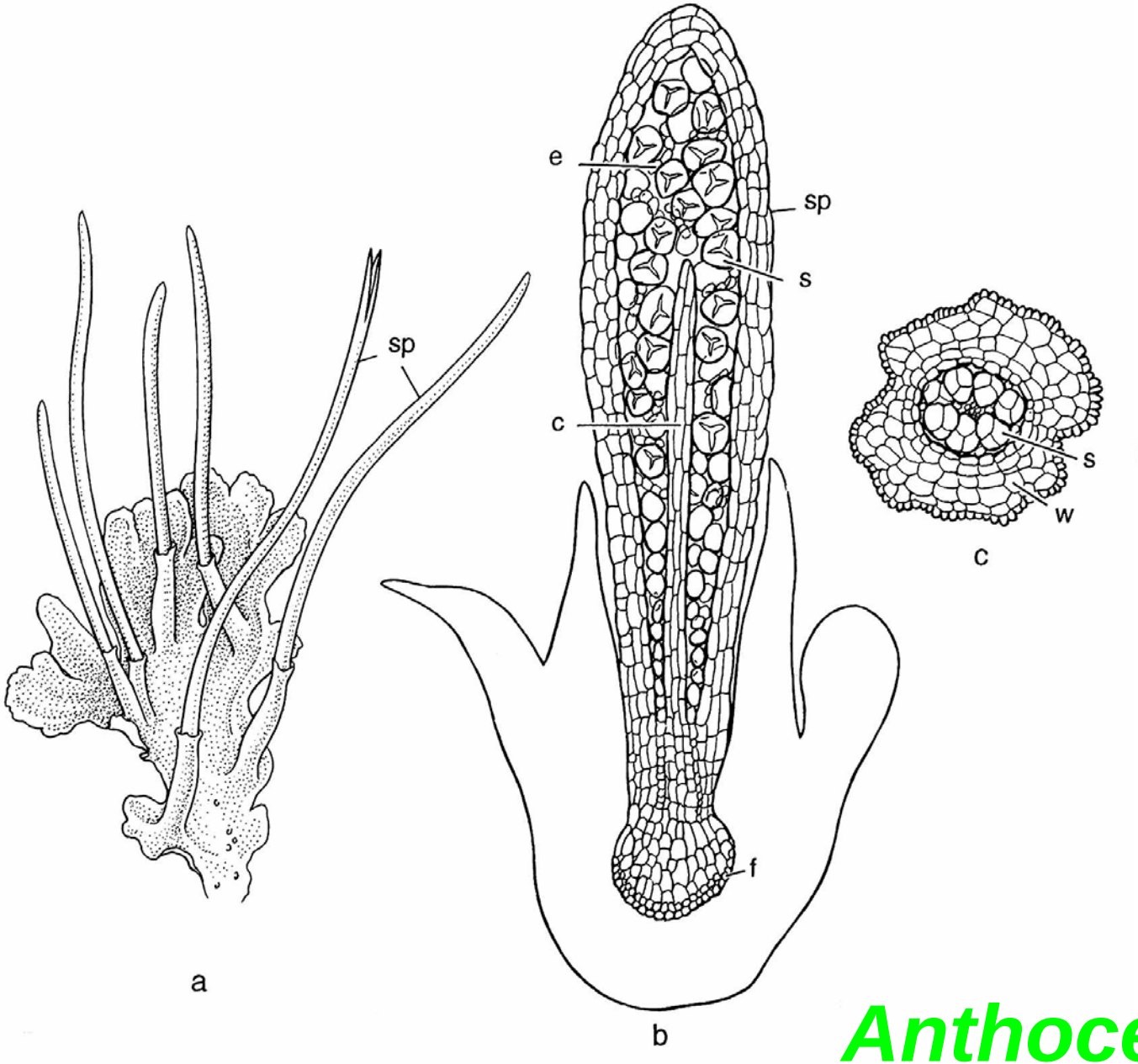
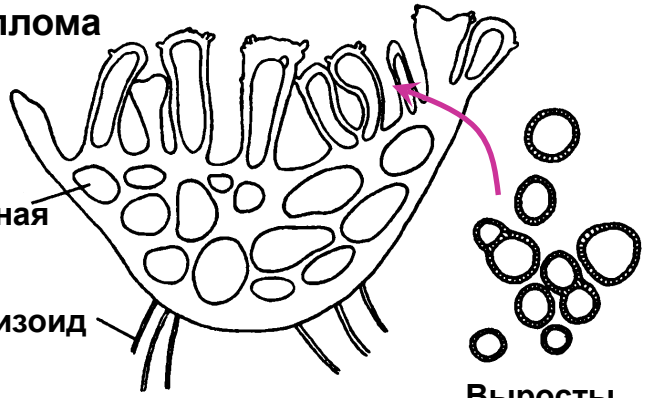


Phaeoceros laevis

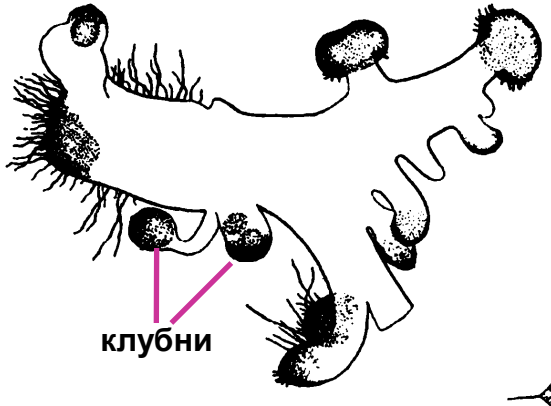
отдел *Anthocerotophyta*

14 родов, 250 видов

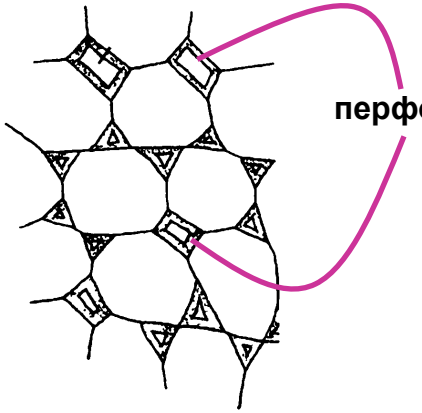
Folioceros appendiculaus, поперечный срез таллома

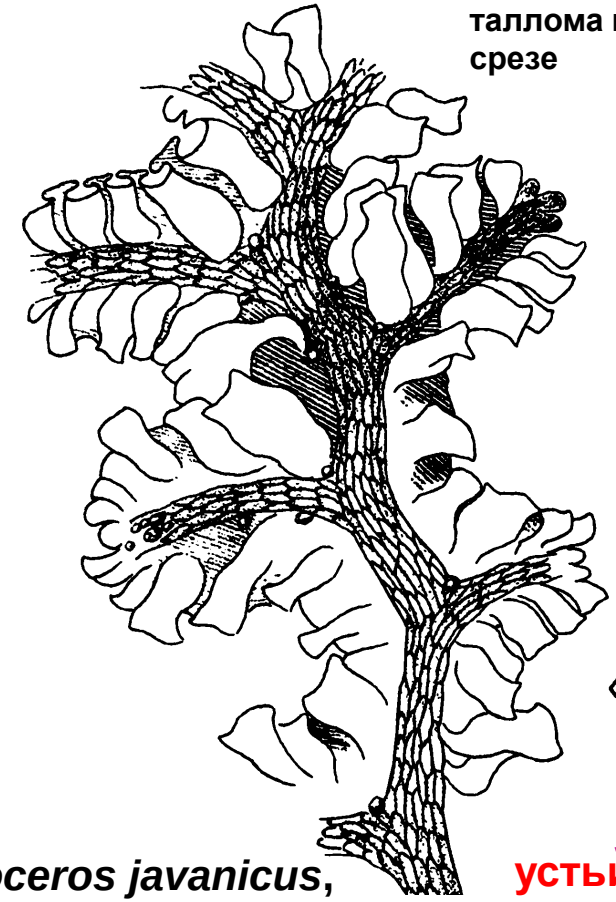


Phaeoceros bulbiculosus, вид таллома с дорзальной стороны

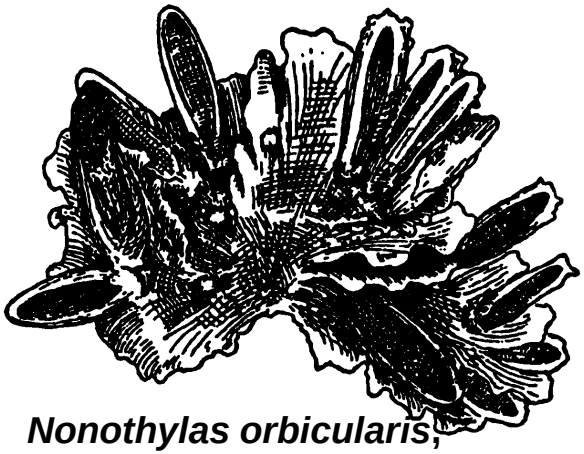


Dendroceros breutelii, однослойный край таллома





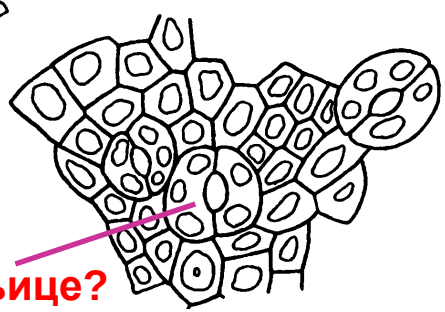
Dendroceros javanicus, таллом



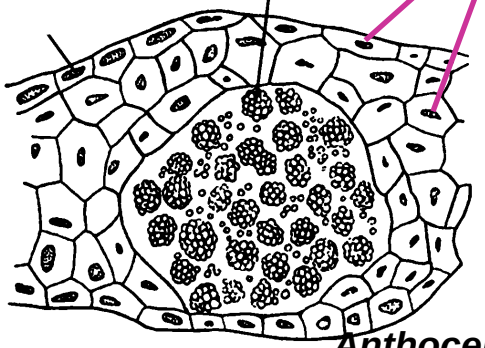
Nonothylas orbicularis, слоевище со спорофитами

