KYLIN (1956): FLORIDEOPHYCIDEAE: 6 orders

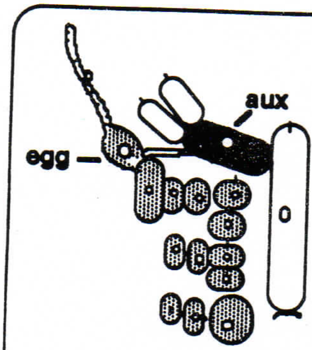
- type of life history
- mode of sexual reproduction

morphological criteria: *fruiting body (cystocarp)* develops from*:*

1) the fertilized egg *(carpogonium)*
2) *auxiliary cells* contacted

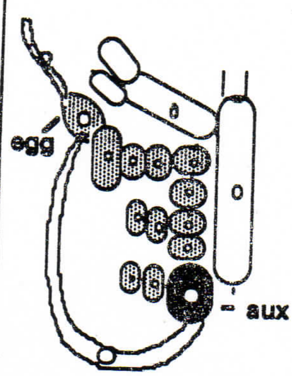
 a) directly by fertilized carpogonium: **procarpial condition*
 b) indirectly by connecting filaments: **non-procarpial condition*
 connecting cells

-Kylin 's 1932 separation of GIGARTINALES & CRYPTONEMIALES:
based on *origin* of *auxiliary cell*



in ordinary vegetative filament

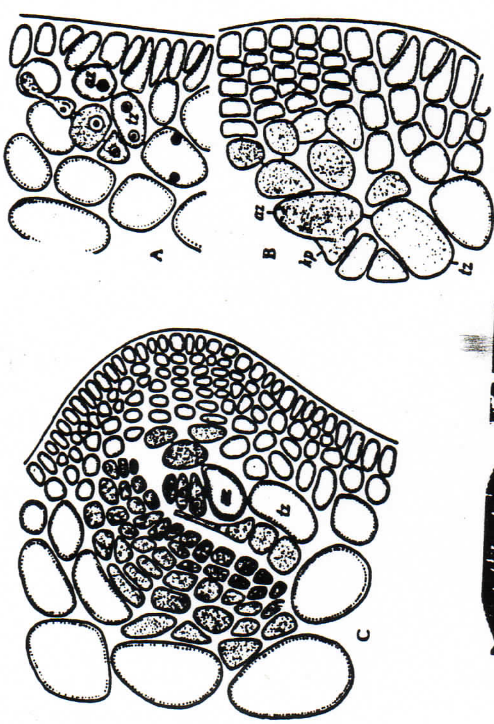
GIGARTINALES



in accessory filament

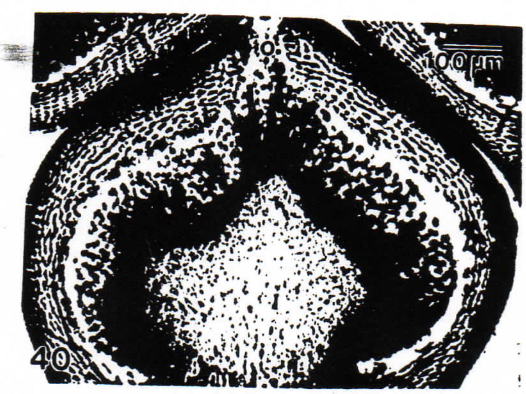
CRYPTONEMIALES

-Kraft and Robins (1985): the 2 orders into Gigartinales *sensu lato*



FRUITING BODY = CYSTOCARP

= morphological manifestation of nutrient-driven interaction between carposporophyte and gametophytic tissues



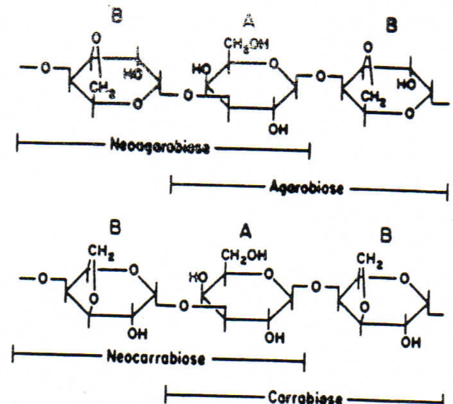


Fig. 10-2. Disaccharide repeating units of agaroses (upper). and carrageenans (lower).

Kylin 's 1956 Florideophyte orders

Nemalionales (=Nemaliales) --> Acrochaetiales
--> Batrachospermales
Gelidiales
Cryptonemiales
Gigartinales --> **Ahnfeltiales**
--> **Gracilariales**
Rhodymeniales --> Palmariales
Ceramiales

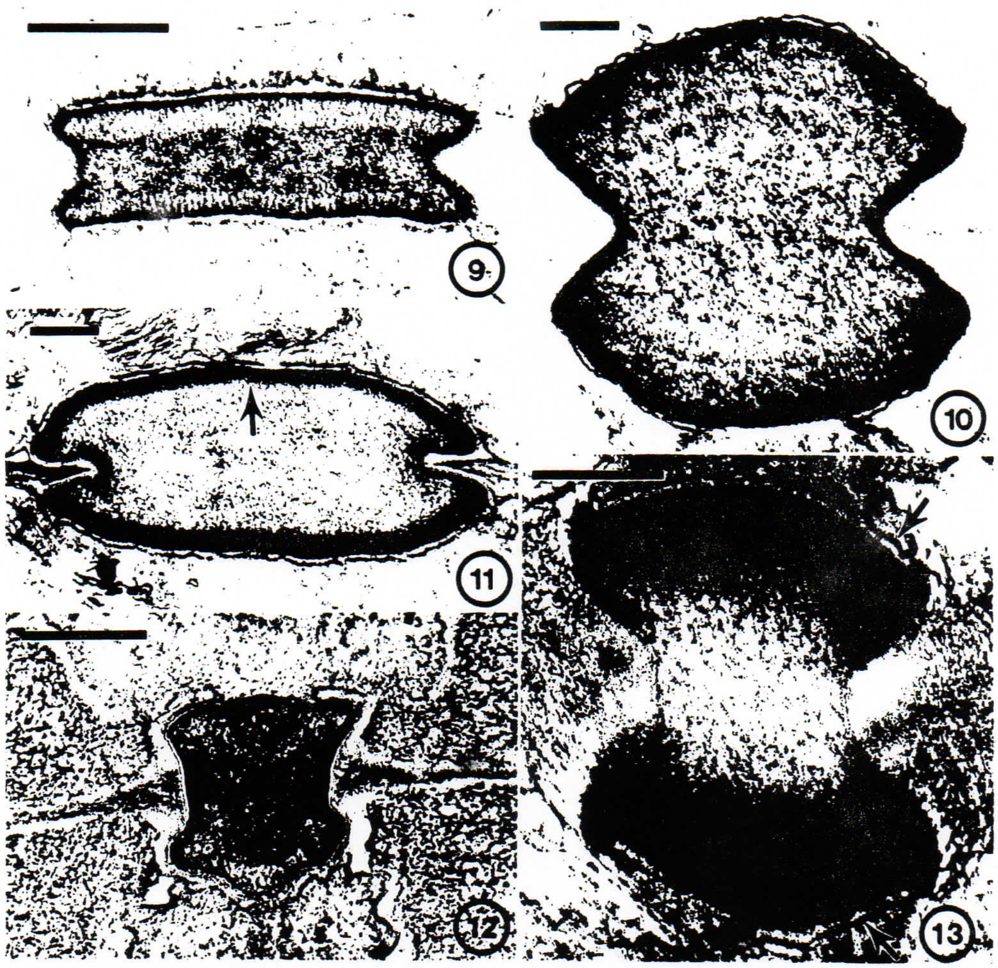
Agarophytes: contain agar

Cell walls of red algae consist of 1) fibrillar part that gives wall its strength & 2) amorphous part in which fibrils are embedded (=phycocolloids).
-most abundant of amorphous cell wall matrix that are commercially exploited are galactans or polymers of galactose which are alternatively β-1,3 and β-1,4 linked **agars** and carrageenans; these mucilages may consitute up to 70% of dry weight of cell wall.
-phycolloid: insoluble in cold water but readily soluble in hot water with a 1% solution being clear & forming solid & elastic gel on cooling: agar composed of 2 polysacharides: agarose & agaropectin
-in traditional processing procedure, plants are bleached in sun with several washings in freshwater; material is boiled for several hours & extract is acidified; extract then frozen & thawed. On thawing water flows from agar, carrying impurities with it & agar that remains is dried & marketed as flakes or cakes
- more modern method extracts agar under pressure in autoclaves: agar is decolorized & deodorized with activated charcoal, filtered under pressure & evaporated under reduced pressure. Further purification by freezing is then undertaken.
- non-toxic: used in food preparation and in pharmaceurtical industry as gelling & thickening agent: canning of meat & fish & for protection against shaking in transit, manufacture of processed cheese, mayonnaise, puddings, creams, jellies
-Japan most important producer of agar, about 3500 tonnes annually
- used on large scale for preparation of gels: **agar-agar**: microbiological investigations: agar gels contain nutrients for bacteria & fungi but gel itself is resistant to degradation by these organisms

Ahnfeltiales: pit plugs lacking cap membrane & cap layers
Gelidiales: pit plugs w. cap membrane w. 1 cap layer, striated plug core
Gracilariales: pit plugs w. cap membrane w. 1 or 0 cap layers, striated plug core

