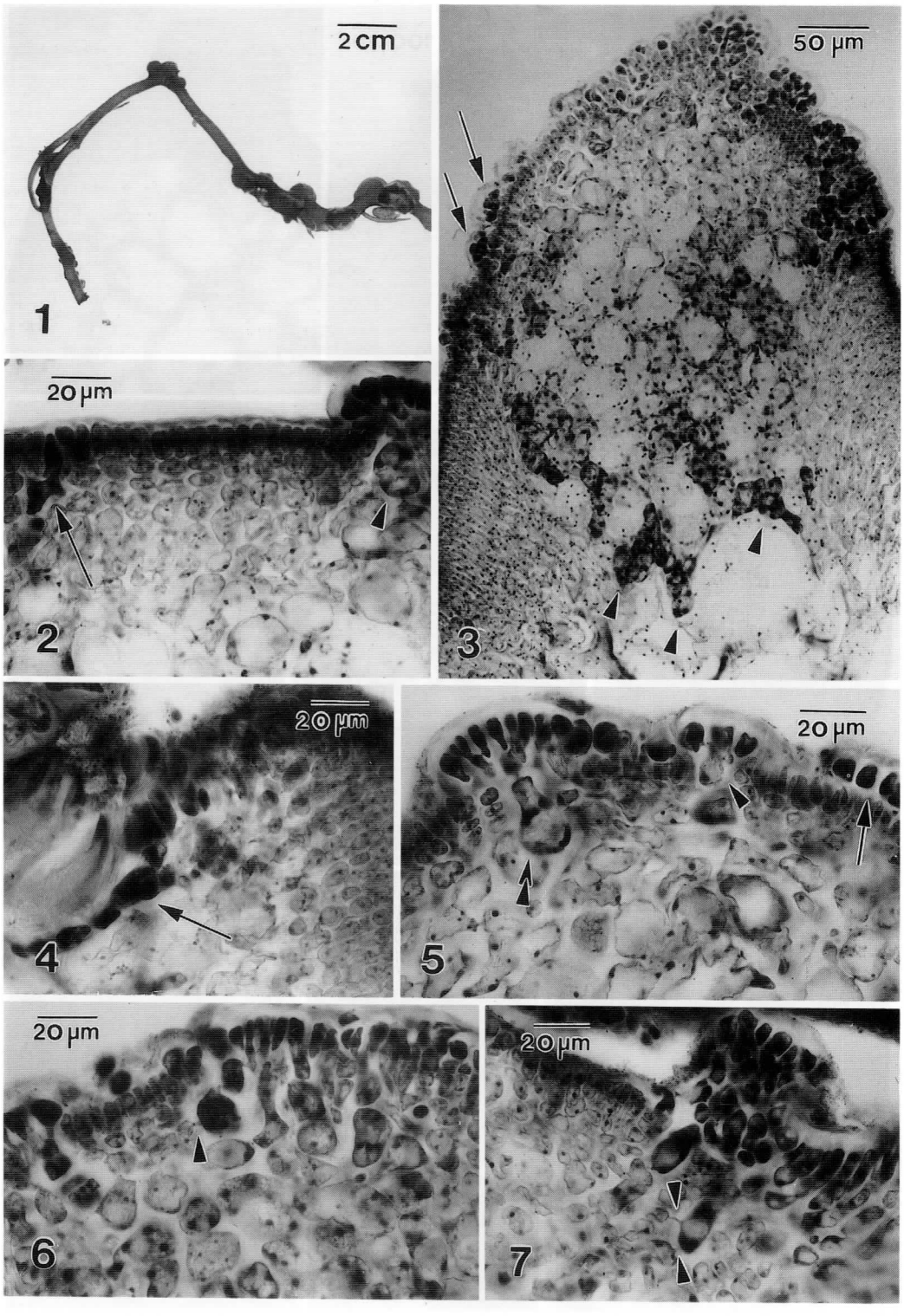
The latter specimens are the first reported for British Columbia and represent its most northern known distribution record (GABRIELSON, pers. comm.)

Results

Vegetative morphology

Gracilariophila oryzoides parasites are characterized by smooth hemispherical, spherical or warty crescent-shaped tubercles or 'pustules' protruding from the infected host (Fig. 1). Although mostly concentrated in the lower thallus portions of the host or in regions priorly epiphytized, such pustules also occur singly or in aggregated clusters over the entire surface of the host. Whereas cystocarpic and tetrasporophytic pustules are variously pigmented, spermatangial ones are typically unpigmented. All pustules investigated were dioecious or tetrasporophytic.

