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STRUCTURE, REPRODUCTION AND EARLY DEVELOPMENT OF *VIDALIA OBTUSILOBA* (RHODOPHYTA-CERAMIALES)

ESTRUTURA, REPRODUÇÃO E DESENVOLVIMENTO INICIAL DO TALO DE *VIDALIA OBTUSILOBA* (RHODOPHYTA-CERAMIALES)

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SUMMARY

A detailed description of the organization and development of vegetative, female, male and tetrasporic structures is presented for material of *Vidalia obtusiloba* collected at the type locality. The apical portion of the thallus is ventrally coiled and presents five pericentral cells. The subapical segments initially cut one dorsal pericentral cell and soon the other four pericentrals following the pattern known for the family. The ventral pericentral is the last cell to be cut. Further divisions of the dorsal and ventral pericentrals make older parts of the thallus with 6 to 8 cells around the central one. Periclinal divisions of the two lateral pericentral cells on each side of the thallus give rise to the lateral wings of the blade. The carpogonial branch arises at the second segment of a trichoblast, from the ventral pericentral cell. The fertile pericentral cuts initially a sterile lateral cell and soon after the carpogonial branch cells. The pericarp starts before fertilization. The anteridial bodies are globoid and are formed from the third segment of a trichoblast. Two tetrasporangia by segment arise at the third or fourth pericentral cells being covered by two large cells that later divide to form a cortical tissue. Of these only one sporangia reaches maturity. Early stages of carpospores development agree in general with the pattern ascribed to the Rhodomelaceae.

RESUMO

O trabalho descreve detalhadamente a organização do talo, o desenvolvimento das estruturas de reprodução e os primeiros estágios da germinação dos tetrásporos de *Vidalia obtusiloba*. As porções apicais apresentam-se enroladas sobre si mesmas, ventralmente, e com 5 pericentrais. Os segmentos sub-apicais cortam inicialmente uma célula pericentral dorsal e, posteriormente, as outras quatro pericentrais, seguindo a seqüência conhecida para a família, sendo a pericentral ventral a última a ser formada. Divisões posteriores das pericentrais dorsais e ventral fazem com que as partes mais velhas se apresentem com 6 a 8 células em torno da central. A parte laminar do talo é formada por divisões anticlinais das quatro pericentrais laterais, sendo duas de cada lado. O ramo carpogonial forma-se no segundo segmento de um tricoblasto, a partir da pericentral ventral. A pericentral fértil corta, inicialmente, uma célula lateral estéril e a seguir as células do ramo carpogonial. O pericarpo inicia-se antes da fecundação. Os corpos anteridiais apresentam forma globóide e desenvolvem-se a partir do terceiro segmento de um tricoblasto modificado. Os tetrasporângios são formados pela terceira e quarta pericentrais, em número de dois por segmento, inicialmente com duas células de cobertura que se dividem, posteriormente, formando um tecido de cobertura. O padrão de germinação dos carpósporos concorda, em linhas gerais, com o descrito na literatura para a família Rhodomelaceae.

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INTRODUCTION

Vidalia obtusiloba (Martens) J. Agadh was described from material collected on the Brazilian Coast (*Fucus obtusilobus* Martens, mscr., apud C. Agardh 1824, p. 161). Since then it has been referred several times to Brazil: Martius (1828 - 34), p. 8; 1833, p. 33) as *Sphaerococcus maximiliani* (Mert.) Martius; Martens (1870, p. 310) as *Rytiphlacea obtusiloba* Ag.; Moebius (1890, p. 1.085) as *Odonthalia microdontha* Grev.; Schmidt (1923, p. 230, in Luetzelburg 1922 - 23) and Schmidt (1924, p. 94); Howe (1928, p. 193) and Taylor (1960, p. 609) all as *Vidalia obtusiloba* (Martens) J. Ag.,

Oliveira Filho (1969), in a general paper on the Ceramiales of the Espirito Santo State, Brazil, called attention to some controversial point about *Vidalia* structure. In the same paper that author recognized three different morphological "forms", provisionally labeled as forms 1, 2 and 3. Of these, the plants assigned to form 1 are the ones whose gross morphology agree better with the original description of C. Agardh 1824. Unfornately it was not feasible to examine the type material of *V. obtusiloba* that should be deposited at Lund.

Considering that the type material was probably collected by the Prince of Wied-Neuwied in Espirito Santo State in 1815 and having a large number of speciments from that place, collected at several seasons and years, we decided to develop a detailed anatomical study of it aiming at a better characterization of this taxon. Spore's development was also included since it is a valuable taxonomic character.