Other higher florideophytes: pit plugs w. cap membrane & 0 cap layers

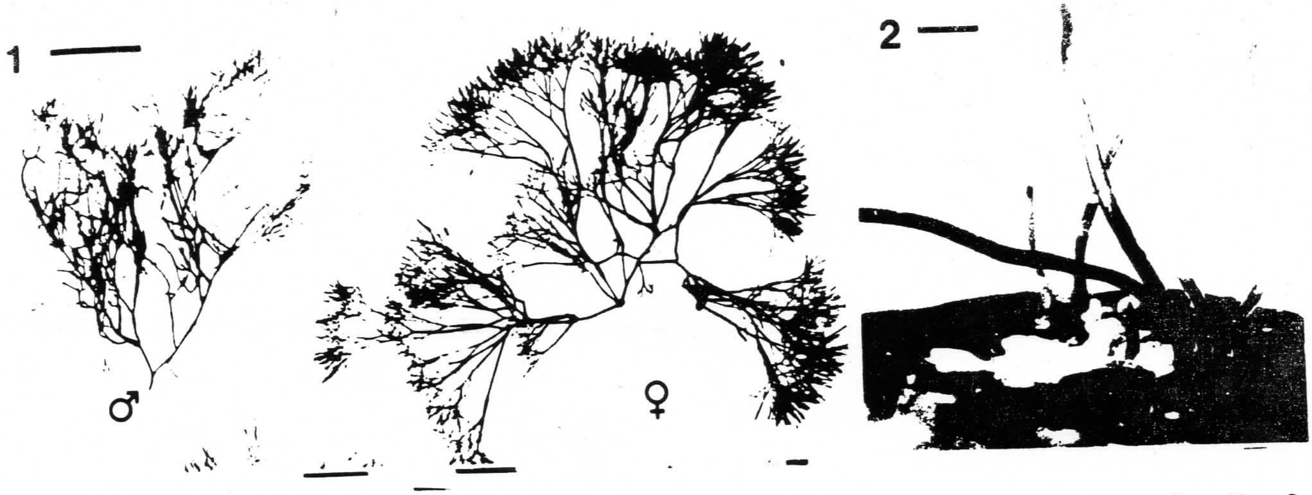
Agarophytes: gonimoblasts arise from fertilized carpogonium; auxiliary cells absent



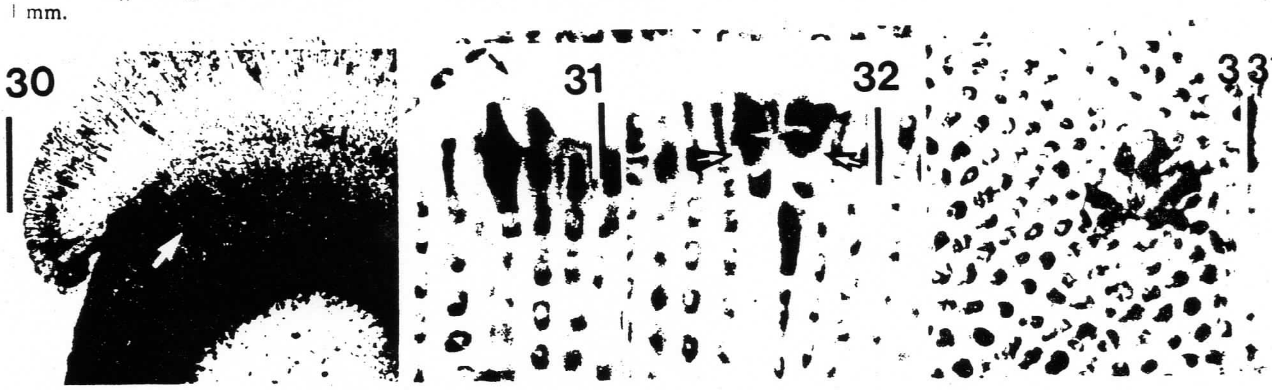
FIGS. 9–13. Pit plugs without a two-layered plug cap. Fig. 9, scale bar = 1 μm. Figs. 10–13, scale bars = 250 nm. FIGS. 9, 10. Comparison of pit plugs of *Gelidiella acerosa* (Gelidiales) and *Gracilaria foliifera* (Gracilariales), respectively. Both have striations of plug core, but striations are less conspicuous in *Gracilaria*. Examples selected to show difficulty of interpreting presence or absence of inner cap layer. FIG. 11. *Dumontia incrassata* (Gigartinales). Dense bands (arrow) at peripheral part of plug core. FIGS. 12, 13. Comparison of pit plugs of *Ahnfeltia plicata* (Ahnfeltiales), *Porphyrodiscus* stage, and *Ahnfeltia gigartinoides* (Gigartinales), respectively. Size differences are representative. Arrows point out cap membranes in *A. gigartinoides*; cap membranes are absent in *A. plicata*.

ORDER AHNFELTIALES

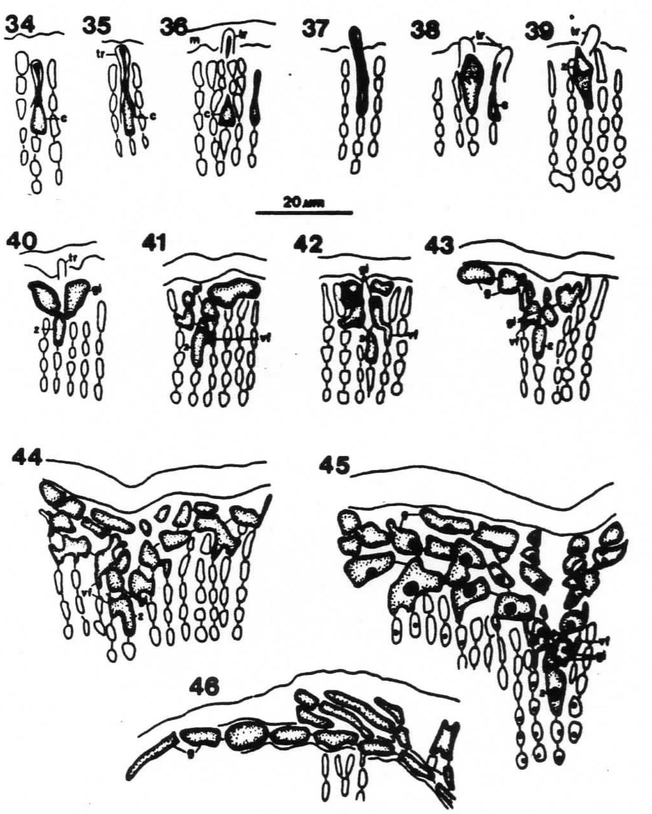
-wiry, intertidal, in temperate regions of Atlantic & E. Pacific
- pit plug lacking both cap layers & cap membranes
-thalli pseudoparenchymatous w.secondary pit connections abundant
-dioecious, triphasic heteromorphic alternation of generations
-spermatangial initials cut off spermatangia by transverse divisions
-only carpogonium, no carpogonial branch, no auxiliary cells
-fertilized carpogonium cuts off gonimoblasts thallus outwards and lower gonimoblast cells fuse back to vegetative cells of female gametophyte; gonimoblast filaments grow into external pustule penetrating thallus surface
-nutrition of carposporophyte is supported by extensive fusions w. gametophytic tissues
-tetrasporophyte is small disc, previously known as *Porphyrodiscus*
-tertasporangia cruciate



FIGS. 1–6. Habit and morphology of *Ahnfeltia plicata*. FIG. 1. Habit of male and female plants from Northwest Cove, Nova Scotia. Both male and female gametophytes vary from irregularly to dichotomously branched. Scale bar = 12 mm. FIG. 2. Groups of young terete axes growing from extensive crustose holdfast; lighter central area is crustose coralline alga overgrowing holdfast. Scale bar = 1 mm.



...nts. Scale bar = 20 µm. FIG. 30. Carposporophyte formed on massive female sorus containing several layers of buried carpogonia (arrow). Scale bar = 100 µm. FIG. 31. Zygote, with trichogyne wall still attached (arrow). Scale bar = 10 µm. FIG. 32. Zygote has cut off gonimoblast initials upward (arrows); these have fused to nearby intercalary cells of female sorus and divided transversely to form apical cells of gonimoblast filaments. Scale bar = 10 µm. FIG. 33. Apical cells of young gonimoblast filaments radiating out over surface of sorus from buried zygote. Scale bar = 10 µm.



FIGS. 34–46. Carpogonia and postfertilization development in *Ahnfeltia plicata*. (Abbreviations used in Figs. 34–46: c: carpogonium; g: gonimoblast cell; gi: gonimoblast initial; m: mucilaginous material; tr: trichogyne; vf: vegetative cell of female sorus; z: zygote = fertilized carpogonium.) FIGS. 34–36. Conical carpogonia with short trichogynes not protruding beyond surface mucilaginous layer. FIG. 37. Possibly abnormal, narrow carpogonium. FIGS. 38, 39. Carpogonia after fertilization (zygotes) with trichogyne walls still visible; in Fig. 38 unfertilized carpogonium also is present. FIGS. 40–46. Young carposporophytes. FIG. 40. Zygote, with trichogyne still attached, has cut off gonimoblast initials obliquely outward to sorus surface. FIG. 41. Zygote has fused with undifferentiated intercalary cell of female sorus and cut off gonimoblast initials, one of which has fused with vegetative cell; gonimoblast initials have formed young gonimoblast filaments. FIG. 42. Gonimoblast initials, but not zygote, have fused with female sorus cells. FIG. 43. Young gonimoblast filaments radiating outward over sorus surface from zygote. FIG. 44. Young carposporophyte, consisting of cone of branched gonimoblast filaments radiating from zygote, occupies depression in sorus. FIG. 45. Young carposporophyte stained with haematoxylin has much enlarged nuclei relative to vegetative cells of female sorus. FIG. 46. Margin of older carposporophyte showing development of gonimoblast cells obliquely upward from periclinal gonimoblast filaments.