1 пластида в каждой клетке

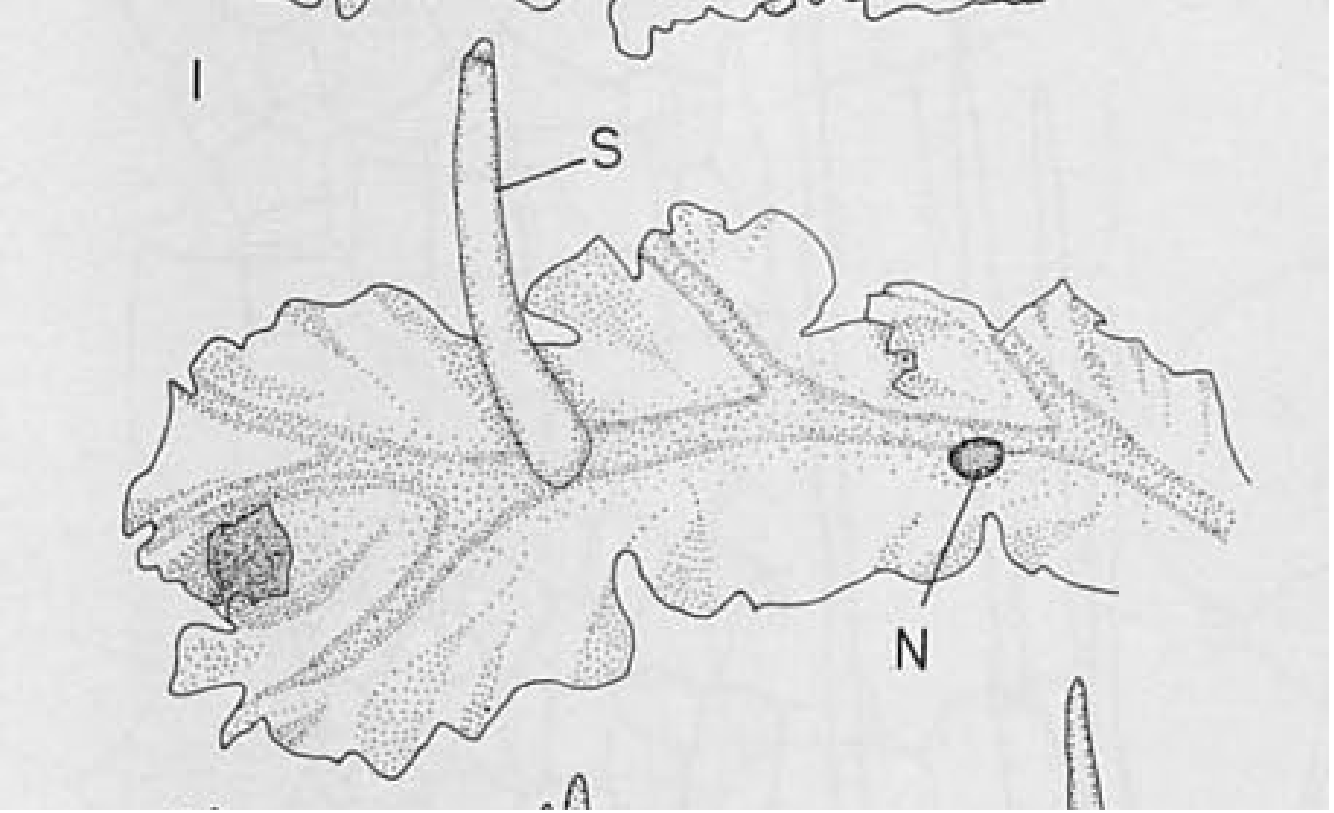
Nostoc

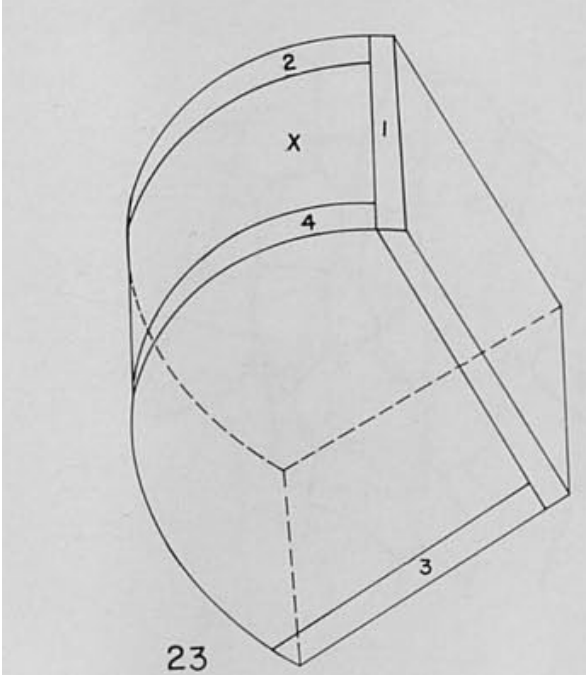


Dendroceros sp., брюшная эпидерма



Anthoceros agrestis, срез таллома

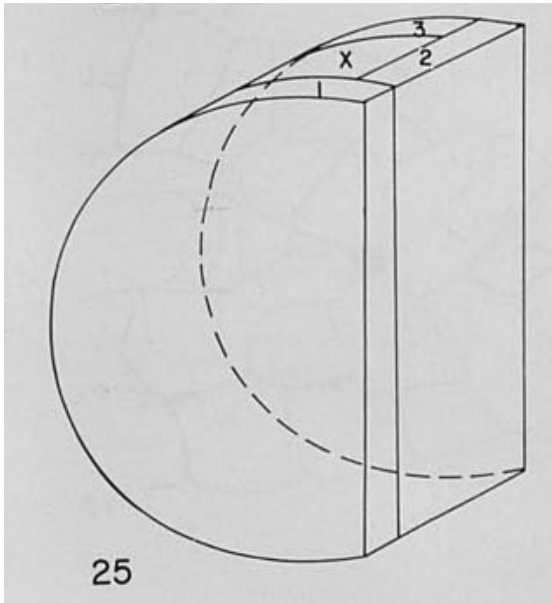




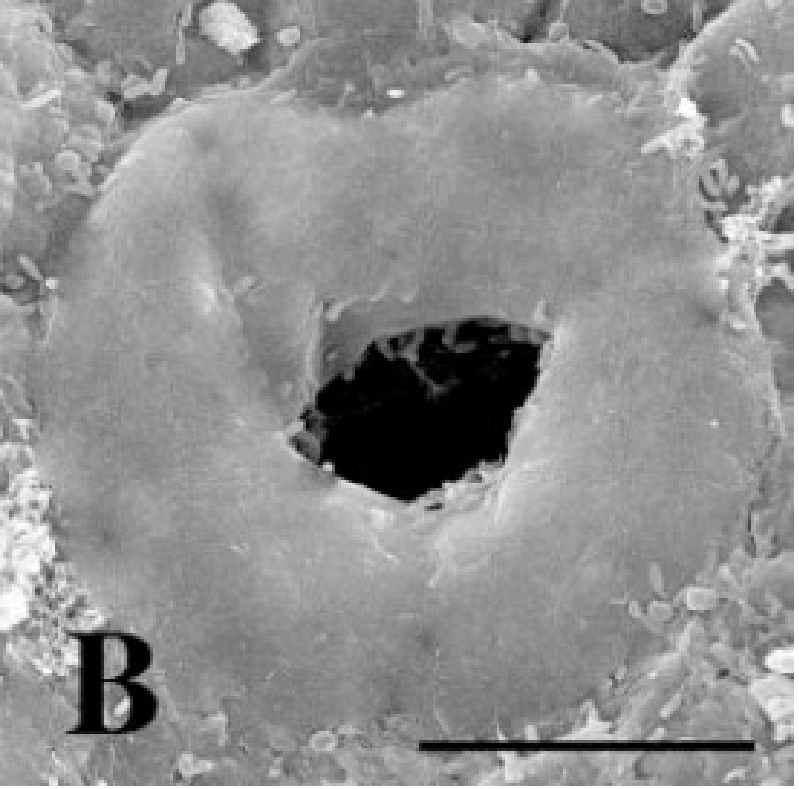
Клиновидная апикальная клетка (все кроме *Dendroceros*)

Dendroceros, дихтомическое ветвление

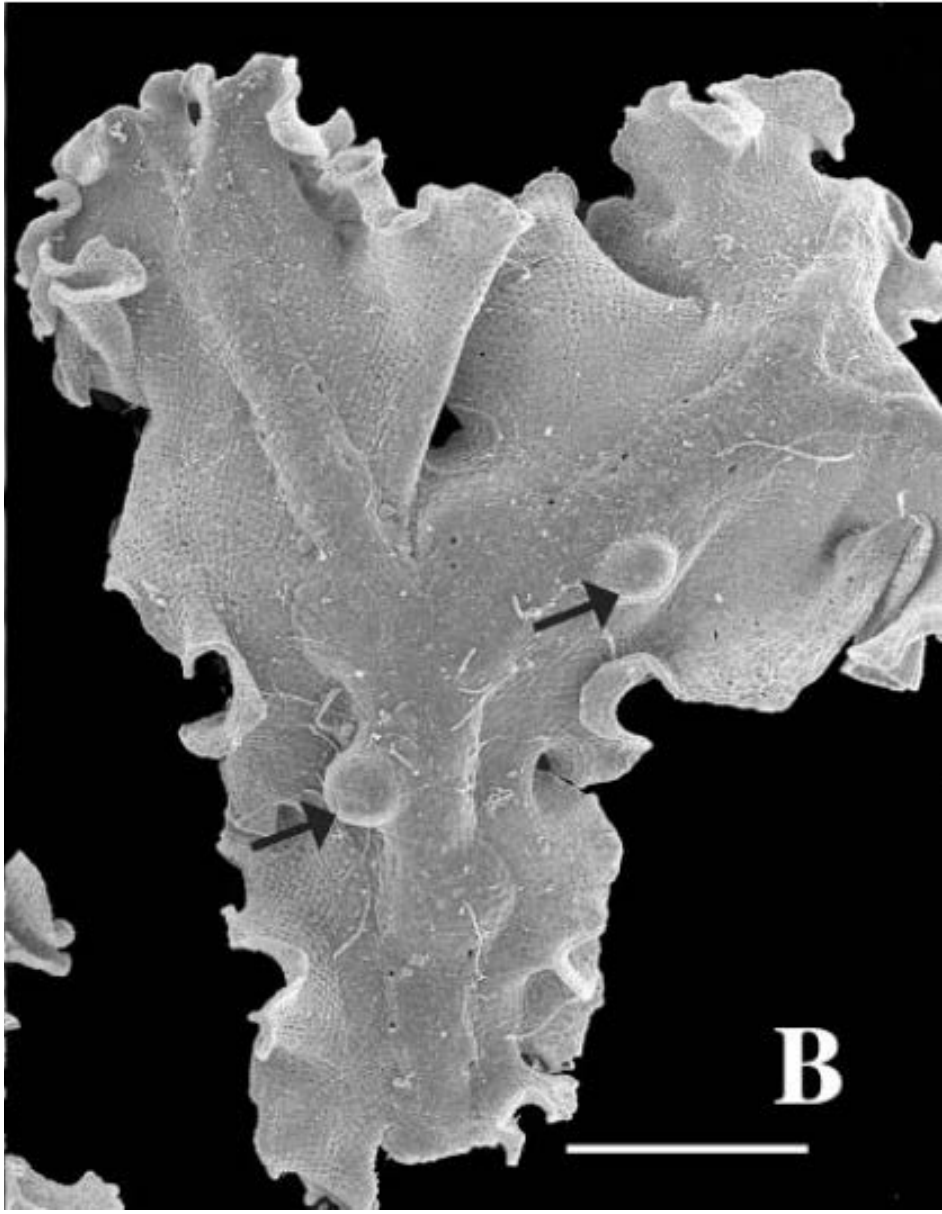
Дихотомическое ветвление установлено у гаметофитов всех изученных в этом отношении антоцеротовых и представляет собой оригинальную особенность этой группы