Spore attachment, germination and host penetration were not seen. According to ZUCCARELLO and GOFF (1988) nuclei are transfer-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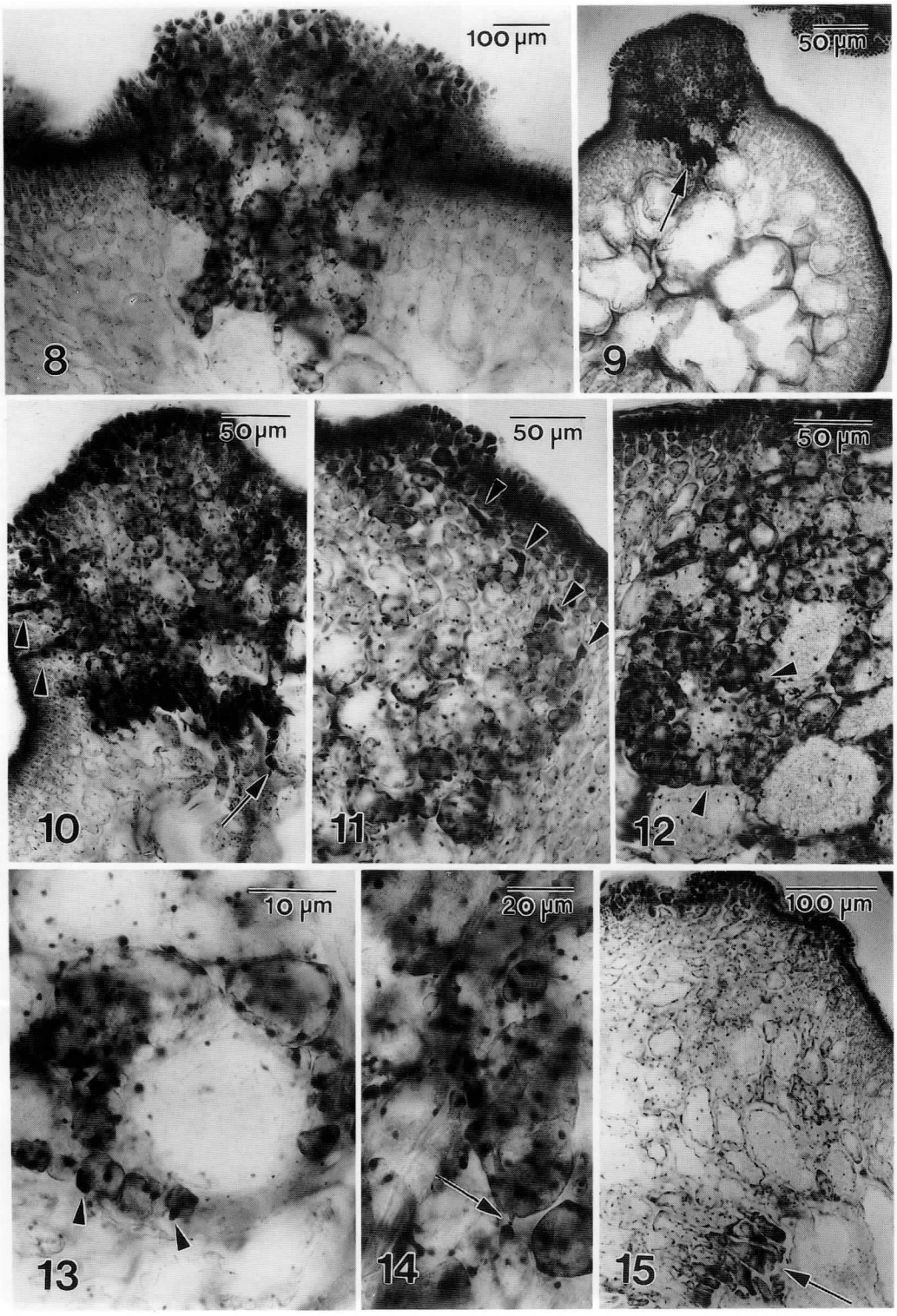
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red directly from the infection peg and 1–2 derivative cells into host cells which, in turn, produce filamentous rhizoidal cells that penetrate the host tissue making secondary pit-connections with host cells. Young pustules stained with hematoxylin reveal what appear to be numerous infection discs on the surface of a single pustule (Figs. 2, 3 and 5). This is interesting in that combined male and female sexes or mixed phases were never seen in the same pustule. Perhaps the discs are non functional.