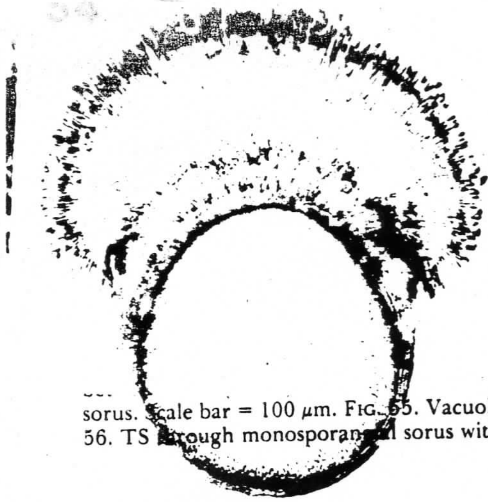
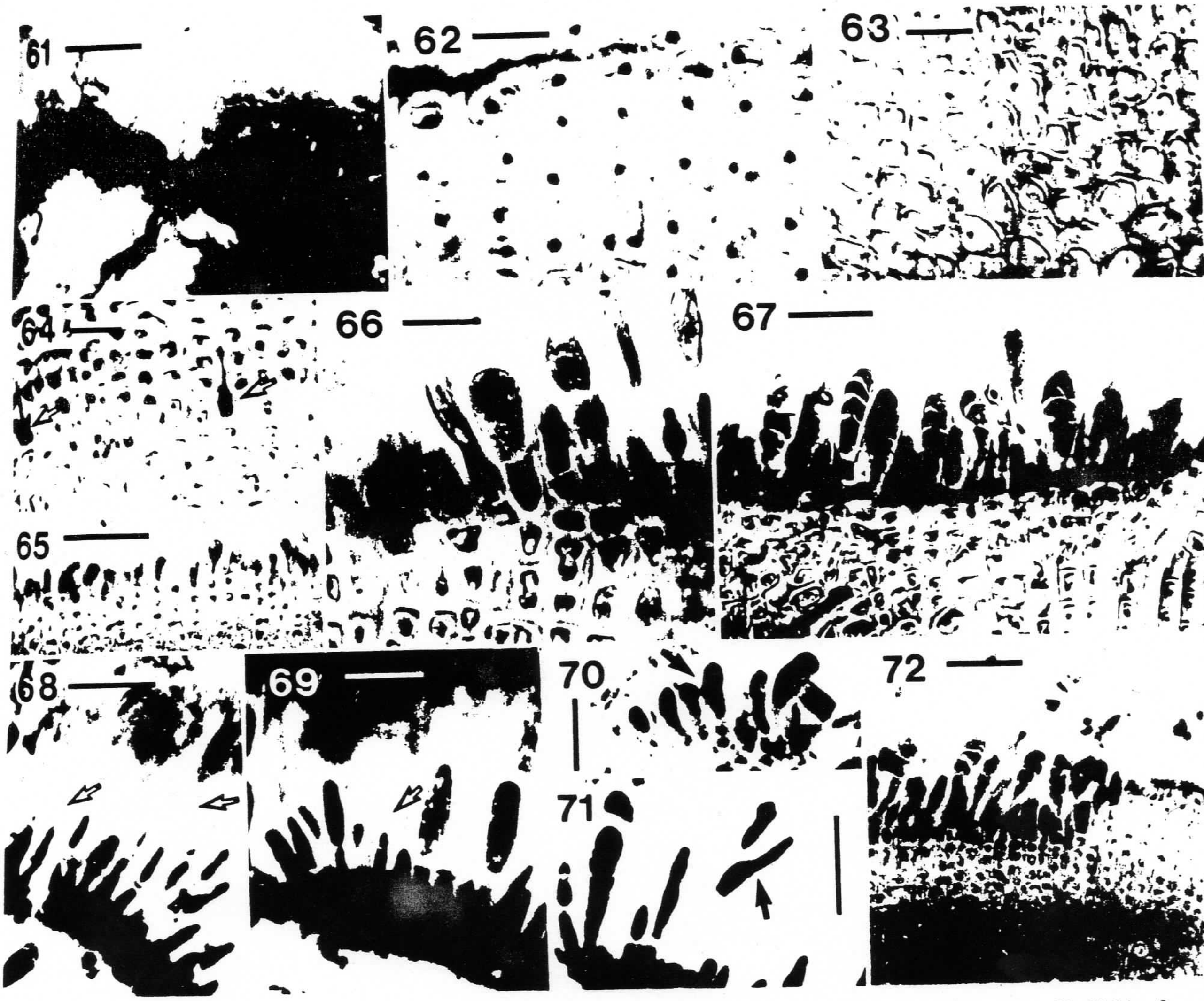


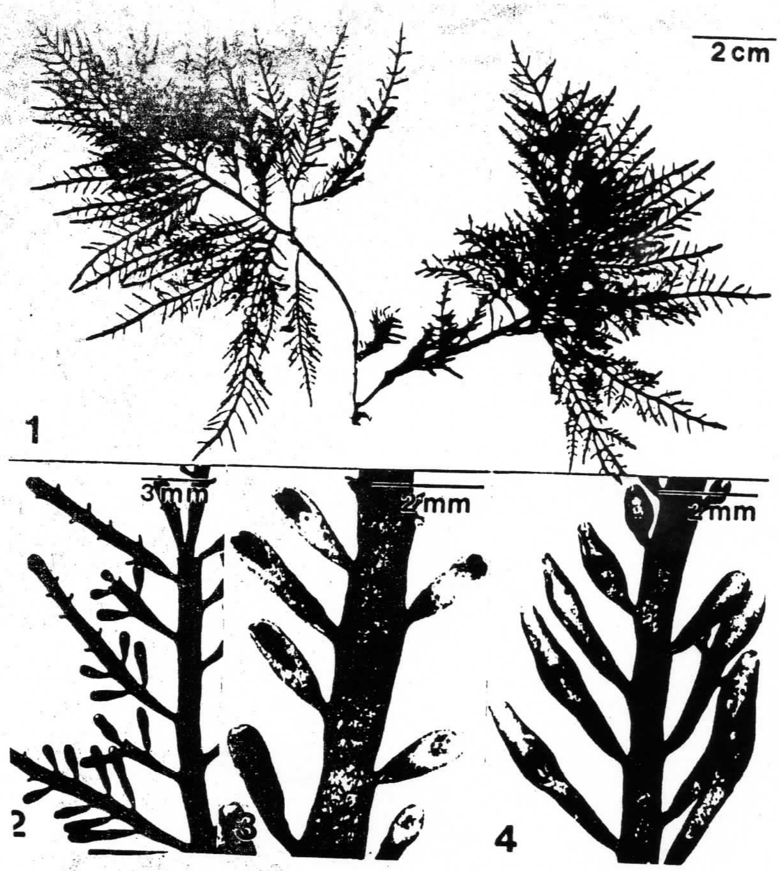
FIG. 54. TS of axis with mature carposporophyte showing carposporophyte borne on female sorus. Scale bar = 100 μm. FIG. 55. Vacuolate gonimoblast filaments terminate in cells bearing carposporangia. Scale bar = 15 μm. FIG. 56. TS through monosporangial sorus with thick mucilaginous covering. Scale bar = 20 μm.

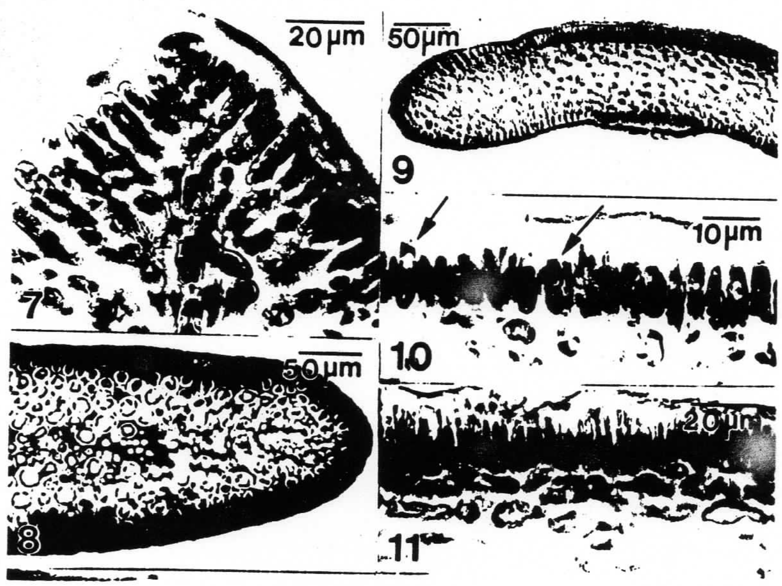


FIGS. 61–72. Vegetative and reproductive morphology of *Porphyrodiscus simulans* phase of *Ahnfeltia plicata*. FIG. 61. Habit of crust with concentric growth rings on quartz pebble. Scale bar = 2 mm. FIG. 62. Vertical section (VS) through upper part of crust stained with haematoxylin showing filaments of uninucleate, thick-walled cells. Scale bar = 10 μm. FIG. 63. VS of lower crust with numerous cell fusions resulting in large, irregularly-shaped cells. Scale bar = 10 μm. FIG. 64. VS of crust with buried hair cells (arrows). Scale bar = 10 μm. FIG. 65. VS of crust surface forming tetrasporangial initials. Scale bar = 40 μm. FIG. 66. Division of clavate tetrasporangial initials yields ovoid tetrasporocytes and smaller subtending cells. Scale bar = 10 μm. FIG. 67. VS of mature sorus with nearly regularly to very irregularly zonate tetrasporangia and dark-staining subtending cells. Scale bar = 20 μm. FIG. 68. Squash of older sorus stained with toluidine blue showing walls of discharged sporangia (arrows) attached apically to subtending cells. Scale bar = 20 μm. FIG. 69. Tetrasporangial subtending cells with old walls attached apically (arrow) enlarge sequentially to form tetrasporocytes. Scale bar = 20 μm. FIG. 70. Pair of fused tetrasporocytes (arrow) resulting from sequential transformation of fused vegetative cells into tetrasporocytes. Scale bar = 10 μm. FIG. 71. Tetrasporocyte (arrow) with another tetrasporocyte attached laterally resulting from the transformation of a pseudodichotomous vegetative filament into tetrasporocytes. Scale bar = 20 μm. FIG. 72. VS of mature tetrasporangial sorus in surface pit formed by erosion of vegetative filaments as they are transformed into sporangia and possibly also from continued apical growth of surrounding vegetative filaments. Scale bar = 40 μm.