METHODS

Thallus structure and reproductive organs were studied on freezing microtome sections of formalin preserved material or on material in paraffin, following the usual technique (Johansen 1940). Female reproductive structures and cystocarp development were also studied in squash preparations after convenient softening of young tips in a 5% solution of sodium hydroxide. Paraffined sections were stained with safranine and fast-green as recomended by Johansen (1940). Spore development was performed following the technique described in Oliveira Filho (1967) and Oliveira Filho &Brinati (1974).

THALLUS STRUCTURE

The genus *Vidalia* has a ribbon-shaped thallus with circinate apices, showing a marked dorsiventrality. It's gross morphology has been described by several authors (cf. Falkenberg 1901, Taylor 1960 and Oliveira Filho 1969). Figure 18 shows the habitus of the "form 1" (after Oliveira Filho 1969), that is the form more closely resembling the original description of C. Agardh (1824, 1. 161), later improved in another paper (1828, p. 51).

The growth of the thallus is given by a dome-shaped apical cell that cuts segments somewhat longer at the dorsal side in such a way the apical portions become ventrally rolled up (figs. 1 and 18).

Five-pericentral cells are alternately cut in each segment bigining from the first or second one. The first two pericentral cells are cut at the dorsal side of the thallus; the others are cut, alternatively, one to the right and one to the left side of the first pericentral. The third and the fourth pericentral cells are lateral in position, the fifth being cut at the ventral side, between the two lateral ones (figs. 2 - 6).

After the five pericentral cells are formed, each one of the two dorsal cells cuts a small cell that takes the dorsal position, so displacing the dorsal pericentral cells to a dorso-lateral position (fig. 7). Later the ventral pericentral divides once, giving rise, in this way, to the apparent eight pericentral cells found in the older parts of the thallus (figs. 8 and 9).

Near the apex, the lateral wings of the thallus have two layers of cells, the dorsal layer being formed from anticlinal divisions of the dorso-lateral pericentral cells and the ventral layer from the lateral pericentral cells (figs. 8 and 9). In older parts of the thallus three or four layers of cortical cells cover the dorsal and ventral side of the blade. The first cortical layer is produced by periclinal and anticlinal divisions of the wing cells as well as of the dorsal pericentrals. Subsequent divisions of the first cortical layer give rise to the other three layers of cortical cells (figs. 9 and 19).

At the basal portions of the thallus there is a development of a secondary cortex around the midrib, formed by periclinal and anticlinal divisions of the primary cortex (fig. 19).

Sterile trichoblasts are not very frequent. Apparently they occur only on tetrasporic plants. They are slightly reddish, monosiphonous, dichotomously ramified and soon deciduous. They arise on the dorsal side of the blade just behind the apex, from the fourth segment on, forming a single row restricted to the apical portion. The trichoblast initial is cut through a periclinal division from one dorsal pericentral cell. This cell gives rise to a three-celled filament that divides dichotomously a few times, forming an inconspicuous trichoblast (fig. 38). In male and female plants only fertile trichoblasts could be found.

PROCARP

Fertile trichoblasts arise in an acropetal sequence on the dorsal side of a short lateral branch (fig. 21). The apical cell of the trichoblast in cut from the dorsal pericentral cells of short lateral branches and the formation of pericentral cells in the fertile trichoblast follows the same pattern described for the vegetative apices of the thallus (figs. 10 - 12).

The second segment of the trichoblast becomes fertile and the ventral pericentral cell gives rise to the carpogonium and to the sterile cells, (figs. 11 - 15). The supporting cell (ventral pericentral) initially cuts a large sterile cell laterally. Soon after that, two divisions, perpendicular to the long axis of the supporting cell, divide it in three cells, that lie almost in a straight line. The third cell enlogates and cuts the terminal carpogonium with a long and wide trichogyne (figs. 13, 15 and 16).

At the time of the first division of the supporting cell, the lateral pericentral cell

of the fertile segment forms the first pericarp initials (fig. 13). As the carpogonial branch develops, the surrounding pericentral cells of the fertile segment, as well as of other segments, start to produce a dense pericarp which makes observations of further development very difficult (fig. 21).

Details of fertilization, production of other sterile cells and of the auxiliary cell were not observed.