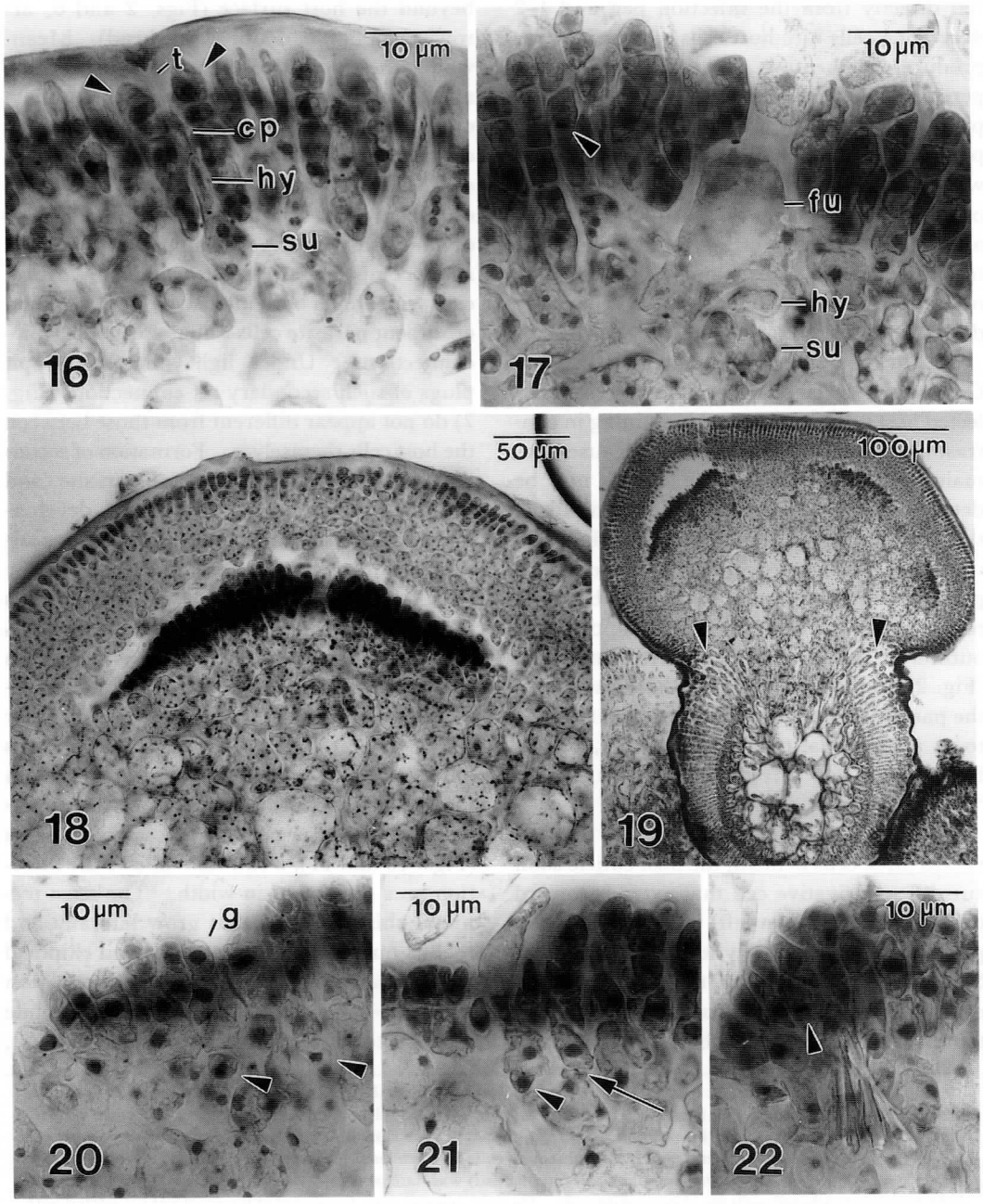
The intrusive part of the infection cycle in *G. oryzoides* starts when a rhizoidal cell or infected host cell becomes darkly staining in contrast to cells of the host cortex. Because a remaining empty spore wall could not be detected on the host cuticle, it seems likely that the entire spore content invades the outer tissues of the host. Initially subspherical, a parasite cell (Figs. 3 and 5, arrows) becomes more irregular in shape by adopting the outline of the intercellular space it occupies (Fig. 2). Once embedded within host tissue, the parasitic component is commonly referred to as a 'rhizoidal cell' (Goff, 1982), or if a filamentous file of rhizoidal cells, as a 'rhizoid' (Fig. 4).

A recently embedded rhizoidal cell that lies two to three cells beneath the host cuticle soon cuts off a derivative cell that extends toward the surface (Fig. 2 on left) where it cuts off a pair of initials bilaterally to the outside (Fig. 5, arrowhead). Each of these initials then divides longitudinally by concavo-convex septa to form files of cells that barely emerge beyond the host surface (Figs. 2 and 6, arrowheads; Fig. 5, double arrowhead). Meanwhile, the embedded rhizoidal cells become multinucleate (Figs. 2 and 5–7) and initiate conjunctor cells that establish secondary pit-connections (Figs. 6–7) with neighboring host cells. Outer cortical host cells overgrown by erumpent parasite cells are stimulated to divide transversely, forming an amplified zone composed of small, squarish cortical cells with which both intrusive (Figs. 5–7) and erumpent parasite cells initiate secondary pit-connections. Under light microscopy, pit plugs of such secondary pit-connections (Fig. 7) do not appear different from those between the host cells themselves. Formation of secondary pit-connections between parasite and host cells takes place throughout development, and results in the continuous deposition of parasite nuclei into host cells.

In addition to initiating conjunctor cells that fuse with host cells, rhizoidal cells simultaneously also cut off derivative cells that grow thallus-inward and continue to proliferate within the confines of intercellular spaces (Figs. 8–13). Once rhizoidal cells have reached the medulla, direction of growth for further expansion shifts from thallus-inward to the margins of the infected areas (Figs. 10 and 11), a shift that allows the infection area to expand in width. The most terminal rhizoidal cells that grow laterally and thallus-outward are uninucleate and elliptical to irregularly shaped with an angular portion (Figs. 10–11). They continue to divide while their subterminal derivatives quickly expand,

Figs. 1–7. *Gracilariophila oryzoides* from British Columbia. Fig. 1. Surface view of mature tetrasporangial pustule on host *Gracilariopsis lemaneiformis*. Fig. 2. *On left*: binucleate rhizoidal parasite cell (arrow) with derivative growing towards surface of host. *On right*: multinucleate rhizoidal cell (arrowhead) with erumpent cell file. Fig. 3. Discs (arrows) and penetrating rhizoidal cells (arrowheads) in host tissue. Fig. 4. Rhizoidal filament (arrow). Fig. 5. *In center*: rhizoidal cell (arrowhead) with lateral pair of derivative cells. *On left*: rhizoidal cell (double arrowhead) with file of derivative cells. *On right*: cellular discs (arrow) that have not yet connected with host cortex. Fig. 6. Rhizoidal cell linked by secondary pit-connection (arrowhead) to cortical cell of host. Fig. 7. Same as in Fig. 6, with rhizoidal cell bearing erumpent derivatives (arrowheads).