Полудисковидная апикальная клетка *Dendroceros*



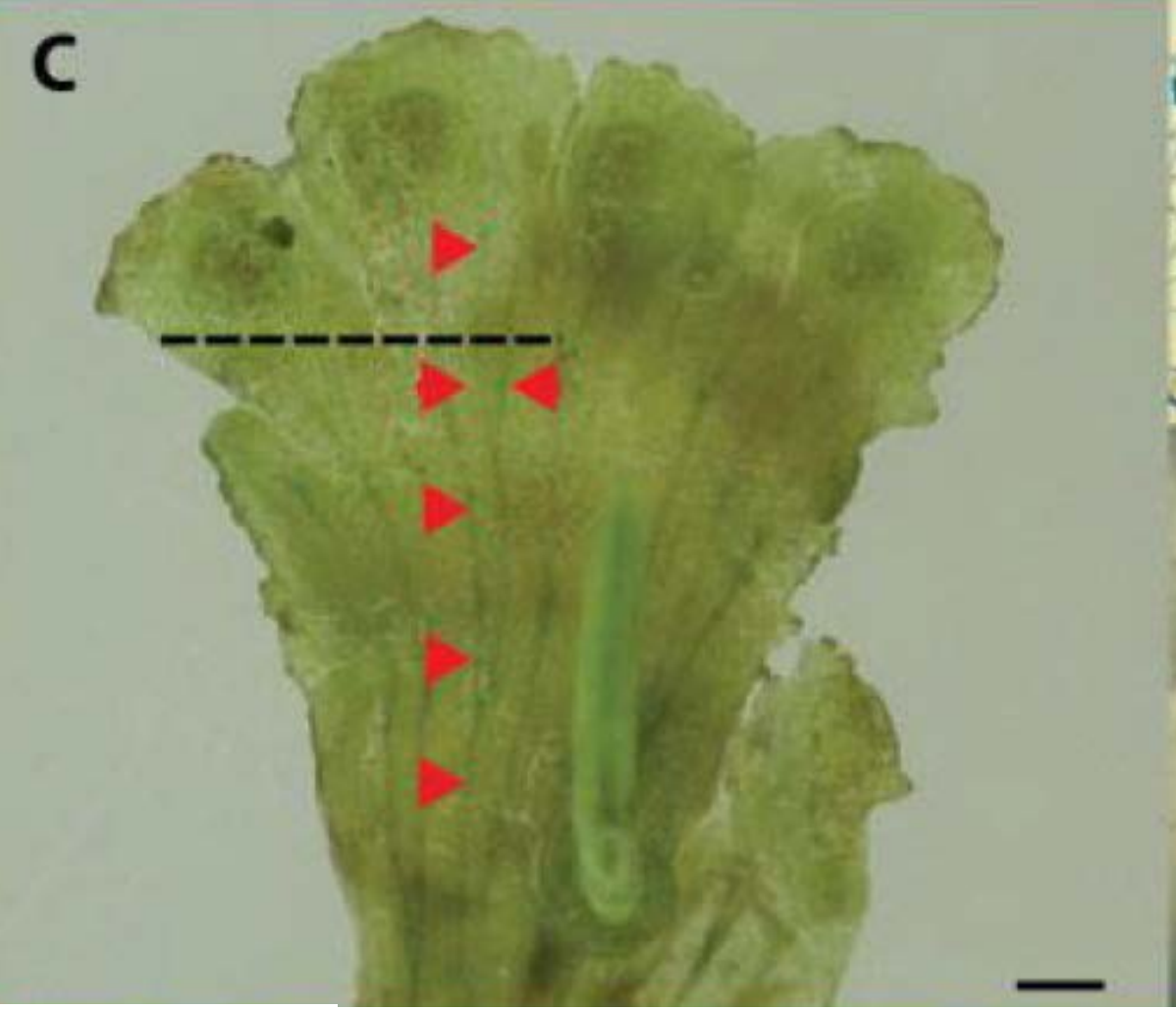
открытое устьице

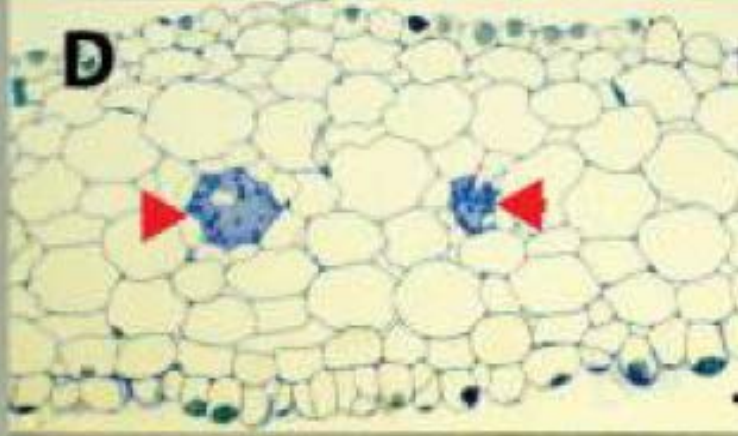


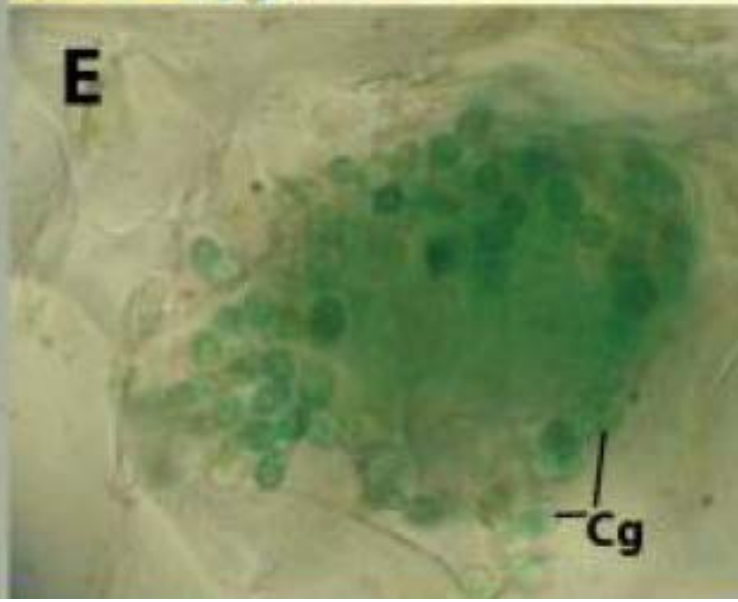
Dendroceros crispatus: слоевище с нижней стороны