A young cystocarp of less than half milimeter already shows a great fusion cell from which the gonimoblastic filaments arise (fig. 17). It is not infrequent to find young cystocarps with 2 and more rarely 3, carpogonial branches. Though it was not possible to trace their, origin, we suppose that they could be formed by two sterile cells derived from the supporting cell.

When fully developed, cystocarps present a thick wall and open through an apical pore.

Only the terminal cells of the gonimoblasts diferentiate in carpospores (fig. 20).

SPERMATANGIA

The spermatangia are disposed in globoid bodies surrounded by a gelatinous sheath. They are arranged in an acropetal sequence on the dorsal side of a short lateral branch, in a single row near the apex.

The spermatangial branch initial arises through a periclinal division from one of the dorsal pericentral cells, forming at the begining a short monosiphonous filament (fig. 36). From the third segment on, pericentral cells give rise to a cluster of spermatangia (fig. 37). When fully ripe the spermatangial bodies are oblong, measuring111 – 136 μm wide to 129 - 172 μm long.

TETRASPORANGIA

The tetrasporangia are formed on short lateral ramified branches. They are marginally disposed or, in form 1, appear on proliferations of the midrib. The tetrasporic branches are alternately ramified with strongly coiled apices (fig. 22). The fertile portions are dorsoventrally flattened, without development of lateral wings, measuring about 450 μm to 180 μm in cross section (fig. 23).

The stichidia grow through an apical cell that cuts segments transversely (fig. 25). Five pericentral cells are formed, following the same sequence as the one described for the apex of the thallus. The sporangia are formed at the fouth or fifth segments from the apical cell, by the two lateral pericentrals, so two sporangia are produced in each segment (fig. 24).

The sporangia are disposed in two opposite rows at the ventral side of the stichidia (fig. 22). Each fertile pericentral first cuts, by a periclinal division, a large cover cell,

and then by another division a second one is produced. Only after that is the sporangium produced through an anticlinal division from the pericentral cell (figs. 24 and 25). In all sections examined, it was seen that the fertile segments have, always a sterile one between them.

The two cover cells are much bigger than the cortical cells and are easily visible when stichidium is seen from the ventral side. Sometimes they do not divide and remain almost completely uncovered by the cortical cells. Sometimes they divide and can no longer be recognized as such (fig. 26).

TETRASPORE'S DEVELOPMENT

Immediately after their liberation from the sporangia the spores become spherical, measuring about 100 μm in diameter. After a variable lenght of time, the spores attach themselves to the substratum. The germination begins by the development of a basal protuberance. The first septum is parallel to the substratum and divides the sporeling in two cells. The larger one will give rise to the thallus (thallus initial) and the smaller to the rhizoids (rhizoidal initial). The following divisions of the thallus initial are perpendicular to the sporeling axis, forming three cells, while the initial rhizoidal elongates. Divisions parallel to the axis of the sporeling occur only after they attain the stage of four or more cells.

In some instances the initial rhizoidal divides parallely to its axis giving rise to more than one rhizoidal cell. Later the rhizoidal cell divides in a perpendicular plane to its axis, forming a multicellular rhizoid.

In our cultures the sporelings stopped development after attaining a few cells, probably due to inadequate culture conditions, made without enrichment of the medium (filtered seawater) or light conditions (natural diffuse light).

Some trials with cystocarpic plants have been done and despite carpospores having been released these did not germinate in the described conditions.

The sequence of developmental stages are pictured in figs. 27 - 35.

DISCUSSION

The general features of the thallus and reproductive structures of the Brazilian material of *Vidalia obtusiloba* agree with the data presented by other authors for the studied genera of the Amansiae (sensu Kylin 1956).

The strong curling of the thallus apex is due to the asymmetry of the pericentral cells, that become larger at the dorsal side, as in *Lenormandia prolifera* (Saenger &Ducker 1971). The primarily dorsiventral thallus has already been remarked on by Hommersand (1963). This dorsiventrality becomes established very soon, at the second segment, where normally occurs the first periclinal division of the central cell to produce the first pericentral cell, that is always the dorsal one.

The presence of 8 cells surrounding the central cell in older portions of the thallus and of 7 in younger ones may lead to a wrong interpretation of the pericentral number (cf. Okamura 1915, pl. CXXXI, and Oliveira Filho 1969, pl. 166). The 5 real primary pericentral cells can be found in the first segments of the thallus, which, due to its strong coiling makes its observation quite difficult. Soon after the 5 pericentral cells are formed, the 2 dorsolateral ones divide once each, in a plane that all the resulting 4 cells remain in contact with the central cell, appearing, in a superficial analysis as pericentrals. Later on also the ventral cell divides similair and 8 pericentrals appear all along the thallus.