Figs. 8–15. *Gracilariophila oryzoides* from British Columbia. Fig. 8. Intrusive penetration of rhizoidal cells in host tissue. Fig. 9–10 (Fig. 10 is close-up of Fig. 9). Young pustule consisting of dark-staining parasite cells and light-staining host cells. Rhizoidal cells extending toward surface (arrowheads) and into the medulla (arrow) of host. Fig. 11. Rhizoidal cells (arrowheads) extending toward surface of host. Fig. 12. Small-celled parasite cells (arrowheads) confined to small intercellular spaces. Fig. 13. Formation of conjunctor cells (arrowheads) from parasite cells encircling a medullary host cell. Fig. 14. Establishment of secondary pit-connection (arrow) between parasite cell and host cell. Fig. 15. Intrusive growth of parasite ceases in medullary region of host (arrow). Distinction between host cells and vegetative cells has become blurred.



becoming spherical (Figs. 11–13). They also continue to initiate conjunctor cells (Figs. 12–13), establishing numerous secondary pit-connections (Fig. 14) with host cells. Rhizoids also course intercellularly into the starch-rich cortex of the host and stop abruptly at the vacuolated, presumably nutrient-poor medulla (Figs. 9 and 10, arrows). Whenever rhizoids penetrate the host tissues without at the same time cutting off derivatives that grow outwards toward the thallus surface, they appear to loose the ability to erupt secondarily above the host cortex (Fig. 4).

While a difference in shape and cyto-

plasmic content is obvious between host cells and parasite cells during the early infection stages, the vegetative tissues of both parasite and host eventually become indistinguishable once both infection and abundant formation of secondary pit-connections has ceased (Fig. 15). Remnant traces of the parasitic component are then revealed by the darkly staining extremities of rhizoidal derivatives (Fig. 15).

Female reproductive apparatus

Mature cystocarpic pustules are variously pigmented, hemispherical and resemble cystocarps of the host. A single continuous pericarp surrounds either one (Figs. 18 and 27) or several carposporophytes (Fig. 19). The latter phenomenon indicates that several carpogonia were simultaneously fertilized and that cells of the sterile branches flanking the carpogonial branch and neighboring cortical cells were concomitantly activated to divide periclinally.

A transverse section through a cystocarpic pustule of *Gracilariophila oryzoides* reveals that the floor is little modified cytologically (Figs. 17, 18 and 27). The cells are morphologically similar to medullary cells, and the cytoplasmic contents of both sporophytic and gametophytic tissues stain darkly.

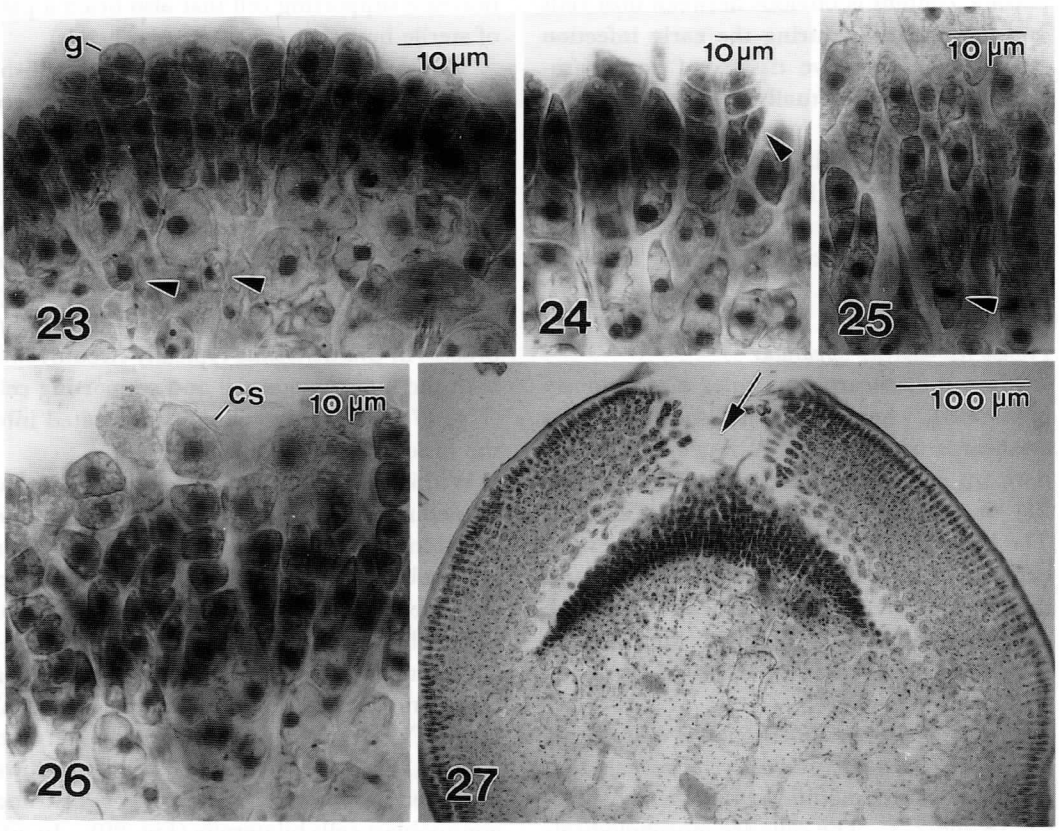
Functional carpogonial branches were not present in the available research material. Unfertilized carpogonial branches are typically two-celled (Fig. 16), consisting of a distal conical carpogonium with a straight trichogyne extending towards the thallus surface, and a hypogynous cell. Such carpogonial branches are borne on a multinucleate supporting cell that also bears a pair of sterile branches (Fig. 16 arrowheads).