стрелки – колонии ***Nostoc***


Folioceros dixitianus
Индия, Западные Гаты
Колонии
Nostoc

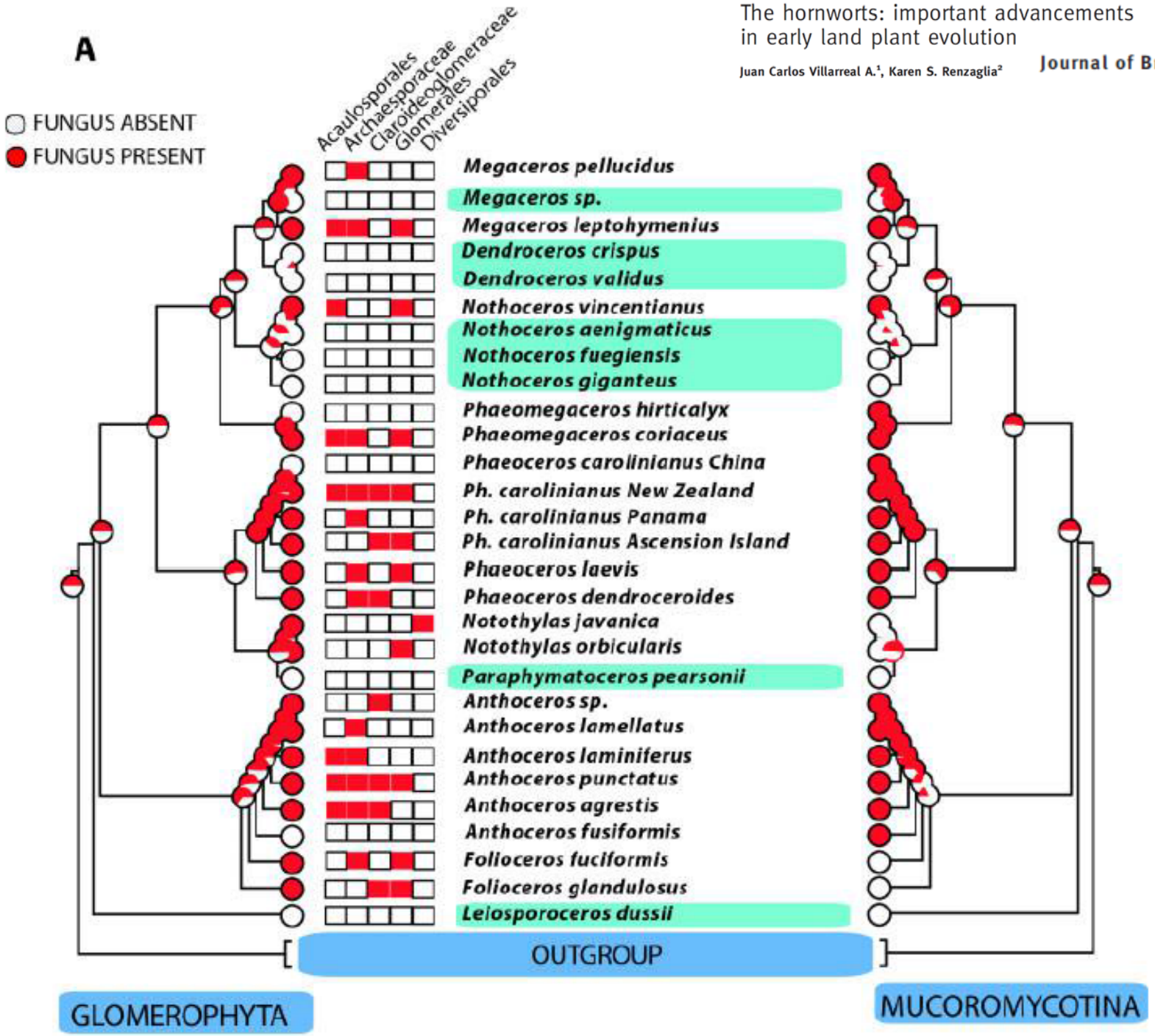


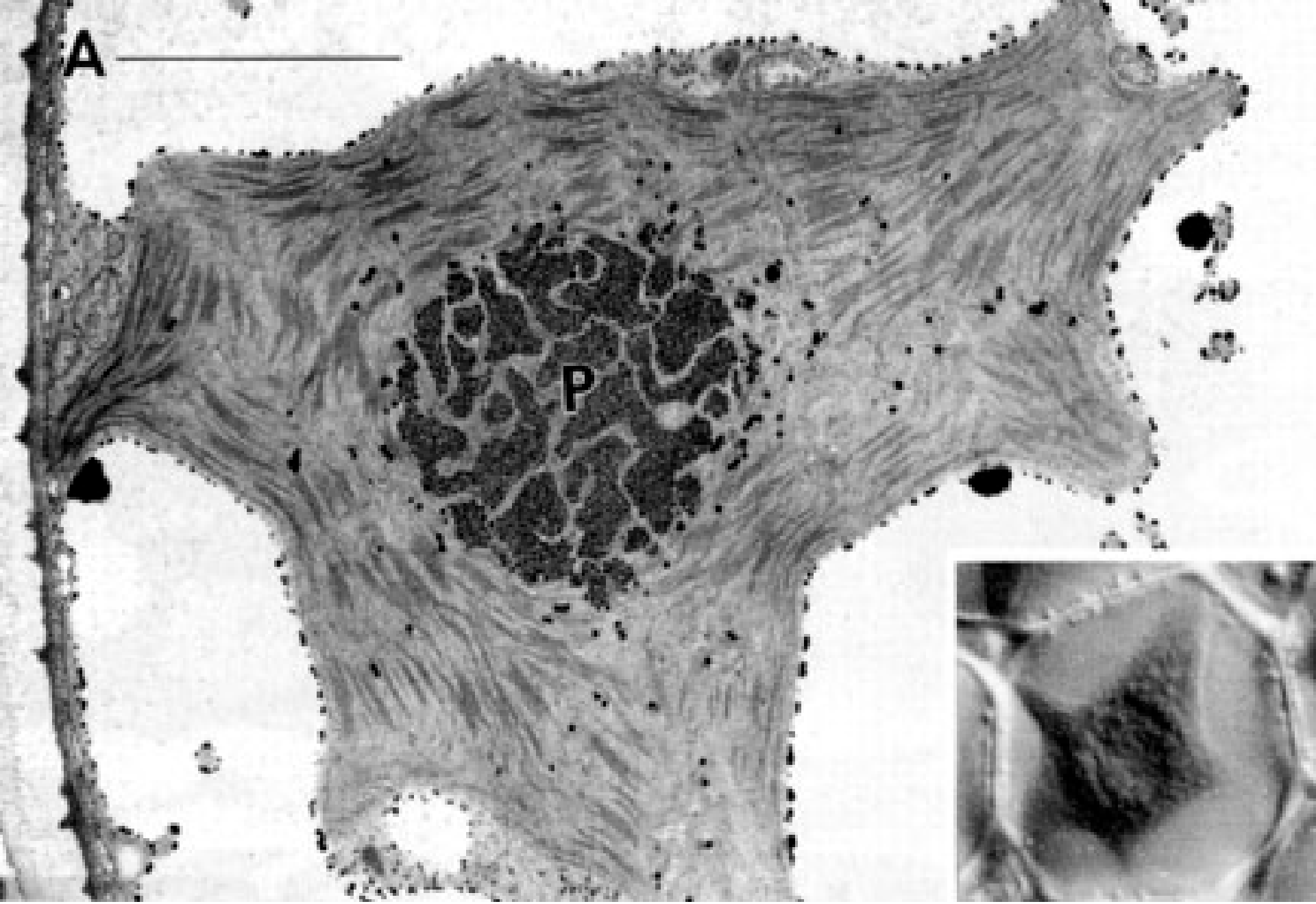




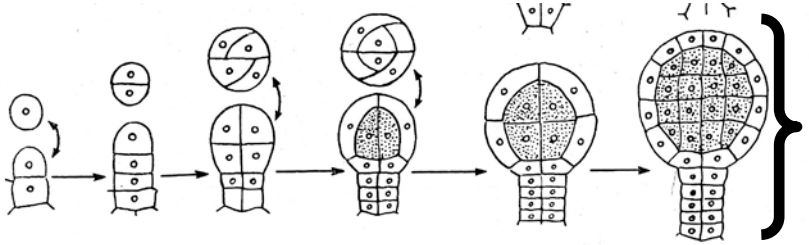
(C) *Leiosporoceros dussii* (Steph.) Hässel. Bifurcating strands of *Nostoc* parallel the main axis of the thallus (red arrows) in a female plant with one sporophyte. A dashed line across represent the transverse section presented in Figure 4D, two opposite arrows represent the two individual strands in Figure 4D. Bar = 2 mm. (D) *Leiosporoceros dussii* (Steph.) Hässel. Transverse section of a mature thallus with two central Nostoc canals (red arrows) at the level of represented by dashed lines in Figure 4C. Bar = 75 μm. (E) Higher magnification of a canal with *Nostoc* (blue-green filaments), note the abundant cyanophycian granules (Cg) in the individual cells (see Villarreal & Renzaglia, 2006 for ultrastructural features). Bar = 10 μm.

Hornworts are arguably the oldest land plant lineage with a widespread symbiosis with cyanobacteria. Most hornwort species develop globose *Nostoc* colonies inside their thalli and multiple re-infections occur throughout their life span. The sole exception is *Leiosporoceros* that has bifurcating strands of *Nostoc* locked inside the thallus, potentially enhancing the transfer of metabolites between partners

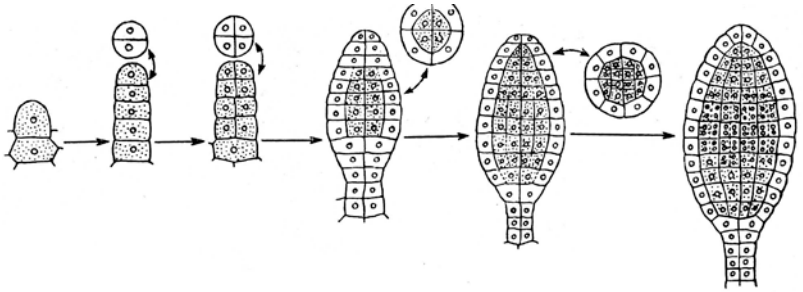

A
FUNGUS ABSENT
FUNGUS PRESENT
Acaulosporales
Archaeosporaceae
Claroideoglomeraceae
Glomerales
Diversisporales
Megaceros pellucidus
Megaceros sp.
Megaceros leptohymenius
Dendroceros crispus
Dendroceros validus
Nothoceros vincentianus
Nothoceros aenigmaticus
Nothoceros fuegiensis
Nothoceros giganteus
Phaeomegaceros hirticalyx
Phaeomegaceros coriaceus
Phaeoceros carolinianus China
Ph. carolinianus New Zealand
Ph. carolinianus Panama
Ph. carolinianus Ascension Island
Phaeoceros laevis
Phaeoceros dendroceroides
Notothylas javanica
Notothylas orbicularis
Paraphymatoceros pearsonii
Anthoceros sp.
Anthoceros lamellatus
Anthoceros laminiferus
Anthoceros punctatus
Anthoceros agrestis
Anthoceros fusiformis
Folioceros fuciformis
Folioceros glandulosus
Leiosporoceros dussii
OUTGROUP
GLOMEROPHYTA
MUCOROMYCOTINA