Okamura (1915), mentions the occurence of trichoblasts on every young segment, a fact also mentioned by Hommersand (1963) for all the Amansiae. However, as in *Lenormandia prolifera* (Saenger & Ducker 1971), we found that the trichoblasts are generally absent. Sterile trichoblasts were found only on tetrasporic plants, and even here, they are very inconspicuous and soon deciduous. In sexual plants only fertile trichoblasts were found.

The lateral branches, either well developed or present as small teeth, are endogenous in origin, as pointed out by Scagel (1953) and Hommersand (1963).

The development of the carpogonial branch follows the same pattern presented by other Rhodomelaceae. The best approach to the procarp development in the Amansiae is the one of Saenger & Ducker (1971, for *L. prolifera*). The fertile trichoblast is very reduced, having only 3 - 4 cells. The carpogonium is produced by the ventral cell of the second segment, being easily recognized by its large size and prominent form. Contrary to what is said by Saenger & Ducker (1.c.) for *L. prolifera* pericarp starts to develop even before the complete differentiation of the carpogonial branch. As in *L. prolifera* there are also 3 sterile cells though they seem to have been produced rather in a lateral than in a basal portion. The trichogine is exceptionally robust and pigmented (brownish). In opposition to what was observed by Saenger & Ducker (1.c.) for *L. prolifera* it is persistent even in well developed cystocarps.

The development of the spermatangial bodies follows the same patern known to the tribe. In the Brazilian material all trichoblasts become fertile in an ordered sequence from apex to base.

The tetrasporangia are formed by the third and fourth pericentral cells as is the case in all the Amansiae studied (cf. Falkenberg 1901). In the examined material the sporangia are not produced in the first 5 - 6 apical, neither in the basal segments, and it seems that a fertile segment always alternates with a sterile one. In cross sections of mature tetrasporic branches it is frequent to find only one tetrasporange per segment, and, observing the tetrasporic branch from the outside, the sporangia appear distributed in two alternated rows. This has already been described by Falkenberg (1901, p. 427), for *Vidalia volubilis,* saying that only one sporange develops in each segment. However, in young portions, one can see that two sporangia are produced in each segment but only one reaches maturity. The fertile pericentral produces first two large cover cells that may remain entire or may divide to produce a few cortical cells.

We could find no references to spores development for the Amansiae, except the one of Saenger & Ducker (1.c.) for carpospores of *L. prolifera.* The pattern of

spores development agrees with the one described for other Rhodomelaceae (cf. Oliveira Filho 1967), presenting, however some minor differences with the first stages pictured by Saenger & Ducker (1971). The young sporeling is erect and radially symmetrical as was already been antecipated by Scagel (1953).