The earliest stages leading to the establishment of a postfertilization fusion cell were also absent in our material; however, a supporting cell subtending a distinct hypogynous cell and fusion cell (Figs. 17 and 18) is a clear indication that fusion cell initiation follows a typical Gracilariacean pattern, in which the sterile cells fuse directly onto the persistent carpogonium. It is evident that the fusion process in *Gracilariophila* typically circumvents both the hypogynous cell and supporting cell (Fig. 17), as neither cell is incorporated into the fusion cell.

Within the cystocarpic cavity, the initial branching pattern of the gonimoblast can be reconstructed from Figure 20. After gonimoblast initials are cut off from the fusion cell, each continues to divide to form files of gonimoblast cells. Division proceeds by concavo-convex septa, followed by oblique or transverse division of the residual subapical cell. The result is a branching pattern in which a basal gonimoblast cell bears two rows of predominantly transversely dividing gonimoblast cells bilaterally (Fig. 20). In addition, intercalary suprabasal gonimoblast cells have the potential to cut off laterals (Fig. 24) that initiate supplementary chains of gonimoblast cells.

In every instance, the lowermost gonimoblast cells closest to the cystocarp floor cut off conjunctor cells from their lower surface (Figs. 20–23) which fuse (Fig. 21, arrow) onto multinucleate floor cells, leaving behind secondary pit-connections. A transversely positioned metaphase plate in a lower

Fig. 16–22. *Gracilariophila oryzoides* from California. Fig. 16. Carpogonial branch apparatus consisting of supporting cell bearing non-functional carpogonial branch and a pair of sterile branches (arrowheads). Fig. 17. Close up of Fig. 18 showing fusion cell bearing gonimoblast, hypogynous cell and supporting cell. Arrowhead points to metaphase stage in basal gonimoblast cell. Fig. 18. Cystocarp with fusion cell (arrow) bearing gonimoblasts. Distinction between floor of cystocarp and medulla has become blurred. Fig. 19. Three cystocarps beneath one pericarp trigger expansion of outer cortex of host (arrowhead), resulting in sharp demarcation between its cortical and medullary region. Fig. 20. Obliquely longitudinal division of apical and subapical gonimoblast cell, and formation of conjunctor cells from lower surface of lowermost gonimoblast (arrowheads). Fig. 21. Initiation of conjunctor cell (arrowhead) and fusion of conjunctor cell (arrow) with a multinucleate vegetative cell. Fig. 22. Metaphase plate (arrowhead) in lower gonimoblast cell will initiate conjunctor cell upon division.
Abbreviations: cp = carpogonium, cs = carposporangium, fu = fusion cell, g = gonimoblast cell, hy = hypogynous cell, su = supporting cell, t = trichogyne.