ORDER GELIDIALES

-common in intertidal worldwide
-agarophytes: *Gelidium*
-triphasic, isomorphic alternation of generations; sexual plants dioecious
-pit plugs with single cap layer, striations in pit plug core
1-2-3 order cell rows
-following nuclear division, most of spore contents pass into germ tube leaving largely evacuated spore which is then cut off: empty spore pattern
-vegetative growth by transverse division of apical cell producing uniaxial thallus
-each axial cell bears two opposite periaxial cells that produce lateral filaments of 2nd order, normally interconnected by 2° pit connections; filaments of 3rd order arise in opposite pairs from cell rows of 2nd order
- wiryness due to internal thick-walled rhizoids developing from cells of 3rd & higher order cortical filaments & descending towards base
-male fertile areas from irregular colorless patches on surface of fertile branchlets
-surface cortical cells elongate & divide anticlinally to produce spermatangial initials
-female reproductive system originates within apical notch of branchlets (pinnules): consist of single carpogonia & nutritive filaments before fertilization
-nutritive filaments branched, short-celled filaments that develop from basal cells of vegetative filaments of 3rd order in fertile area, or sometimes on higher orders
-functional carpogonia intercalary, occur along sides of central furrow in fertile area
-fertilized carpogonium enlarges & forms processes that cut off gonimoblast initials
-pit conneciions of cortical cells attached to carpogonium enlarge leading to cytoplasmic continuity with fertilized carpogonium
-gonimoblast filaments grow & ramify between files of nutritive filaments producing laterals that fuse w. terminal or intercalary cells of nutritive filaments
-additional gonimoblast cells may fuse forming fusions cells
-cystocarps raised, oval to circular in outline
- either unilocular with one ostiole (*Pterocladia*, *Pterocladiella*), or bilocular w. 2 ostioles (*Gelidium*)
-inner sterile cortical cells elongate during cytocarp enlargement
-tetrasporangia cruciate
-genera are mostly segregated based on how carposporophyte develops in relation to vegetative growth (where are carpogonia formed) & how nutritive cells are incorporated in the establishment of the cystocarp
-*Gelidium, Pterocladia, Pterocladiella, Suhria...*





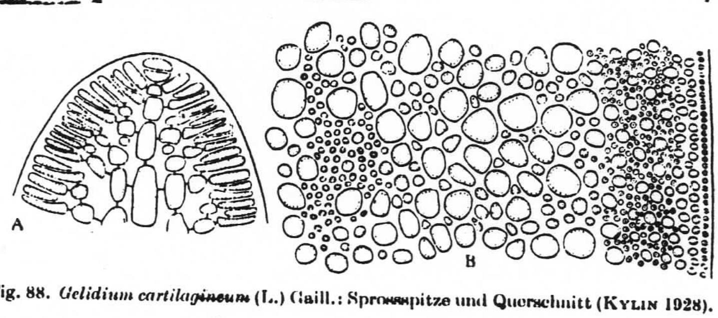


Fig. 88. *Gelidium cartilagineum* (L.) Gaill.: Sprosspitze und Querschnitt (Kylin 1928).

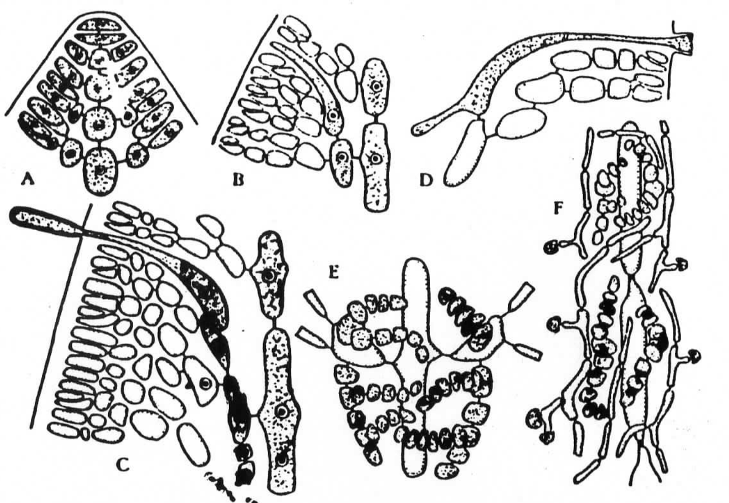
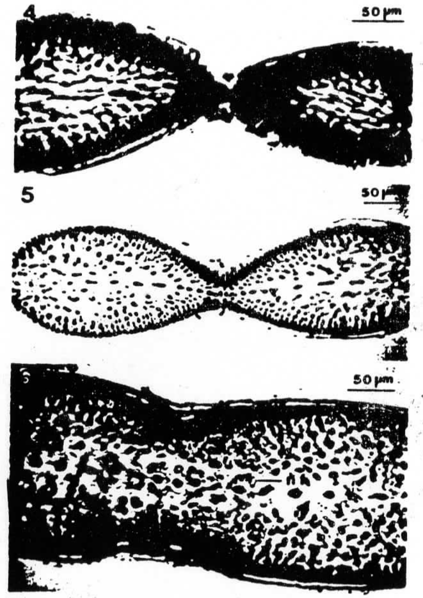
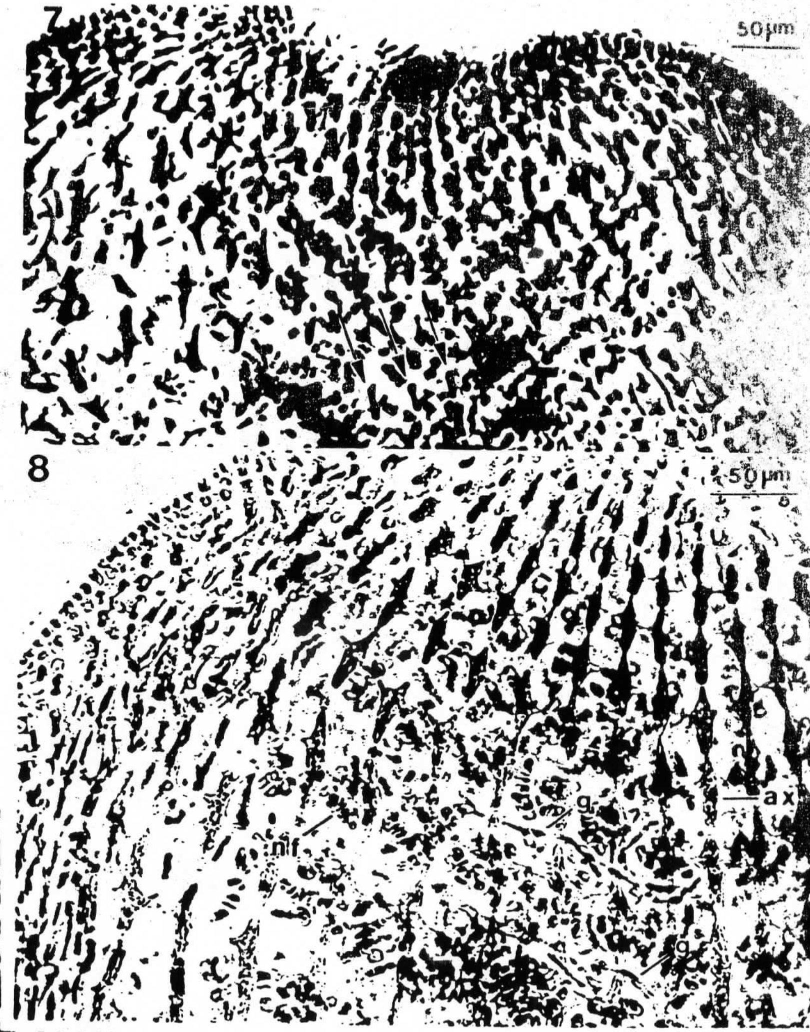


Fig. 90. *Gelidium cartilagineum* (L.) Gaill.: *A* fertile Sprosspitze im Längsschnitt, *B* Anlage eines Karpogons, *C* befruchtungsreifes Karpogon, *D* Karpogon nach der Befruchtung mit einem Gonimoblastfaden, *E* Nährzellen, *F* Gonimoblastfäden mit jungen Karposporen (KYLIN 1928).



Figs 4–6. *Gelidium pteridifolium.*
Fig. 4. Cross-section of young female pinnule at level of apical cell.
Fig. 5. Cross-section of young female pinnule 6–7 segments behind apex.
Fig. 6. Cross-section of female pinnule about 10 segments behind apex with nutritive filaments (nf).



Figs 7, 8. *Gelidium pteridifolium.*
Fig. 7. Oblique periclinal section of tip showing early development of nutritive filaments and carpogonia with trichogynes (arrows).
Fig. 8. Median periclinal section of fertile tip showing central axis (ax) and rows of second-order filaments to left united in columns by secondary pit connections and enveloped by nutritive filaments (nf) with young gonimoblast filaments (g) coursing between.

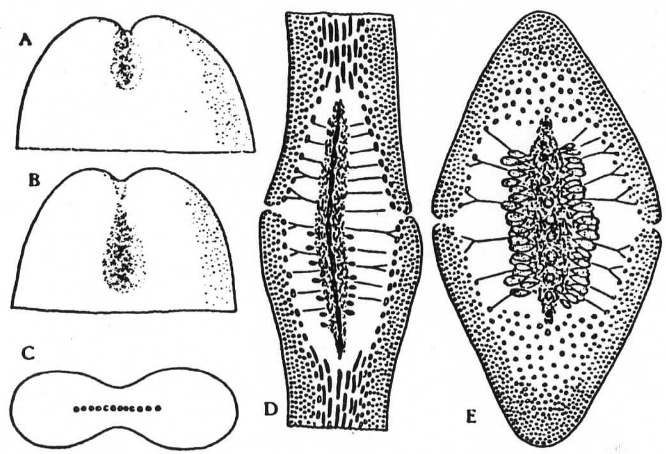
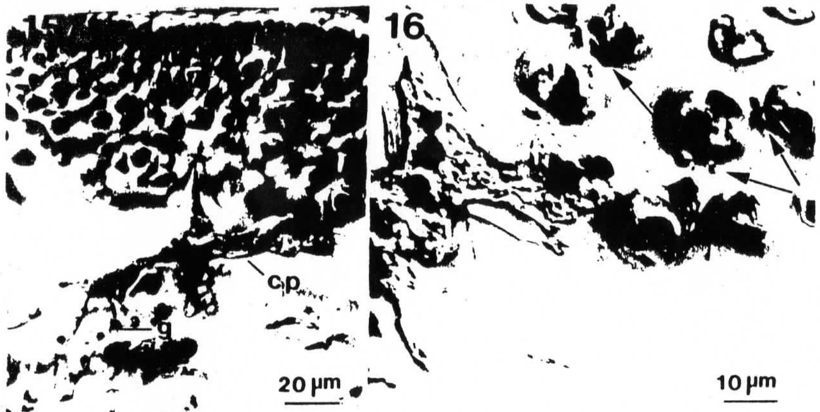
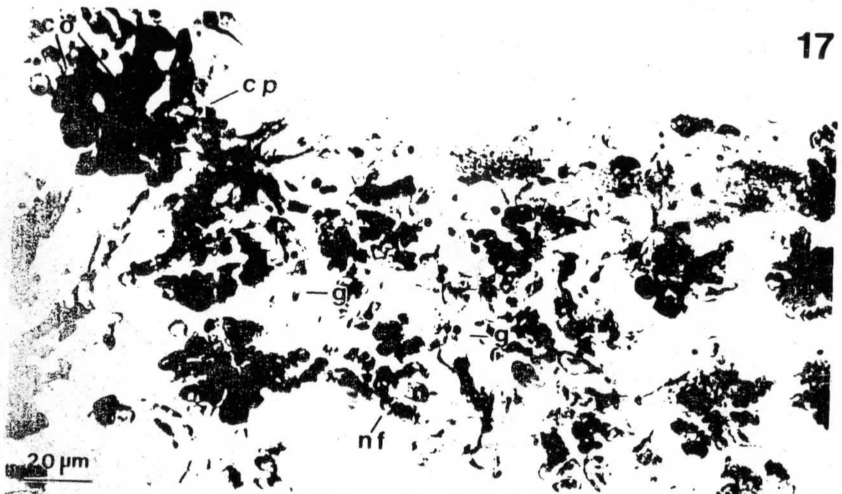
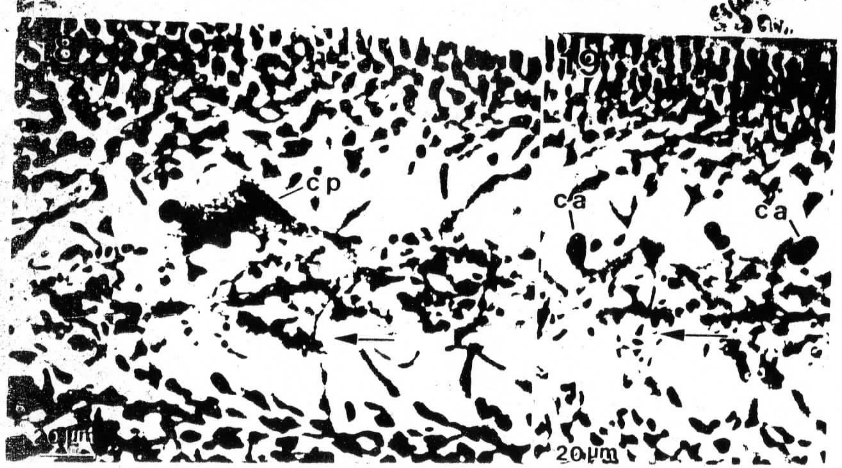