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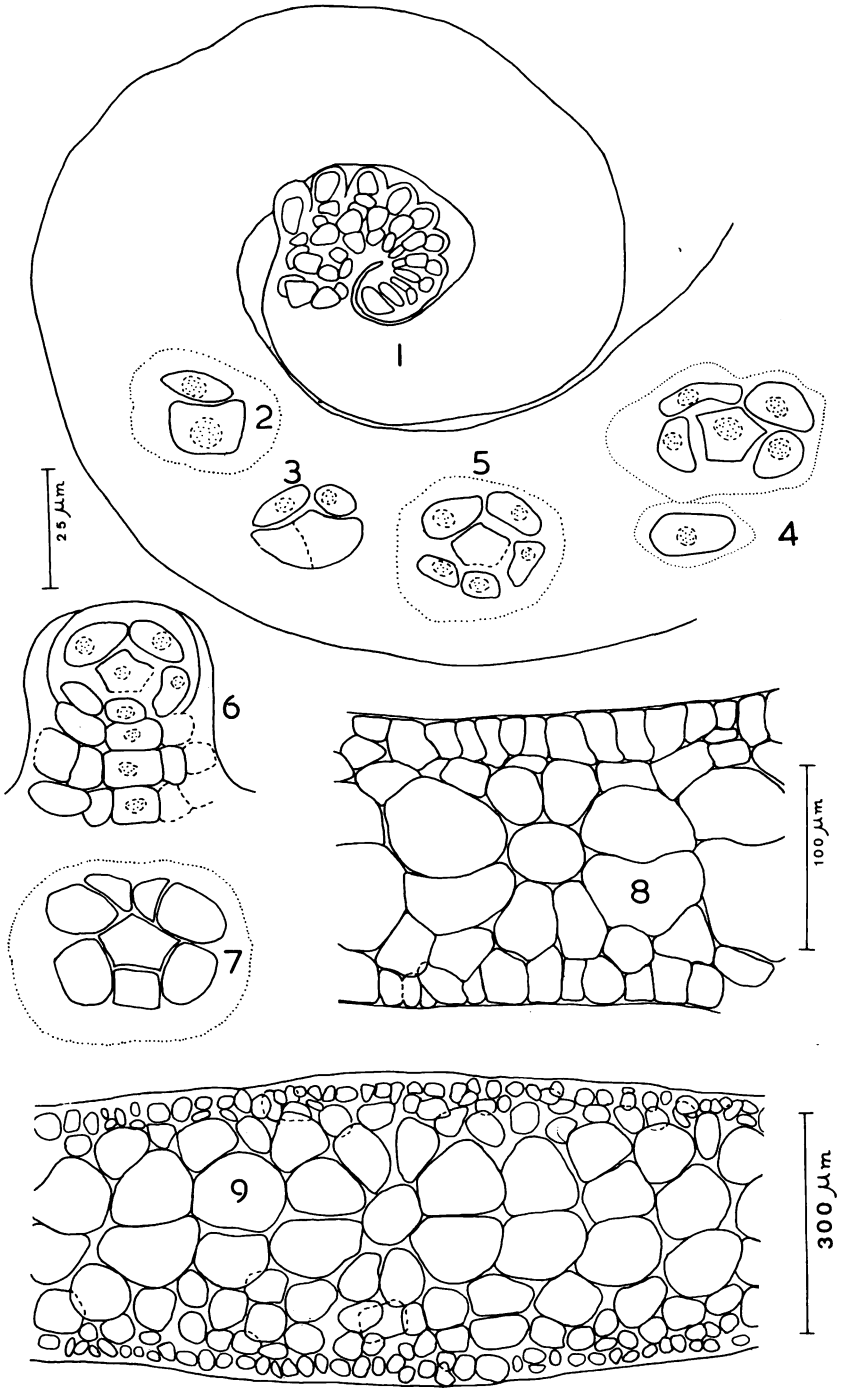
1. Longitudinal section of the thallus, perpendicular to the margin. Note development of trichoblasts from the dorsal pericentral; 2 - 6. Cross-section through successive segments in a growing apex showing the sequence of pericentral sectioning; 7. Cross-section of a young tip, showing the division of the dorsal cell. Thallus appears as with 6 "pericentrals"; 8 - 9. Cross section of successively older parts showing the division of the ventral pericentral, development of the wings and the increasing cortication (see also fig. 19). The 25 μm scale is for figures 1 - 7.