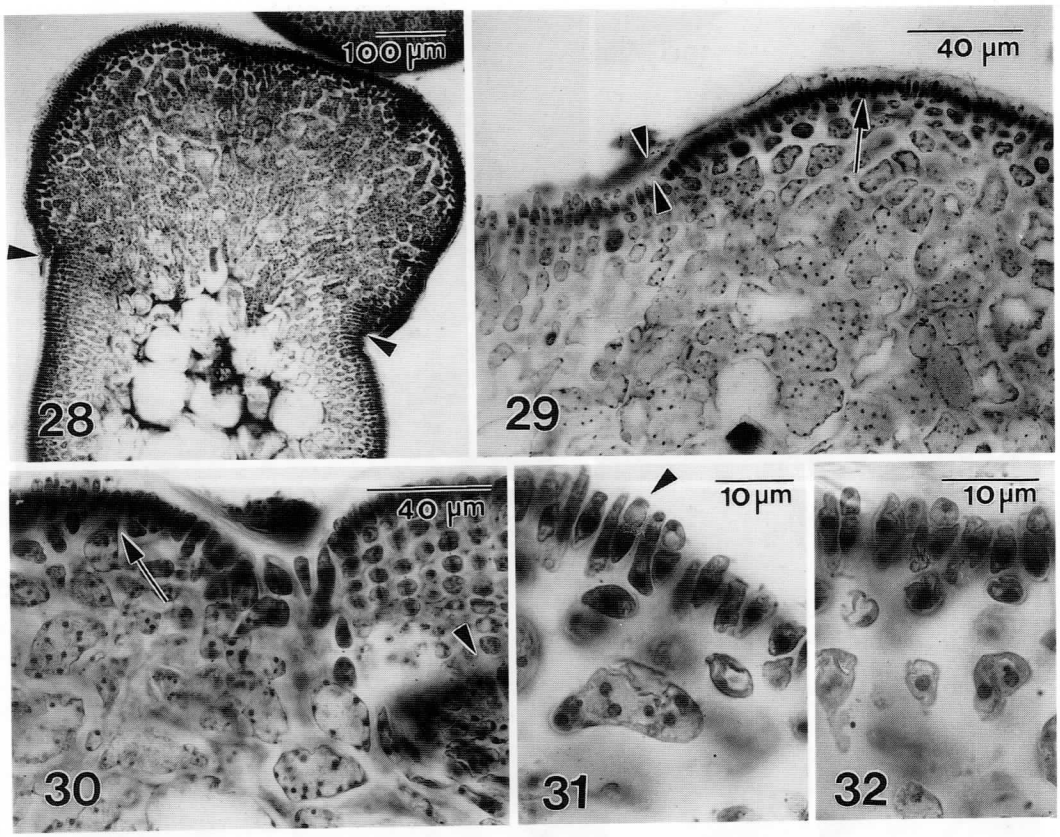


Figs. 23–27. *Gracilariophila oryzoides* from California. Fig. 23. Abundant formation of secondary pit-connections (arrowheads) cut off from lower gonimoblast cells. Fig. 24. Suprabasal gonimoblast cell that has cut off small lateral derivative (arrowhead) by a concavo-convex septum. Fig. 25. Metaphase plate (arrowhead) in lower gonimoblast cell will initiate conjunctor cell upon division. Progressive maturation of gonimoblast into short chains of elongate carposporangial initials. Fig. 26. Basipetal transformation of gonimoblast cells into chains of spherical carposporangia. Fig. 27. Mature cystocarp with well developed central ostiole (arrow), and chains of carposporangia.
For abbreviations see the legend of Figs. 16–22.

gonimoblast cell (Figs. 22 and 25) indicates that gonimoblast cell division and conjunctor cell formation are independent processes. Lower gonimoblast cells become progressively vacuolate, while the distal ones stain darkly (Figs. 23 and 24) and are progressively transformed into elongate carposporangial initials (Fig. 25) that become spherical carposporangia (Fig. 26) upon release through the ostiole (Fig. 27). The pericarp is formed entirely of host tissue surrounded by an outer cuticle that is continuous with that of the vegetative axis (Fig. 19). At maturity, the pericarp consists of about 9–12 layers of small isodiametric cells. Terminal pericarp cells are typically elongate and pointed (Figs. 19 and 27). Numerous carposporophytes beneath one pericarp trigger expansion of the outer cortex of the host, and result in sharp demarcation between its cortical and medullary regions (Fig. 19).

Male reproductive apparatus

Male pustules (Fig. 28) are hemispherical and smooth. The entire outer cortex becomes transformed into a zone of spermatangial parent cells (Figs. 29 and 30) that are barely distinguishable from surface cells of the host. Each pair of spermatangial parent cells (Figs. 31 and 32) is the product of



Figs. 28–32. *Gracilaria oryzoides* from California. Fig. 28. Confluence of spermatangial pustule with host cortex (arrowheads). Fig. 29. Same as in Fig. 28. Fig. 30. Spermatangial pustule with superficial spermatangial parent cells (arrow), and aborting cystocarp of host (arrowhead). Fig. 31. Superficial spermatangial parent cells with transversely divided spermatangia (arrowhead). Fig. 32. Same as in Fig. 31.

an oblique longitudinal division by a concavo-convex septum in a uninucleate outer cortical cell. Both spermatangial parent cells are basally pit-connected, remain uninucleate and each cuts off a single colorless, uninucleate spermatangium distally by a single transverse division (Figs. 31 and 32).

Tetrasporangia

Tetrasporangial pustules are typically crescent-shaped and warty (Figs. 1, 33 and 34). Each tetrasporangial initial (Fig. 35, arrowhead) is transformed from the terminal product of a longitudinal concavo-convex division of an outer cortical cell (Fig. 35, arrowhead). Usually, the resulting subapical bearing cell also divides by a longitudinal concavo-convex septum (Fig. 36), with the apical derivative potentially becoming a new sporangium after release of tetraspores from the first tetrasporangium. Tetrasporangial initials (Fig. 35) typically are larger and stain darker than surrounding cortical cells. The tetrasporocytes typically undergo two successive divisions, giving rise to four cruciately arranged tetraspores of approximately equal size (Fig. 37), although these are frequently divided in an irregular fashion (Fig. 37).