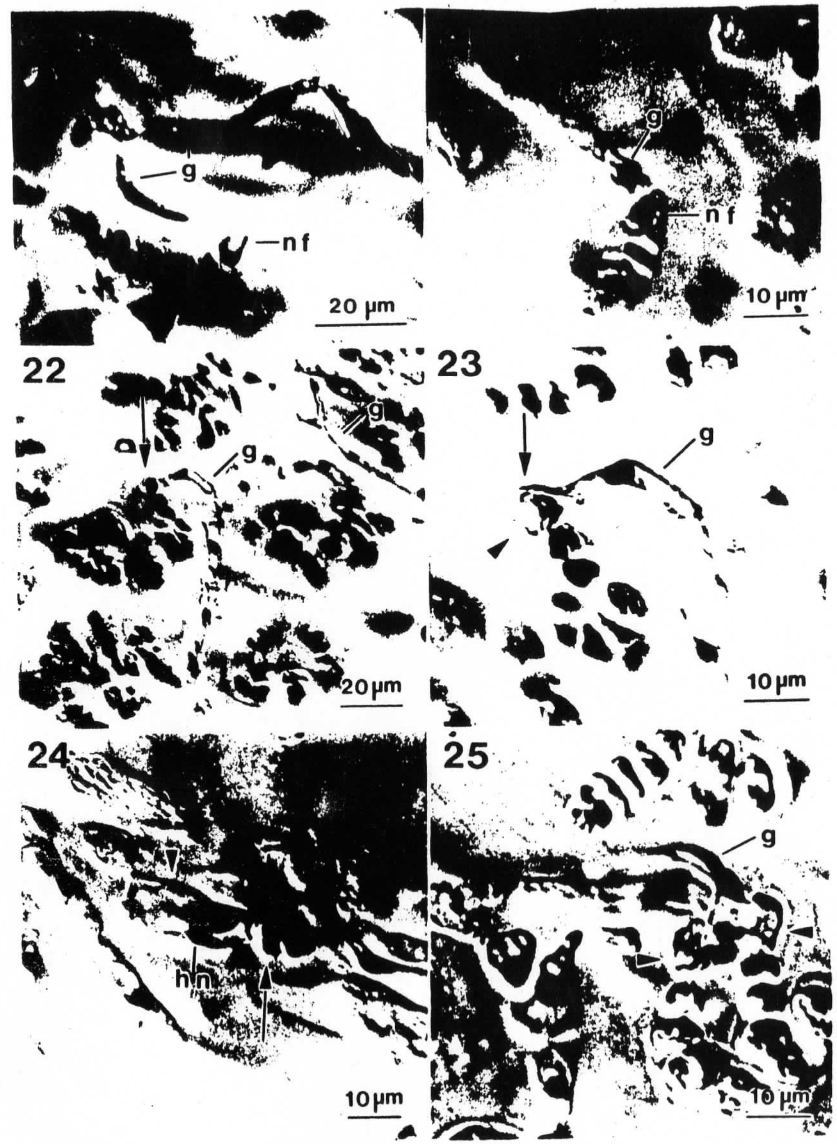
Fig. 89. *Gelidium cartilagineum* (L.) Gaill.: *A-C* Sprosspitzen mit karpogontragenden Gruben, *D* junges Zystokarp im Längsschnitt, *E* altes Zystokarp im Querschnitt (KYLIN 1928).



Figs 13–16. *Gelidium pteridifolium.*
Fig. 13. Attached multinucleate carpogonium (cp) bearing modified cortical filaments (co) and two young gonimoblast filaments (g).
Fig. 14. Distended multinucleate carpogonium (cp) that has probably aborted, with cortical filaments (co) and a few one-celled gonimoblast initials (g).
Fig. 15. Detached multinucleate carpogonium (cp) bearing several inwardly growing gonimoblast filaments (g). (Gonimoblast cells are uninucleate.)
Fig. 16. Enlarged view of multinucleate carpogonium bearing pair of cortical filaments in which innermost cells are binucleate. Fusion has occurred through septal plugs of cortical cells (arrows).

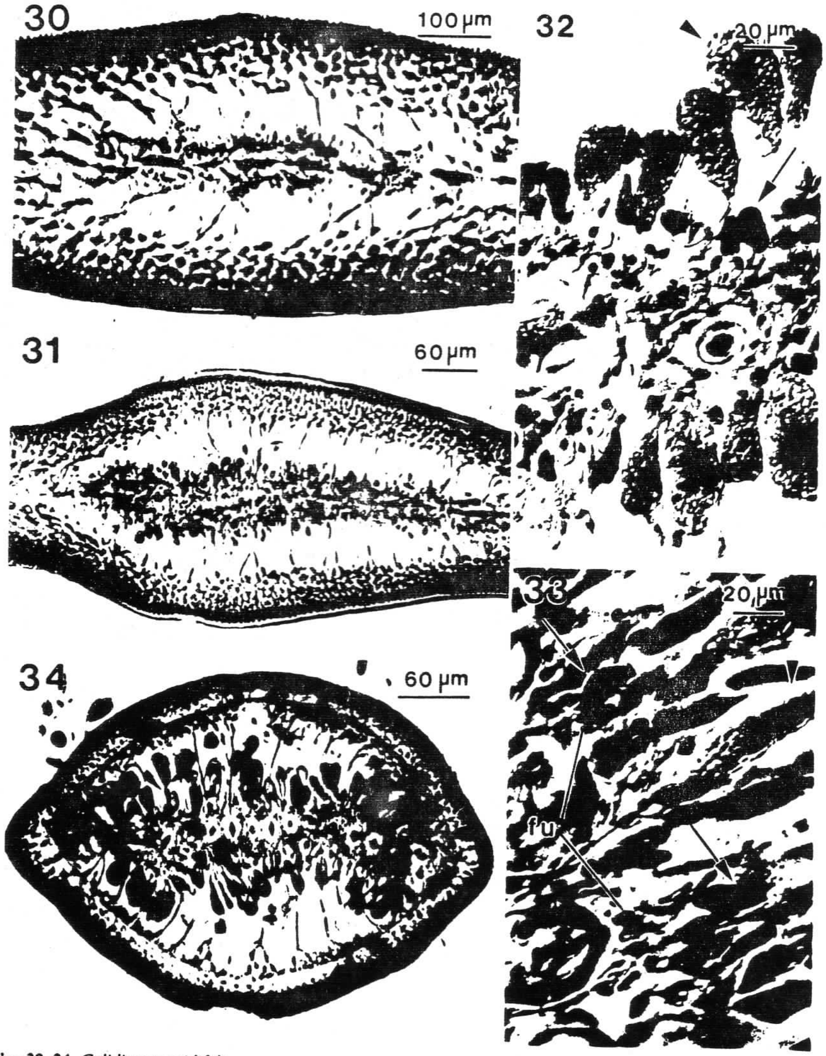






Figs 20–25. *Gelidium pteridifolium.*
Fig. 20. Stage showing branching and directed growth of gonimoblast filament (g) in vicinity of nutritive filament (nf).
Fig. 21. Terminal gonimoblast cell (g) prior to contact with terminal cell of nutritive filament (nf).

Figs 17–19. *Gelidium pteridifolium.*
Fig. 17. Fertile area in which cortex has been stripped away to reveal carpogonium (cp), fused cortical cells (co), and gonimoblast (g) ramifying between rows of nutritive filaments (nf).
Fig. 18. Carpogonium (cp) and gonimoblast filaments at stage of fusion (arrow) with terminal cells of nutritive filaments.
Fig. 19. Gonimoblast filaments bearing young carposporangia (ca). Gonimoblast cell has fused with terminal cell of nutritive filament (arrow).



Figs 30–34. *Gelidium pteridifolium.*

Fig. 30. Longitudinal section of young cystocarp with carposporangial initials and elongated inner cortical filaments.

Fig. 31. As in Fig. 30 at older stage.

Fig. 32. Cross-section of network of gonimoblast and nutritive filaments (now largely vacuolate) with mature primary (arrowhead) and immature secondary (arrow) carposporangia.