Dendroceros tuberculatis: хлоропласт с пиреноидом



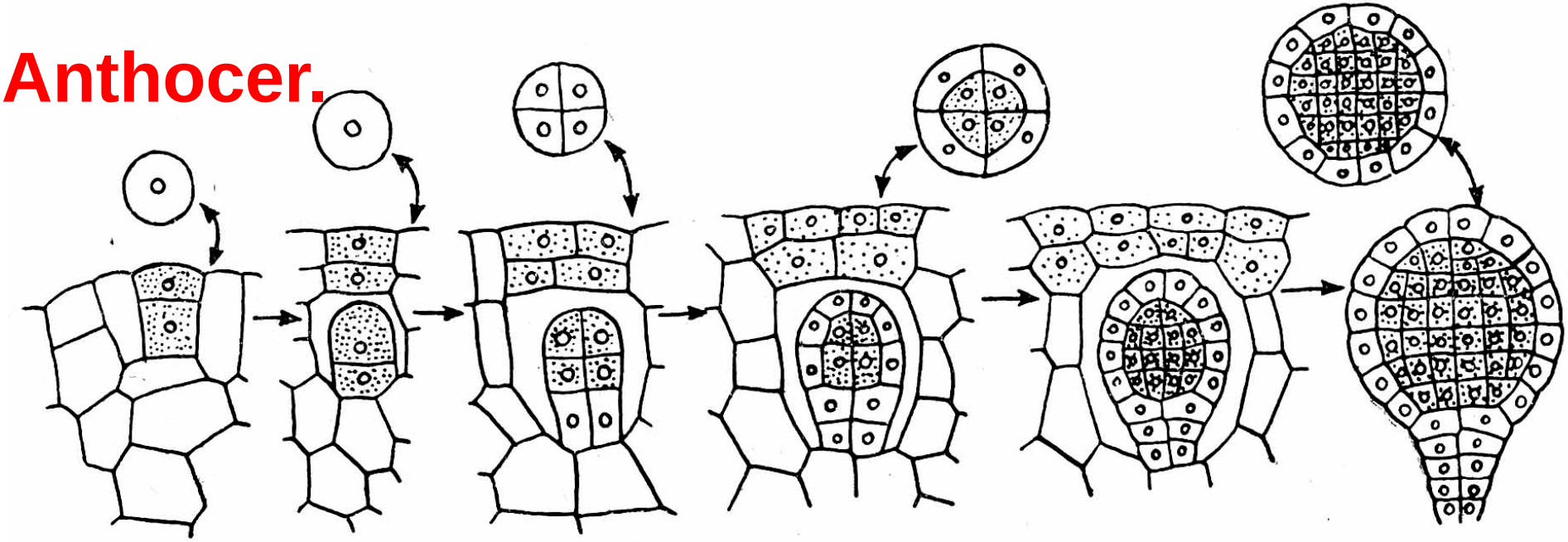
Jungermann.
Metzger.

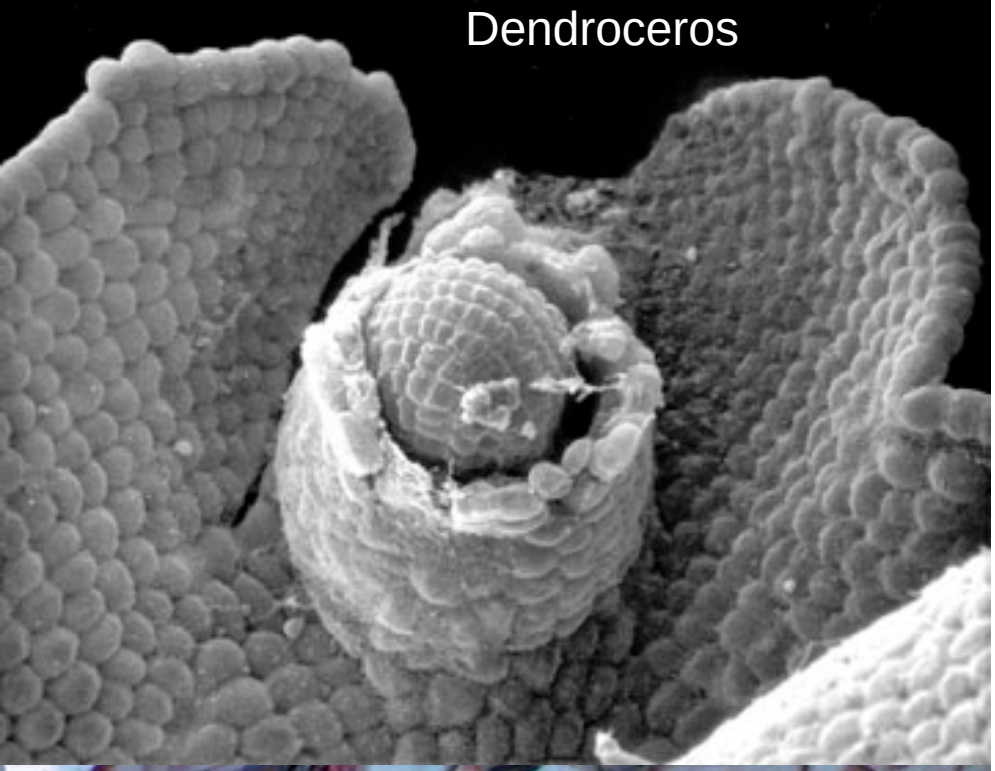


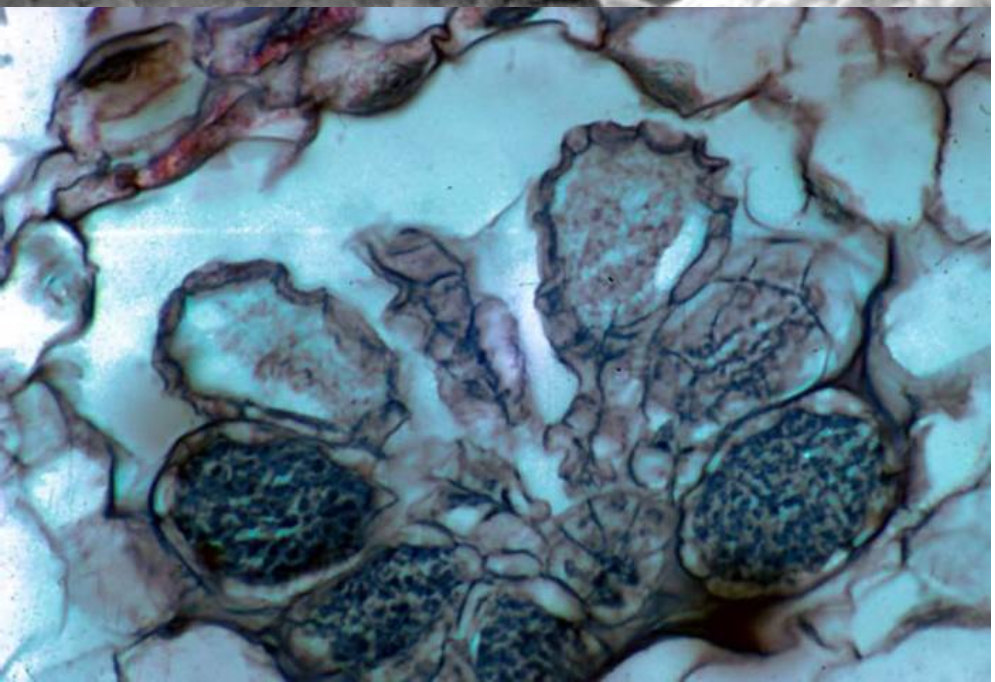
Marchant.

Развитие антеридиев

Anthocer.







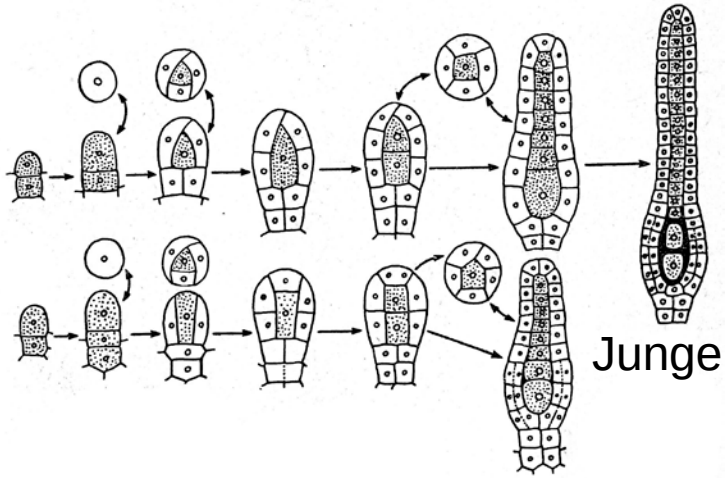
Антеридии

Anthoceros

Folioceros dixitianus
Индия, Западные Гаты

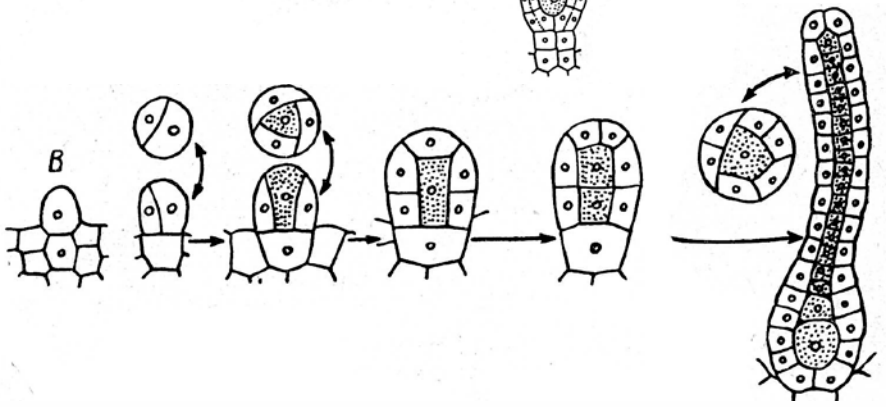

Folioceros dixitianus
Индия, Западные Гаты

Развитие архегониев



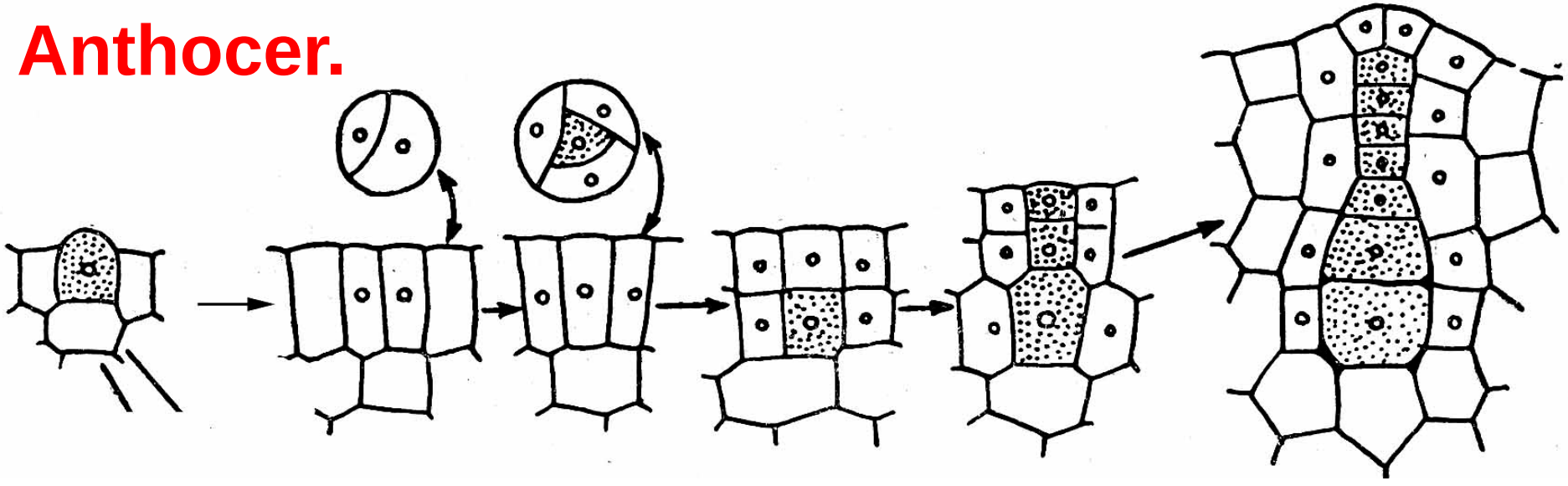
Haplomitr.