Discussion

Gracilariophila clearly belongs to the Gracilariaceae based on features of early reproductive development. Family characters include a supporting cell bearing a two-celled carpogonial branch flanked by a pair of

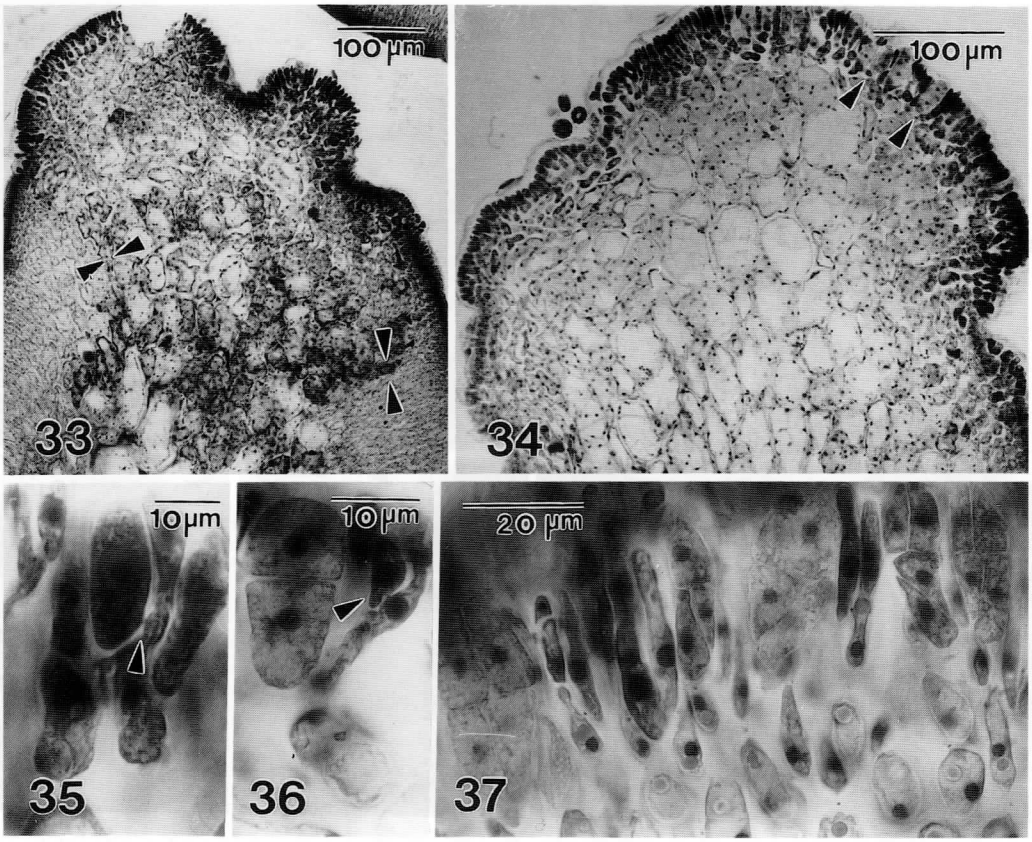


Fig. 33–36. *Gracilariophila oryzoides* from British Columbia and Fig. 37 from California. Fig. 33. Tetrasporangial pustule consisting of mixture of host cells and parasite cells. Sharp demarcation between inner parasite cells and host tissue (arrowheads). Fig. 34. Tetrasporangia (arrowheads) embedded between cortical filaments. Fig. 35. Tetrasporangial initial subtended (arrow) by its bearing cell. Fig. 36. Potential tetrasporangial initials (arrowhead) and bisporangium (*on left*). Former subapical cell has undergone an oblique division potentially resulting in tetrasporangial initial (arrowhead). Fig. 37. Regularly and irregularly cruciately divided tetrasporangia.

sterile branches, direct fusion of cells of sterile branches onto the persistent carpogonium, and formation of a generative multinucleate fusion cell that cuts off gonimoblast initials (FREDERICQ and HOMMERSAND 1988a).

Recently, ZUCCARELLO and GOFF (1988) corraborated by cross inoculation experiments the observations of DAWSON (1949) that *Gracilariophila* is an obligate parasite of its closely related host *Gracilariopsis lemaneiformis* (as *Gracilaria lemaneiformis*). The present study reinforces this idea of adelphoparasitism.

The cystocarps of most red algal parasites typically consist of multiple lobes [e.g. *Gardnerella* (GOFF and HOMMERSAND 1982), *Tikvahiella* (KRAFT and GABRIELSON 1983)] because each individual carposporophyte is surrounded by a separate pericarp. In contrast, the carposporophyte of *Gracilariophila* is hemispherical and surrounded by a single, continuous pericarp.

In transverse section the cystocarpic pustule in *Gracilariophila* is scarcely distinguishable from the cystocarp of its host, *Gracilariopsis*. Both lack the tubular nutritive cells characteristic of *Gracilaria* that fuse with cells of the pericarp. In both, gonimoblast filaments are organized into comparatively straight chains, the initial shape of lowermost gonimoblast cells is retained, and

gonimoblast conjunctor cells fuse with cells in the floor of the cystocarp.