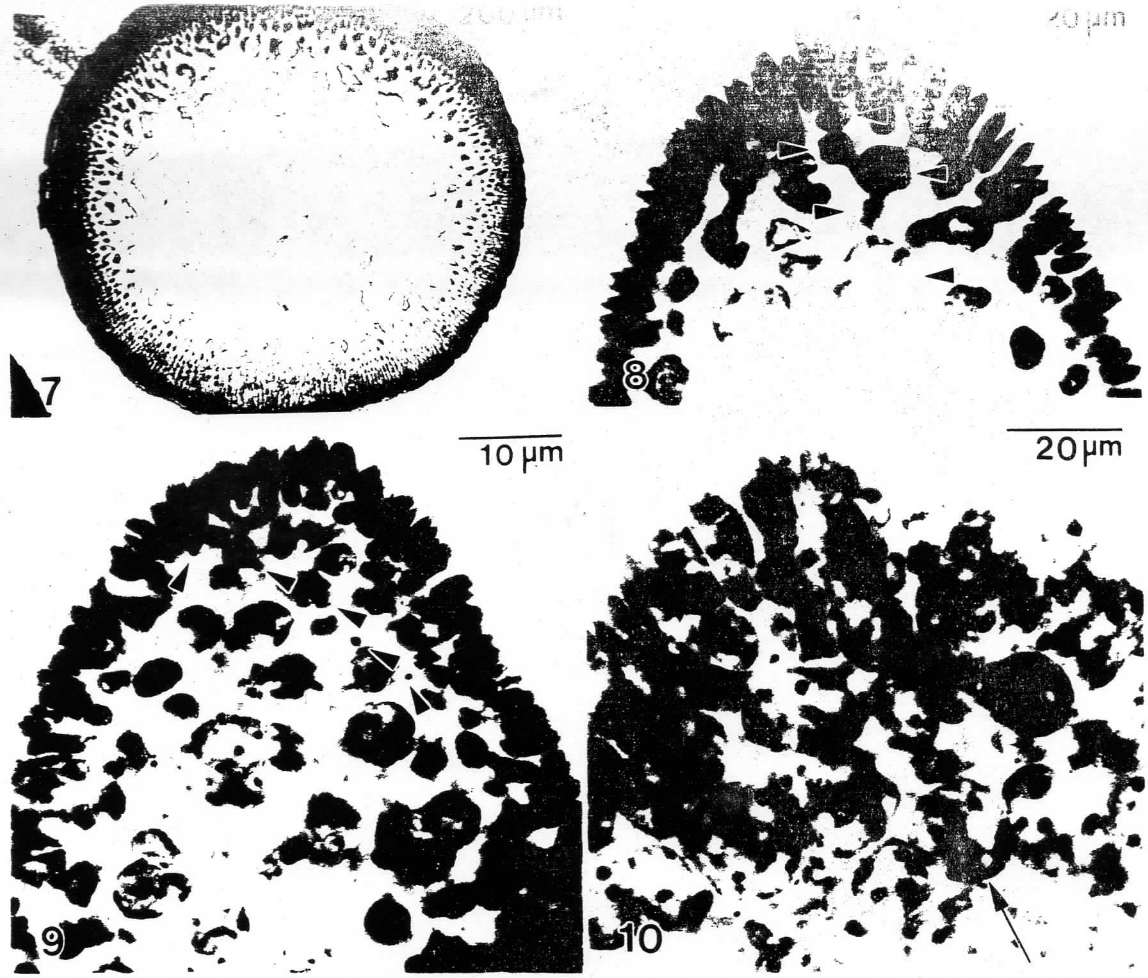
Fig. 33. Close up view of fusion network with mature primary carposporangia (arrowhead) and secondary carposporangia (arrow) from multinucleate fusion cells (fu).

Fig. 34. Median cross-section of cystocarp with mature carposporangia and opposite ostiolar regions.

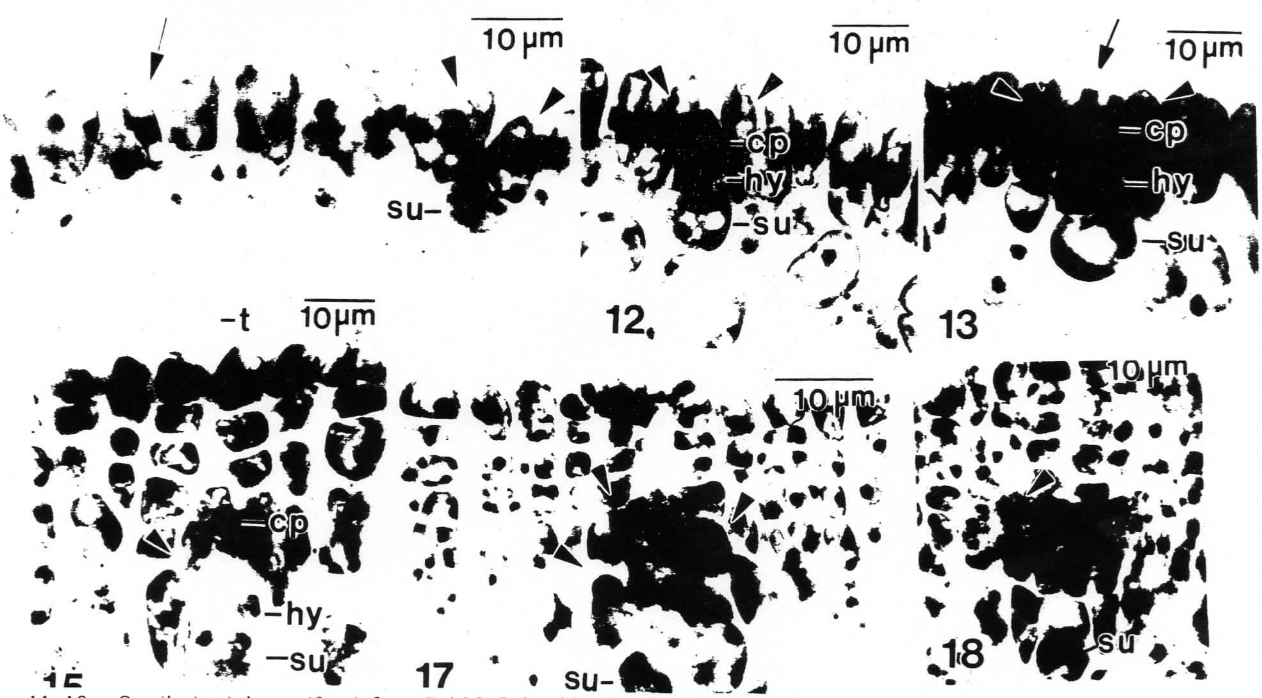
ORDER GRACILARIALES

-thalli of various forms, pseudoparenchymatous, also parasites on other Gracilariaceae
- growth apparently uniaxial w. rapid concealment of central axis
- seconday pit connections numerous between vegetative cells
-pit plugs with membrane w. either 1 or 0 plug cap layer; striations in plug core
-triphasic, isomorphic alternation of generations
-female gametophytes w. outwardly directed 2-celled carpogial branches flanked by sterile branches borne on supporting cell
-diploid nucleus remaining in carpogonium after fertilization
-cells of sterile branches fusing directly onto persistent carpogonium, forming generative fusion cell that cuts off multiple gonimoblast initials laterally & towards surface
-gonimoblast derivatives establish secondary fusions w. cells of gametophytic tissues in pericarp or floor of cystocarp (by conjunctor cells or nutritive tubula cells)
-cells of inner gonimoblast interconnected by secondary pit connections
-outer gonimoboast cells transformed into chains or clusters of carpospornagia
-tetrasporangia cruciate

-genera differentiated by presence, nature or absence of tubular nutritive cells linking gonimoblast & pericarp, organization of spermatangia (superficial, in conceptacles), presence or absence of thick-walled sterile inner gonimoblast tissues, how carposporangia are organized
Gracilaria, *Gracilariopsis*, *Hydropuntia*, *Melanthalia*, *Curdiea*, parasites *Gracilariophila* & *Congracilaria*

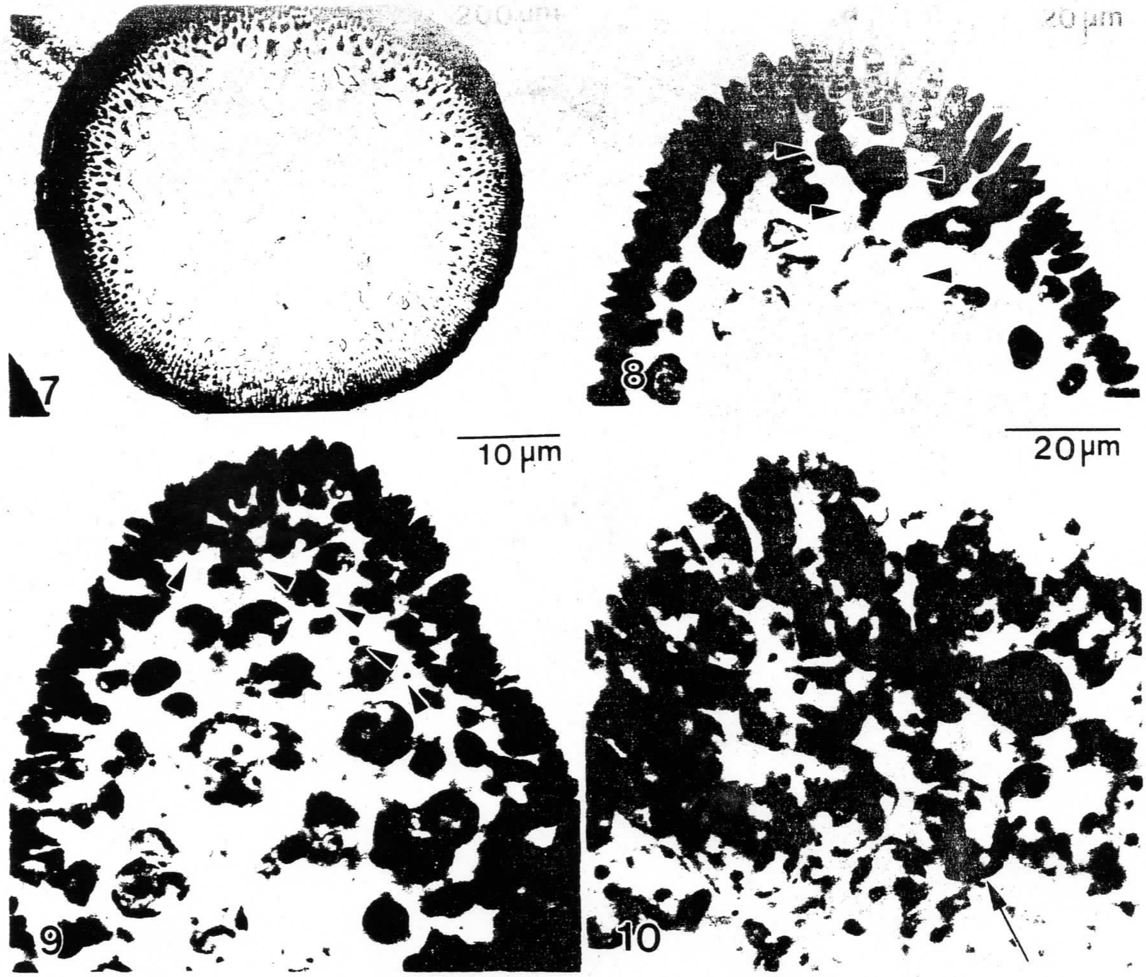


FIGS. 7–10. *Gracilariopsis lemaneiformis.* Fig. 7: British Columbia specimen; Figs. 8–10: California specimen. FIG. 7. Transverse section through main branch showing small-celled palisade arrangement of cortex and vacuolated, large cells of the medulla. FIG. 8. Longitudinal section through branchlet tip showing leading apical cell and six axial cells (arrowheads). FIG. 9. Longitudinal section through branchlet tip showing abundant formation of conjunctor cells (arrowheads) obscuring inherent growth pattern. FIG. 10. Longitudinal section through branchlet showing synchronous mitotic divisions in medullary cell (arrow).