1. Corte longitudinal do talo, perpendicular à margem. Note a formação de tricoblastos à partir da primeira pericentral; 2 -6. – Corte transversal de um ápice em crescimento passando por sucessivos segmentos e mostrando a seqüência na formação das pericentrais; 7. Corte transversal próximo ao ápice mostrando a divisão da pericentral dorsal, simulando 6 pericentrais; 8 - 9. Cortes tranversais de porções mais velhas mostrando a divisão da pericentral ventral, o desenvolvimento das alas e o aumento da corticação. (Veja também a fig. 19). A escala de 25 μm vale para as figs. de 1 a 7.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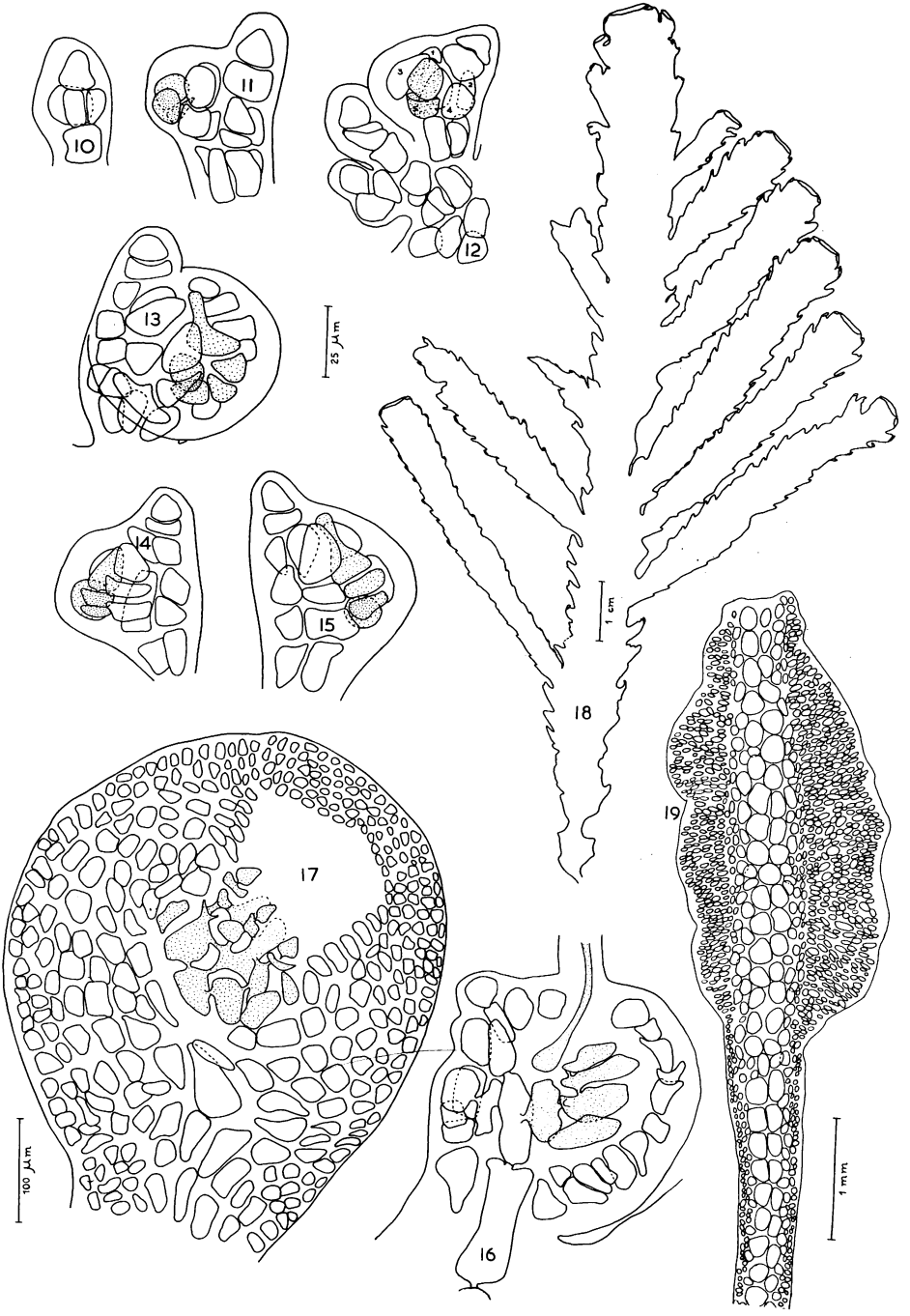
10 - 15. Successive stages in carpogonial branch development from fertile trichoblasts. Note the beginning of pericarp development in fig. 13. The numbers of fig. 12 point the sequence of appearing pericentrals; 16. Mature carpogonial branch with the large trichogyne; 17. Gonimoblast development in a young cystocarp (see also figs. 20 and 21); 18. Gross morphology of a branch from form 1; 19. Cross section through the mid-rib showing the cortication. The 25 μm scale is the same for figs. 10 - 16.