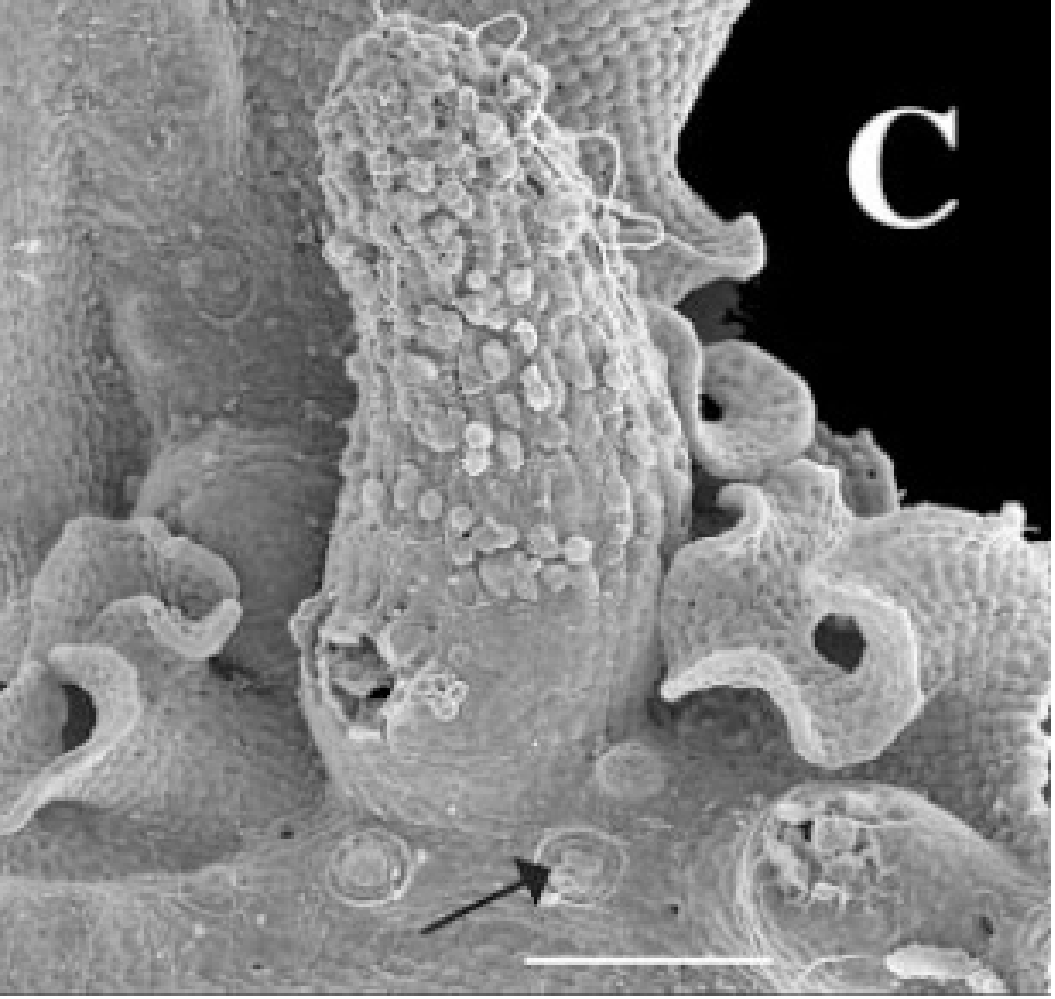
Jungermann.+Metzger.



Marchant.

Anthocer.

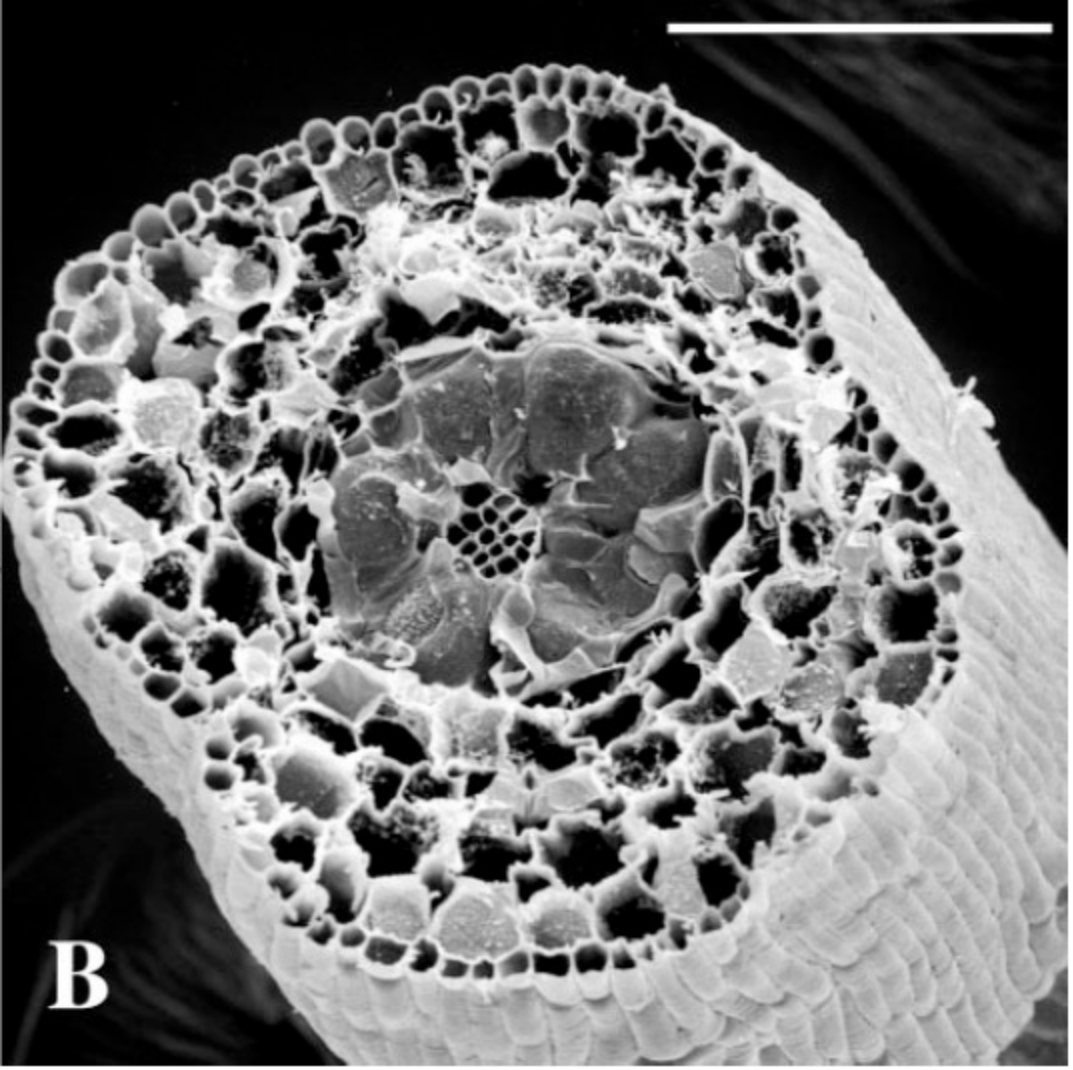




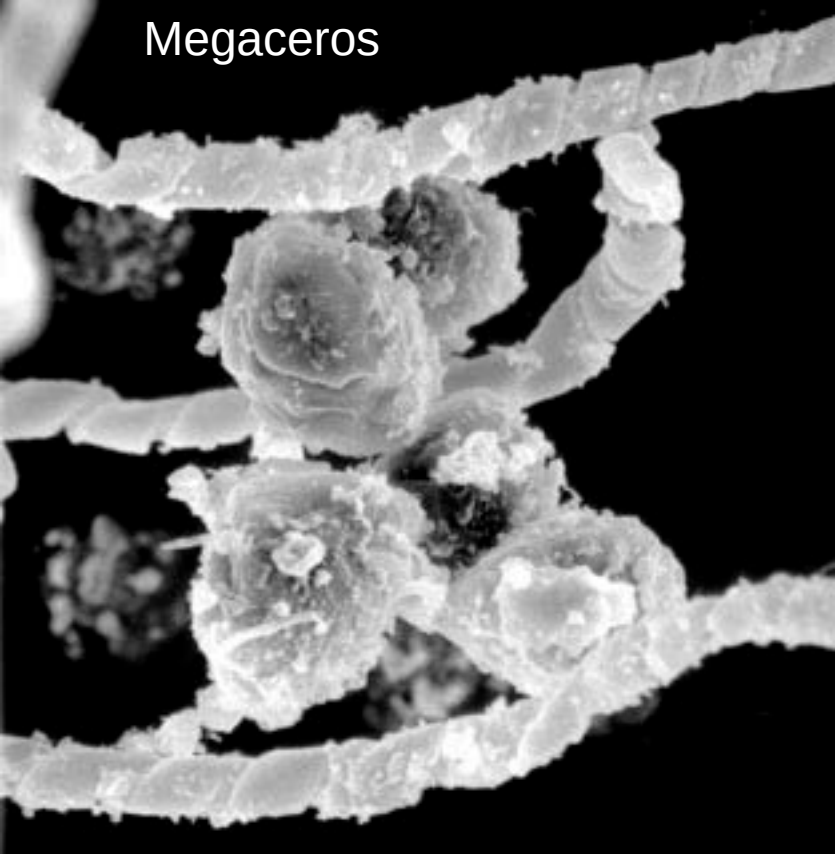
Dendroceros crispatus: группа **архегониев**, в одном из них – молодой спорогоний