The fundamental difference between host and parasite genera is seen in features of the floor of the cystocarp. In *Gracilariopsis*, a special nutritive tissue, the inner pericarp, is generated from the inner portion of cortical filaments that also produce the outer pericarp. Cells of the inner pericarp develop enlarged nuclei, are densely filled with cytoplasm, and appear to function as a 'sink' for the accumulation of nutriment that can support the growth of the carposporophyte during the course of gonimoblast development and the differentiation of the carposporangia (FREDERICQ and HOMMERSAND 1989b). In contrast, there is not a sharp demarcation between gonimoblast tissues and the tissues of the floor of the cystocarp in *Gracilariophila*. Indeed, inner gonimoblast cells are cytologically and morphologically similar to host medullary cells. This continuum between reproductive and vegetative tissues is, so far, unique to *Gracilariophila* among red algal parasites. This special feature can, perhaps, best be understood as a refinement for supplying nutriment to the developing carposporophyte. Being a parasite, *Gracilariophila* presumably has a continuous, ambient supply of nutriment at its disposal obtained directly from the host, most cells of which by this time contain parasite nuclei owing to the abundance of secondary pit-connections. The formation of a secondarily transformed nutritive tissue that functions as a 'sink' (HOMMERSAND and FREDERICQ 1989) would be a superfluous nutritive strategy, since food reserves have already been commandeered through the host/parasite interaction.

WILSON (1910) illustrated spermatangia borne in chains flanked by elongated sterile filaments. This pattern was never observed in our material. Instead, the present study documents that the spermatangial parent cells are produced from surface cortical cells, forming a superficial continuous layer, and that they cut off spermatangia by transverse division as in *Gracilariopsis* (FREDERICQ and HOMMERSAND 1989b).

WEBER VAN BOSSE (1928) and YAMAMOTO (1986) both questioned whether the penetration of the parasite comes about by means of rhizoids or by pit-connections. In agreement with ZUCCARELLO and GOFF (1988), we found that connection between a parasite cell and a vegetative host cell is established by means of secondary pit-connections in *G. oryzoides*. A multinucleate rhizoidal cell was never seen to fuse directly with a host cell. Instead it always cuts off one or more conjunctor cells that fuse with the host cells, leaving behind pit-connections.

As was mentioned earlier, WEBER VAN BOSSE (1928) subdivided *Gracilariophila* based on the absence (Malaysian species) or presence (California species) of rhizoids. In our opinion the compactness of the cortical region (and hence the size of intercellular spaces) may affect the outline of parasite cells (roundish rhizoidal cells vs. elongate rhizoids). We found both shapes in *G. oryzoides*.

The erumpent component of other red algal parasites is known to consist predominantly of unpigmented parasitic tissue interspersed with pigmented host cells, as for example in *Gardnerella* (GOFF and HOMMERSAND 1982) or *Tikvahiella* (GABRIELSON and KRAFT 1983), both adelphoparasites belonging to the Solieriaceae. In *Gracilariophila*, in contrast, the erumpent component is minimal and a well-defined pustule in which parasitic tissue is distinguishable is lacking.

GOFF and COLEMAN (1985) recently discussed the role of secondary pit-connection formation in red algal parasitism as a mechanism for transferring parasite genetic information into the host. Using fluorescence microscopy, ZUCCARELLO and GOFF (1988) noted that the only independent stages of *Gracilariophila* are the spore, the penetrating infection peg which cuts off 1–2 additional cells that transfer nuclei directly into adjacent host cell, establishing a heterokaryotic host cell, and the limited filamentous growth that occurs at the infection site. In their view,

once initial nuclear transfer has taken place by means of secondary pit-connections, the parasite cell then spreads throughout the host tissues as an intracellular parasitic nuclear genome. An alternative interpretation may be that, in addition to establishing heterokaryotic cells, rhizoidal cells may preserve their parasitic individuality until they have completely ceased to undergo cell division. In each instance that we observed, the establishment of a heterokaryotic cell is directed unilaterally, with rhizoidal conjunctor cells fusing with host cells and not vice versa. The main portion of the proliferating rhizoidal system does not appear to harbor vegetative nuclei. Only at the very last stages of infection, do parasite and host tissues eventually become cytologically and morphologically indistinguishable from one another.

The fact that secondary pit-connections do not seem to be structurally modified suggests that few incompatibility barriers exist between host and parasite cells, as would be expected of an adelphoparasite. The evolutionary success of this unusual parasite clearly lies in the abundance and flexible formation of secondary pit-connections at each stage of development. Pit-connections are initially formed when a rhizoidal cell links up with host vegetative cells, when the parasite ramifies and spreads, and when it taps food reserves for the developing carposporophytes.

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Suzanne Fredericq[*1,2] · Max H. Hommersand[*1] · James N. Norris[*2]：

アデルフォ寄生藻 *Gracilariophila oryzoides*（紅藻，オゴノリ科）の形態観察

Gracilariophila oryzoides は生殖器官の初期発達過程からオゴノリ科に属し，*Gracilariopsis lemaneiformis* の新しい時代に現われたアデルフォ寄生藻（宿主と極めて近縁な寄生種）と考えられる。寄生種の生殖器官が宿主のそれと酷似する点は，嚢果には果皮細胞と融合する管状の栄養細胞を欠き，造胞糸は比較的直線的に連なって形成され，造胞糸の結合細胞は嚢果底の細胞と融合しているなどである。嚢果に分化した栄養組織を欠くことを，寄生という生活様式と関連づけて考察した。精子嚢は表層細胞から作られた精子母細胞の横分裂によって切り離される。胞子の侵入，寄生種の細胞と宿主の栄養細胞との結合，それに続くイボ状組織への成長についても記載した。

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