10 - 15. Estágios sucessivos no desenvolvimento de um ramo carpogonial a partir de tricoblastos férteis. Note já um início de formação de pericarpo na fig. 13. Os números na fig. 12 indicam a seqüência de formação das pericentrais; 16. Ramo carpogonial maduro; 17. Desenvolvimento dos gonimoblastos em um cistocarpo jovem (veja também figs. 20 e 21); 18. Aspecto geral de um ramo da forma 1; 19. Secção transversal através da nervura central mostrando a corticação. A escala de 25 μm vale para as figuras. 10 - 16.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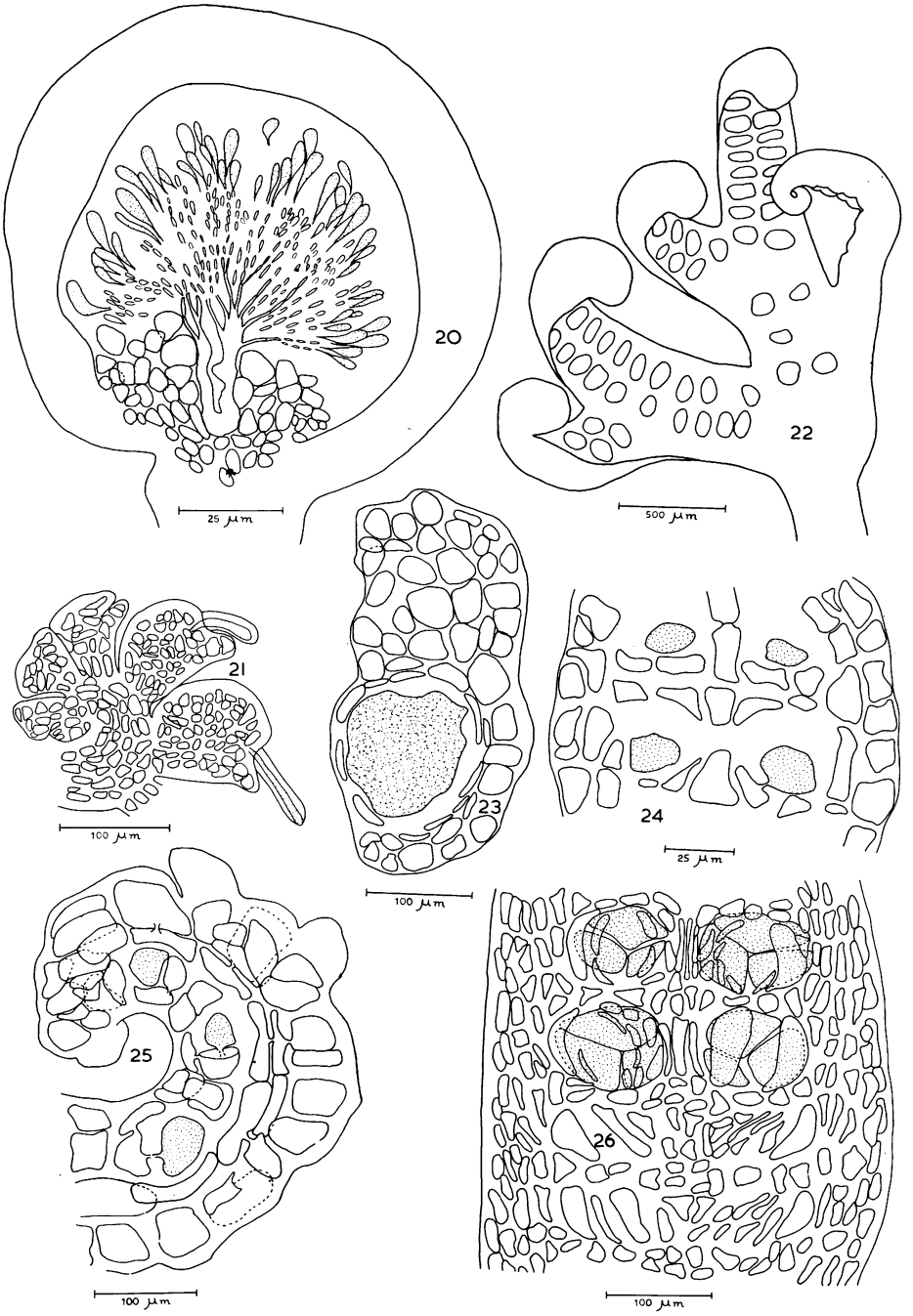
20. Median section of a mature cystocarp. Note the terminal carpospores; 21. Female plants showing the position of cystocarps. Note the thick trichogyne; 22. General view of a tetrasporic branch with tetrasporangia; 23. Cross section of a tetrasporic branch; 24 -25. Longitudinal sections of a tetrasporic branch through two different planes; 26. Surface view of a trasporic branch showing the cover cells.