Phaeoceros laevis,
ЗБС

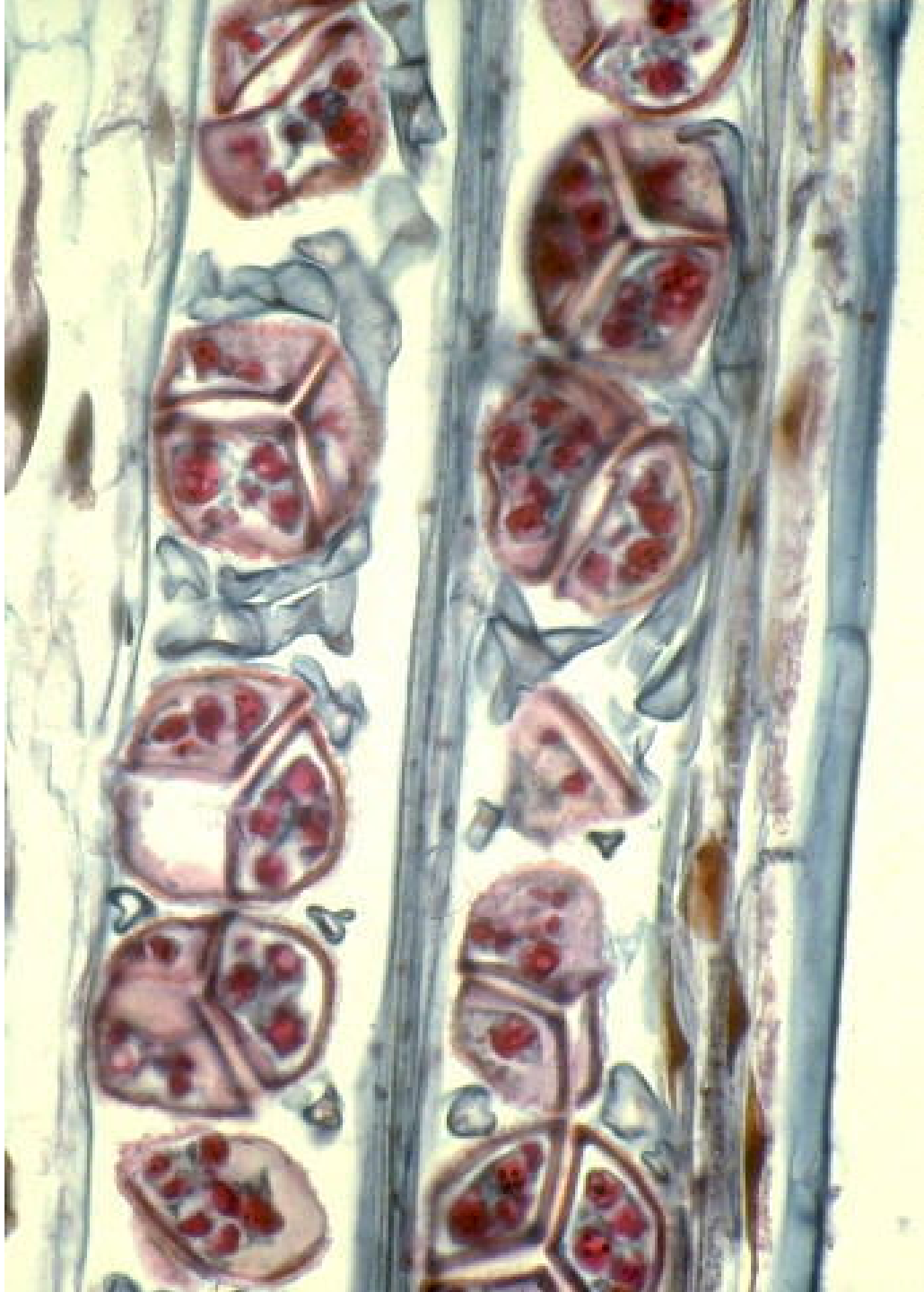

Phaeoceros,
ЗБС



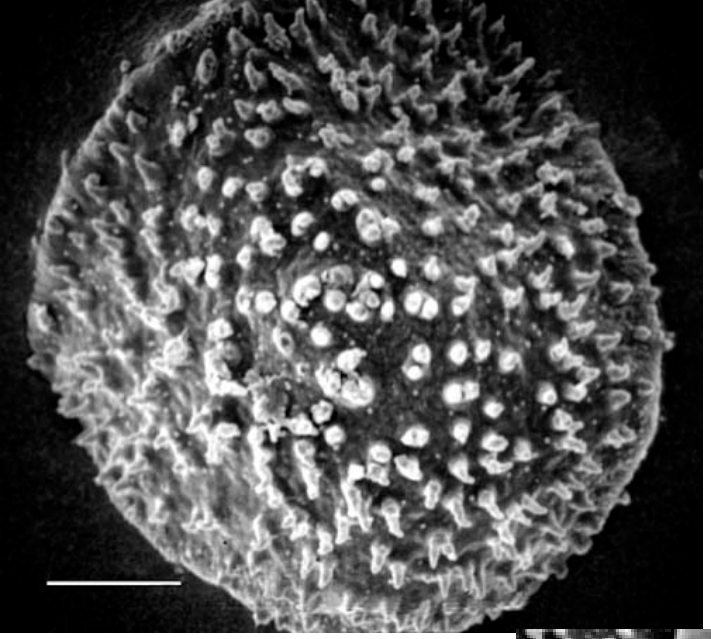
Phaeoceros carolinianus



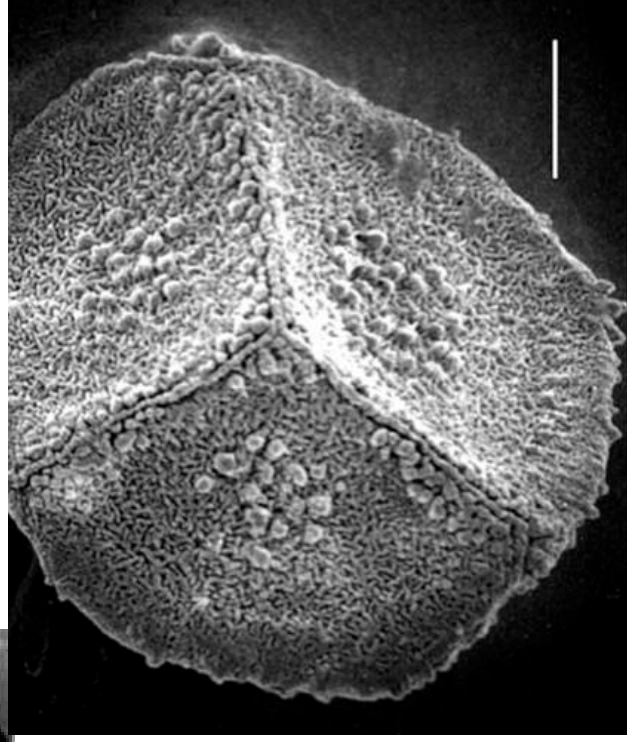
споры и
(псевдо)элатеры



Phaeoceros carolinianus

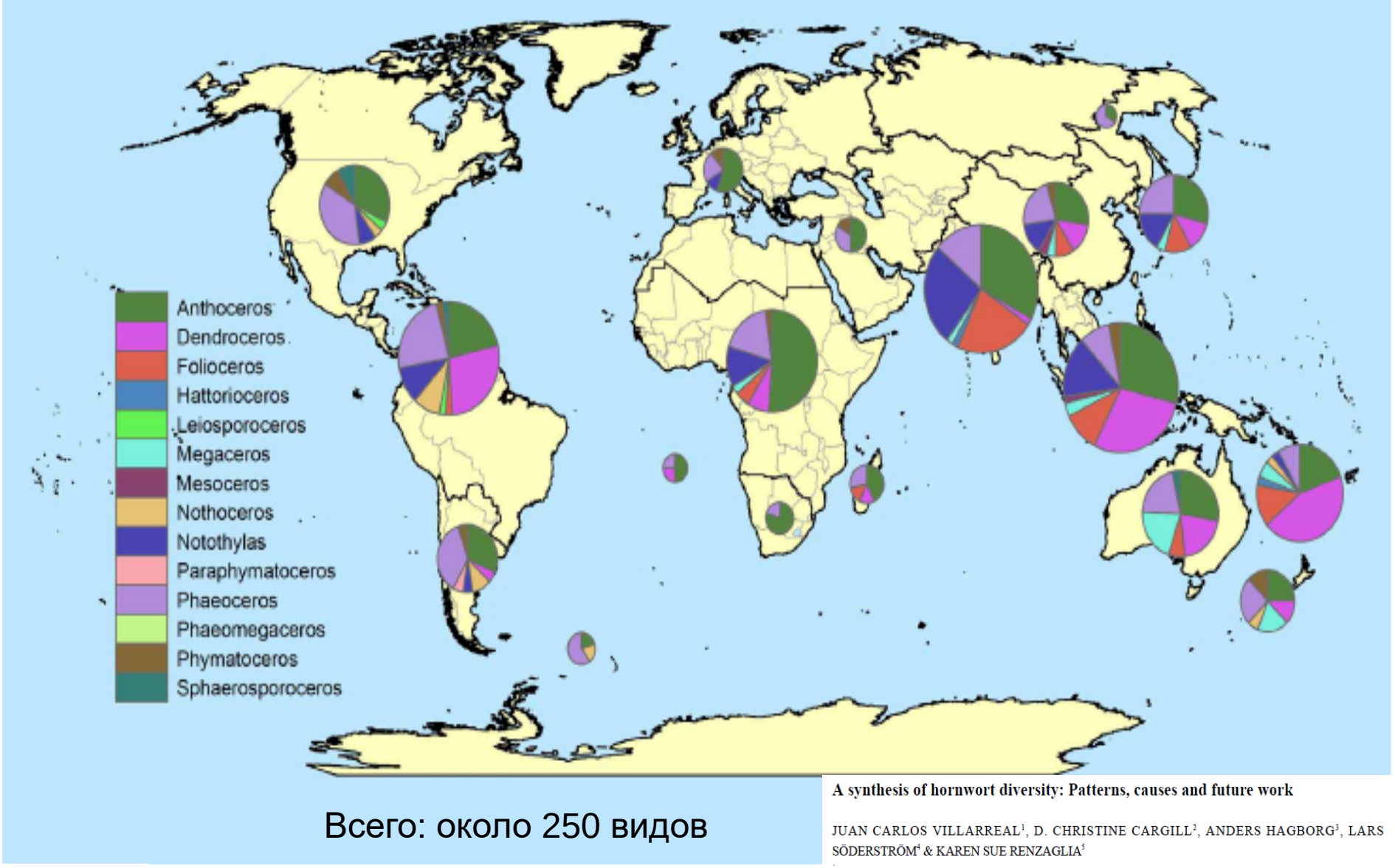


спора с дистальной стороны



спора с проксимальной стороны

тетрада спор

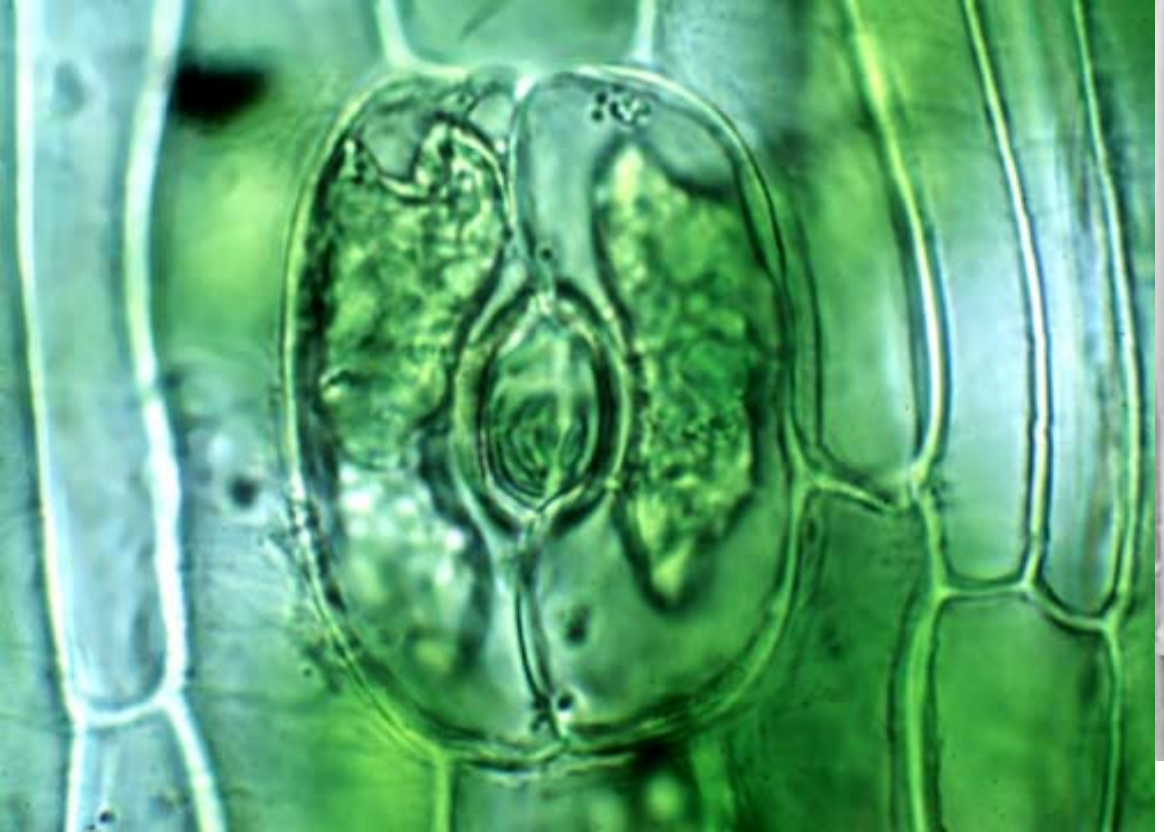


Всего: около 250 видов

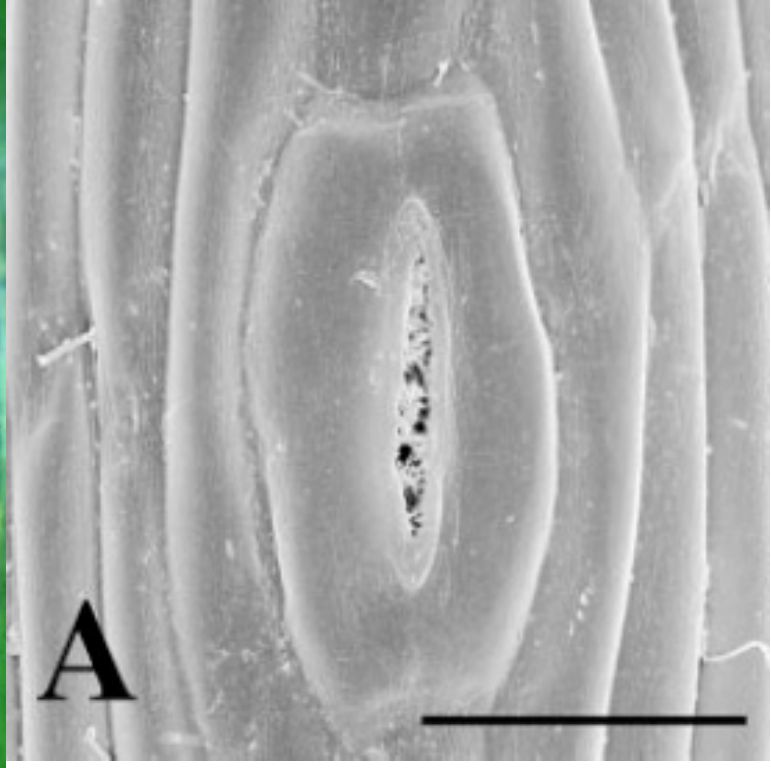