FIGS. 11–19. *Gracilariopsis lemaneiformis* from British Columbia. FIG. 11. Initiation of carpogonial branch apparatus: concavo-convex division in uninucleate outer cortical cell (arrow) is followed by concavo-convex division of subapical cell resulting in supporting cell and initials of sterile branches (arrowheads). FIG. 12. Young carpogonial branch apparatus with sterile branches (arrowheads) prior to trichogyne formation. FIG. 13. Carpogonium with trichogyne initial (arrow) and uniseriate 3-celled sterile branches (arrowheads). FIG.

FIG. 15. First fusion of basal cell of sterile branch into lower end of carpogonium (arrowhead). FIG. 16. Progressive lateral fusion (arrow) of sterile cell with carpogonium. Fusion of conjunctor cells (arrowheads) onto basal cell of sterile branch, and between incipient pericarp cells (curved arrowheads). FIG. 17. Expanding carpogonial fusion cell and individual sterile cells (arrowheads). FIG. 18. Cytoplasmic protrusion (arrowhead) developing from upper part of fusion cell.



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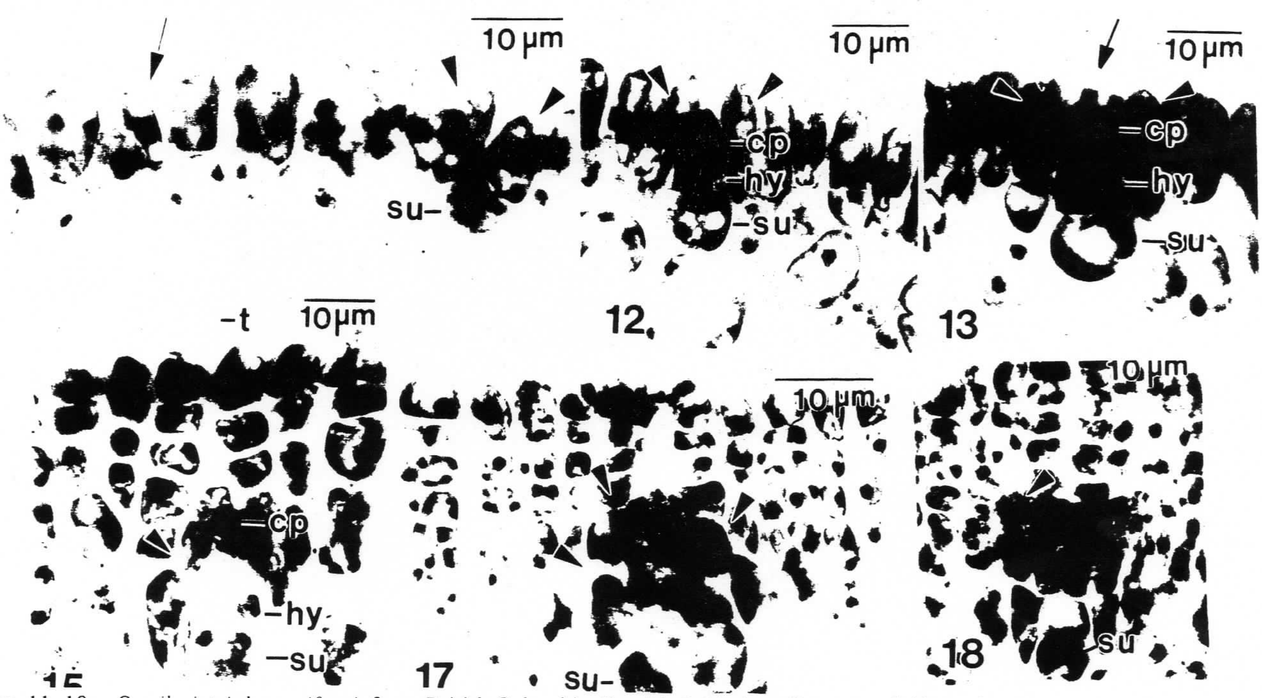

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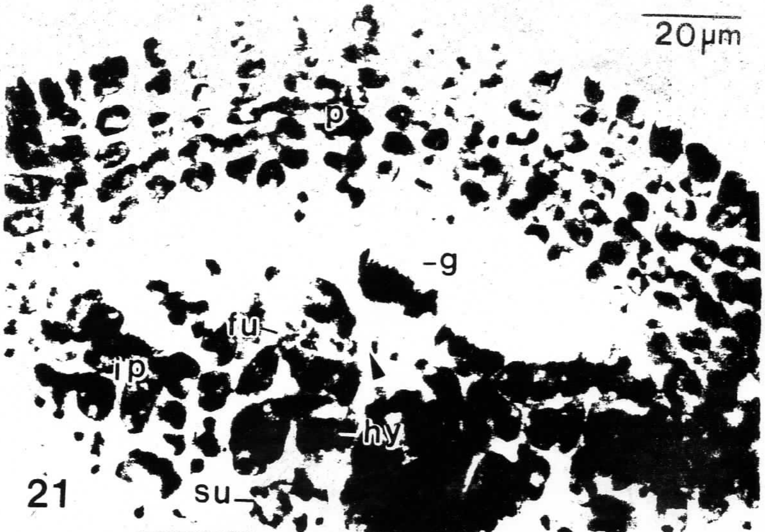
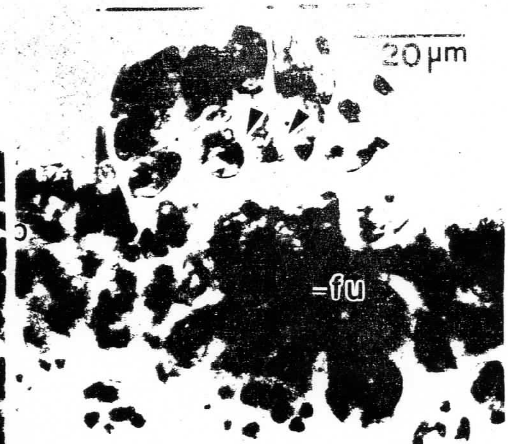
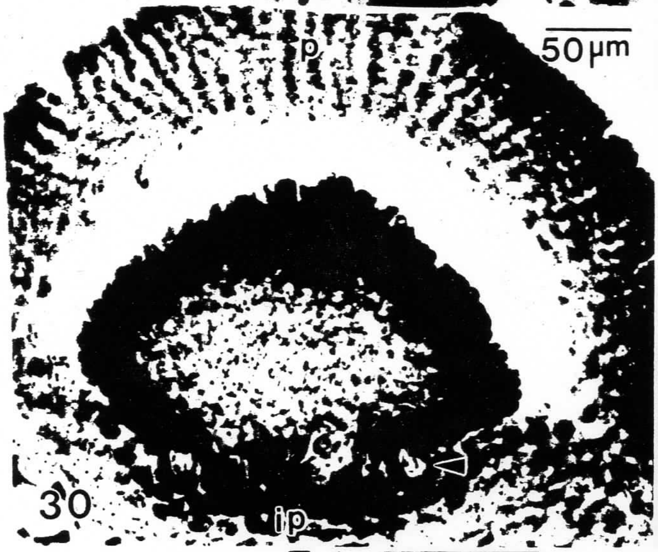
FIG. 15. First fusion of basal cell of sterile branch into lower end of carpogonium (arrowhead). FIG. 16. Progressive lateral fusion (arrow) of sterile cell with carpogonium. Fusion of conjunctor cells (arrowheads) onto basal cell of sterile branch, and between incipient pericarp cells (curved arrowheads). FIG. 17. Expanding carpogonial fusion cell and individual sterile cells (arrowheads). FIG. 18. Cytoplasmic protrusion (arrowhead) developing from upper part of fusion cell.







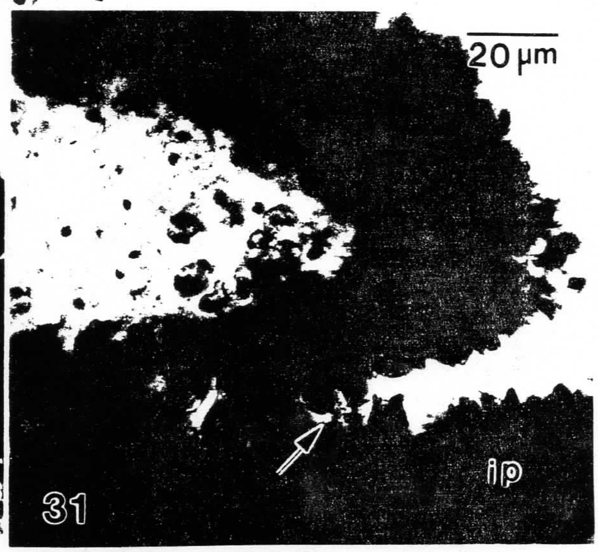
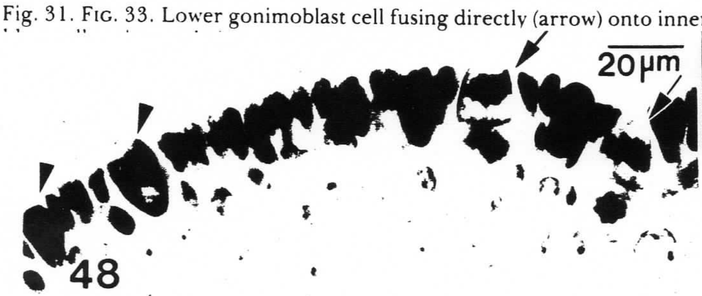
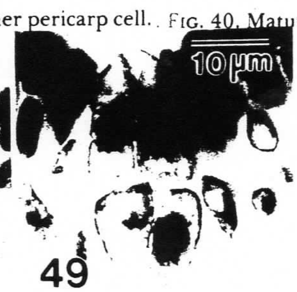


FIG. 21. Young gonimoblast and early development of cystocarp cavity. Gonimoblast cells with pit-connection to fusion cell (arrowhead) and spreading laterally above darkly staining inner pericarp.