20. Corte mediano de um cistocarpo maduro. Note os carpósporos terminais; 21. Plantas femininas mostrando a posição dos cistocarpos; 22 e 23. Vista geral e secção transversal de um ramo tetraspórico; 24 - 25. Cortes longitudinais, em diferentes planos, de um ramo tetraspórico; 26. Vista superficial de um ramo tetraspórico mostrando as células de cobertura.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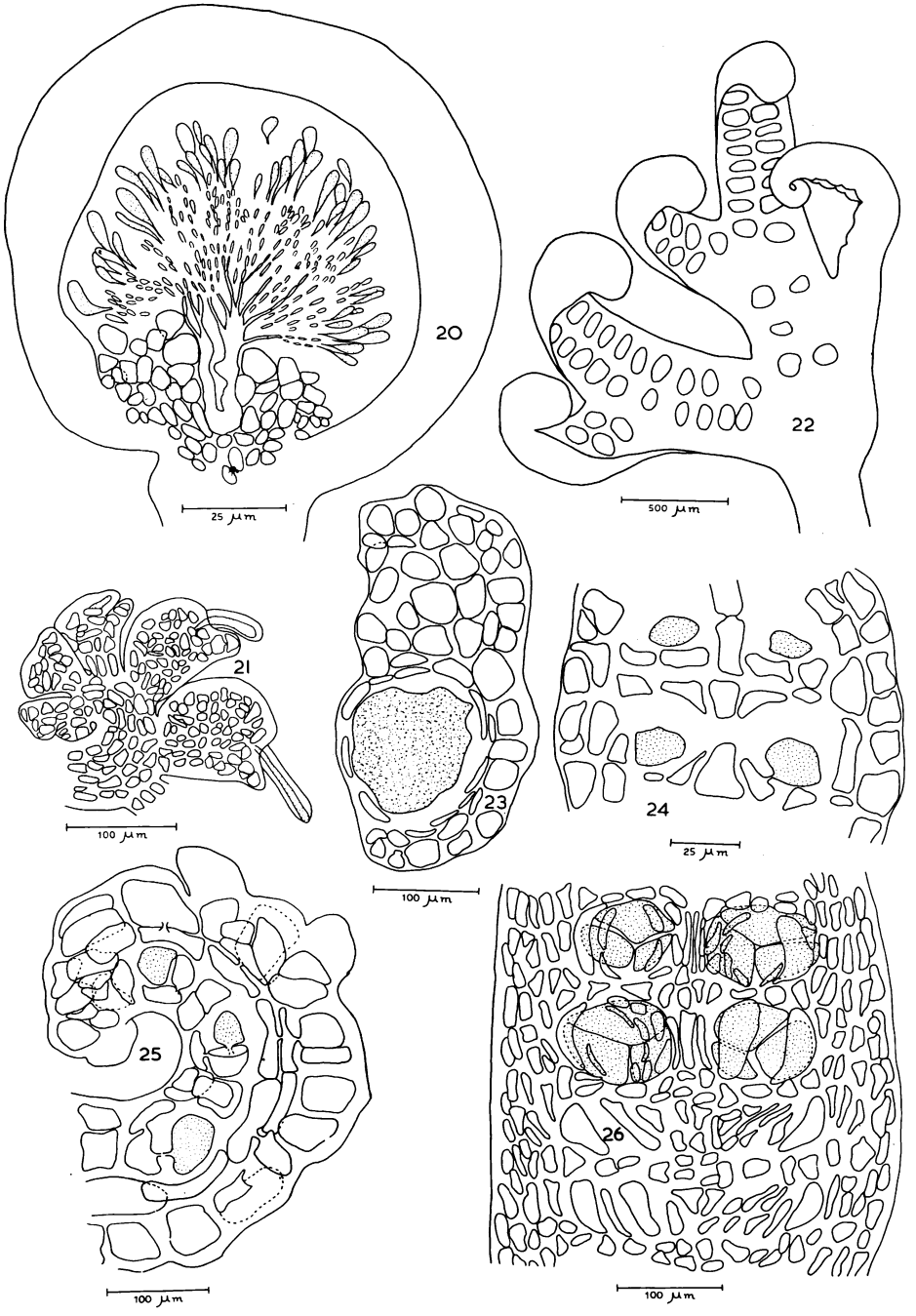
27-35. Development sequence of tetraspores germination **(form 2)** 36-37. Development of spermatangia from trichoblasts; 38. Development of sterile trichoblasts.

27 - 35. Seqüência no desenvolvimento de tetrásporo em germinação (forma 2); 36 e 37. Desenvolvimento de espermatângios a partir de tricoblastos férteis; 38. Desenvolvimento de tricoblastos estéreis.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27-35. Development sequence of tetraspores germination **(form 2)** 36-37. Development of spermatangia from trichoblasts; 38. Development of sterile trichoblasts.

27 - 35. Seqüência no desenvolvimento de tetráporo em germinação (forma 2); 36 e 37. Desenvolvimento de espermatângios a partir de tricoblastos férteis; 38. Desenvolvimento de tricoblastos estéreis.