FIG. 32. Close up of Fig. 31. FIG. 33. Lower gonimoblast cell fusing directly (arrow) onto inner pericarp cell. . FIG. 40. Mature cystocarp with ostiole.





48. Tetrasporangial initials (arrowheads) and tetrasporangia (arrows) scattered in cortex. FIG. 49. Cruciately divided tetrasporangium.

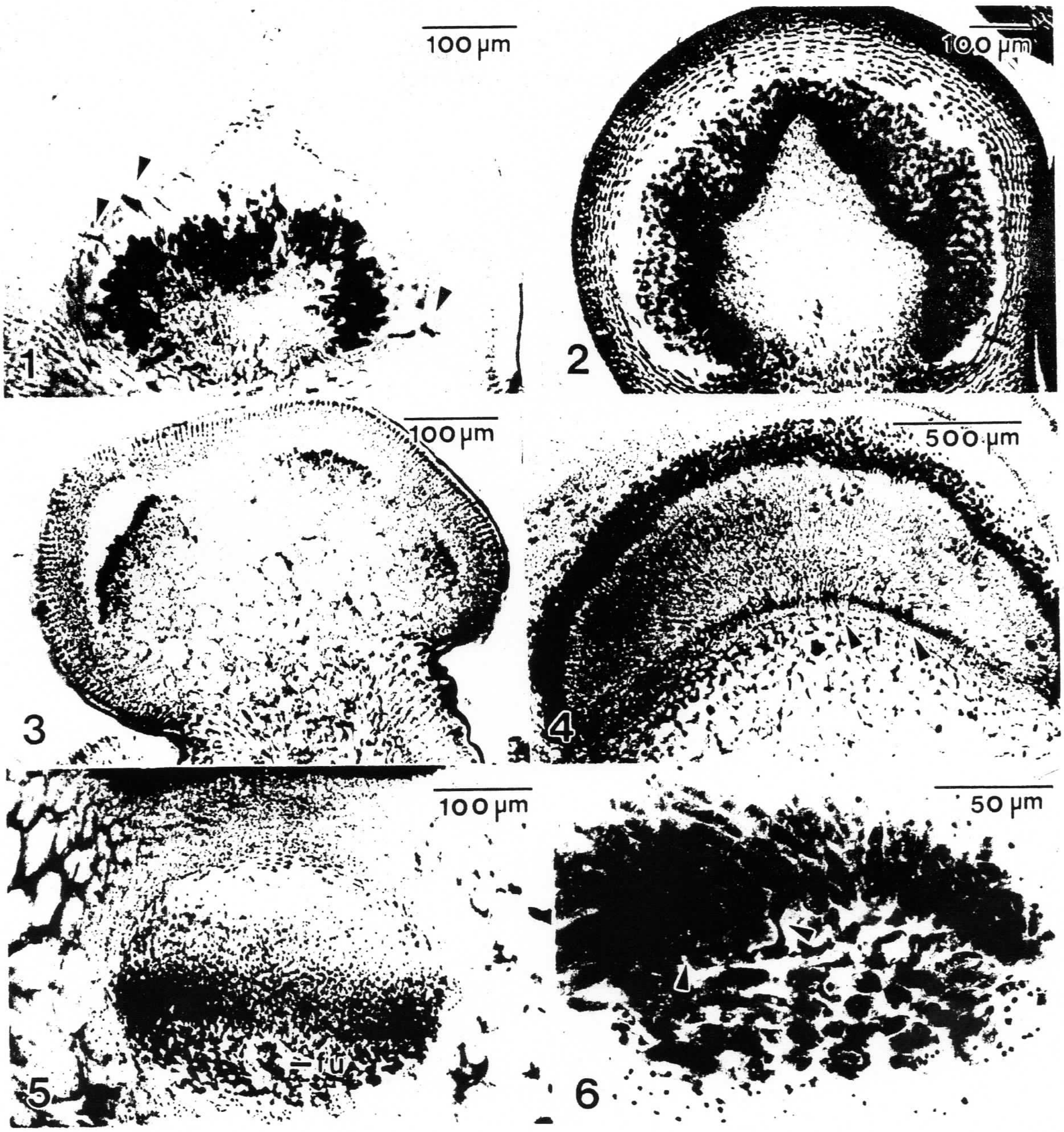
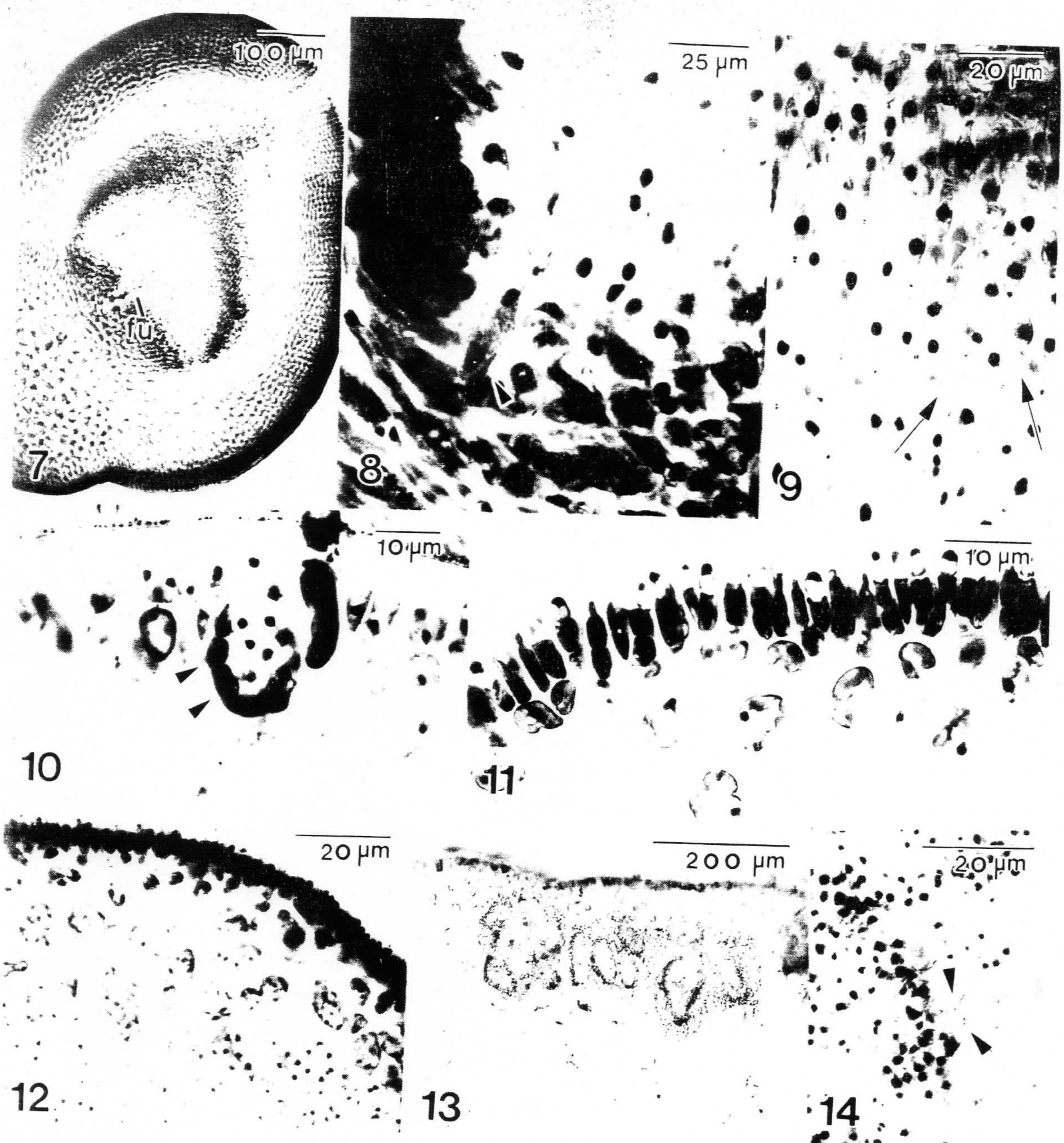


Fig. 1. Gracilaria verrucosa. Cystocarp with tubular nutritive cells fusing both with cells of pericarp (arrowheads) and cystocarp floor. *Fig. 2. Gracilariopsis lemaneiformis.* Cystocarp lacking tubular nutritive cells. *Fig. 3. Gracilariophila oryzoides.* Pustule of three cystocarps underneath one pericarp. *Fig. 4. Hydropuntia crassissima.* Cystocarp with tubular nutritive cells fusing (arrowheads) solely with cells of cystocarp floor. *Figs. 5 & 6. Curdiea flabellata. Fig. 5.* Mature cystocarp. *Fig. 6.* Absence of sterile gonimoblast filaments, except for gonimoblast cells fused with cells in floor of cystocarp (arrowheads).



Figs. 7–9. Melanthalia obtusata var. *abscissa. Fig. 7.* Mature cystocarp showing fusion cell (fu), and gonimoblast completely filling cystocarp cavity. *Fig. 8.* Fusion of lower gonimoblast cell with cell in cystocarp floor (arrowhead). *Fig. 9.* Inner gonimoblast cells linked by secondary pit connections with broadened pit plugs (arrowhead) around which they fuse (arrows). *Fig. 10. Gracilaria verrucosa.* Spermatangial pit with spermatangial parent cells (arrowheads) and spermatangia. *Fig. 11. Gracilariopsis lemaneiformis.* Superficial spermatangial parent cells and spermatangia cut off by transverse division. *Fig. 12. Gracilariophila oryzoides.* Superficial spermatangial parent cells and spermatangia cut off by transverse division. *Figs. 13–14. Hydropuntia crassissima. Fig. 13.* Confluent spermatangial pits. *Fig. 14.* Secondary pit connections (arrowheads) left behind after fusion of spermatangial parent cells onto vegetative cell.