A synthesis of hornwort diversity: Patterns, causes and future work

JUAN CARLOS VILLARREAL[1], D. CHRISTINE CARGILL[2], ANDERS HAGBORG[3], LARS SÖDERSTRÖM[4] & KAREN SUE RENZAGLIA[5]

Proportion of hornwort species in the different genera across regions of the world. Size of the pie diagrams reflects the total number of species in that area (maximum 21 species).



Phaeoceros laevis



Phaeoceros carolinianus

устьице на стенке коробочки

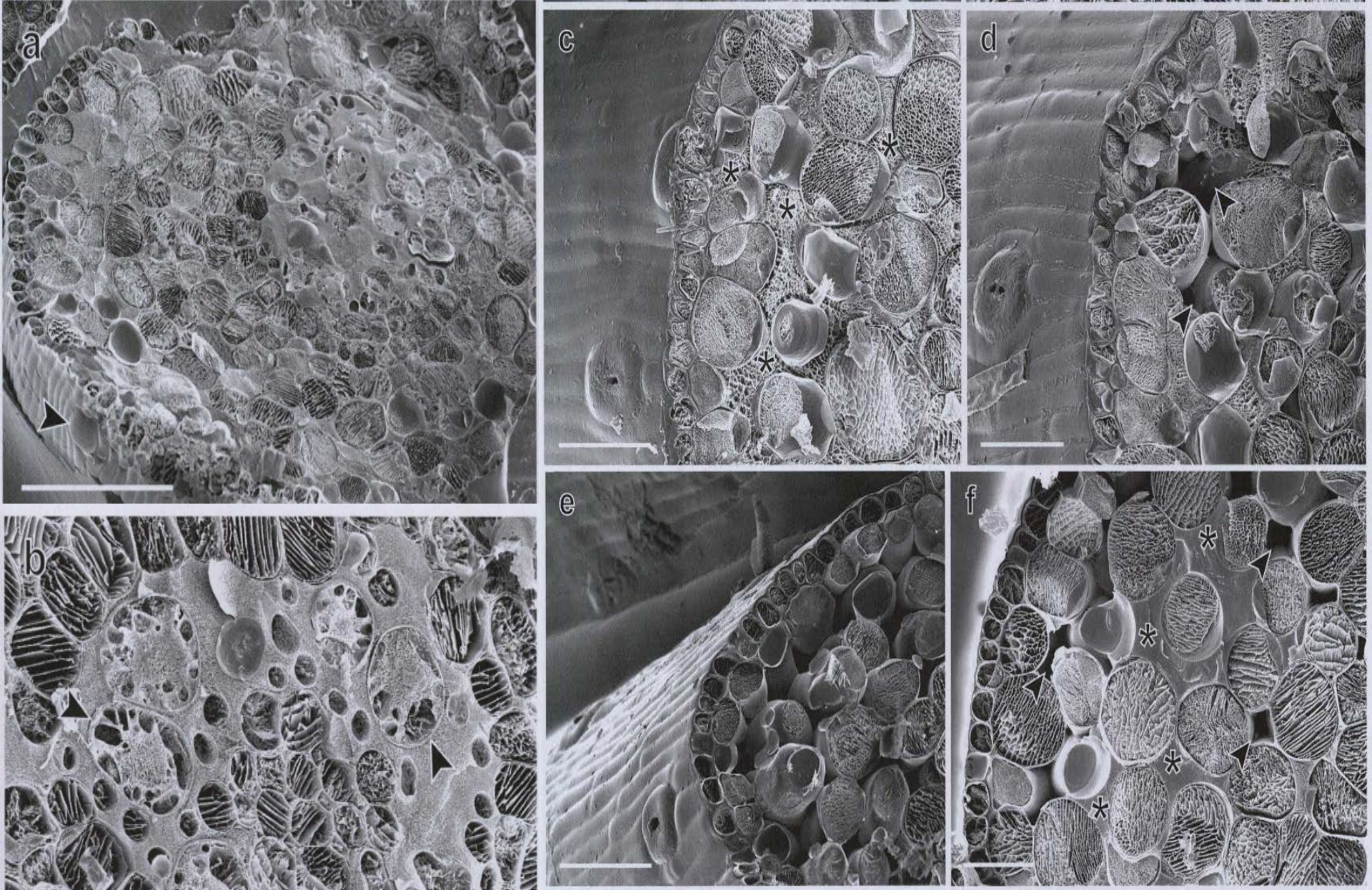
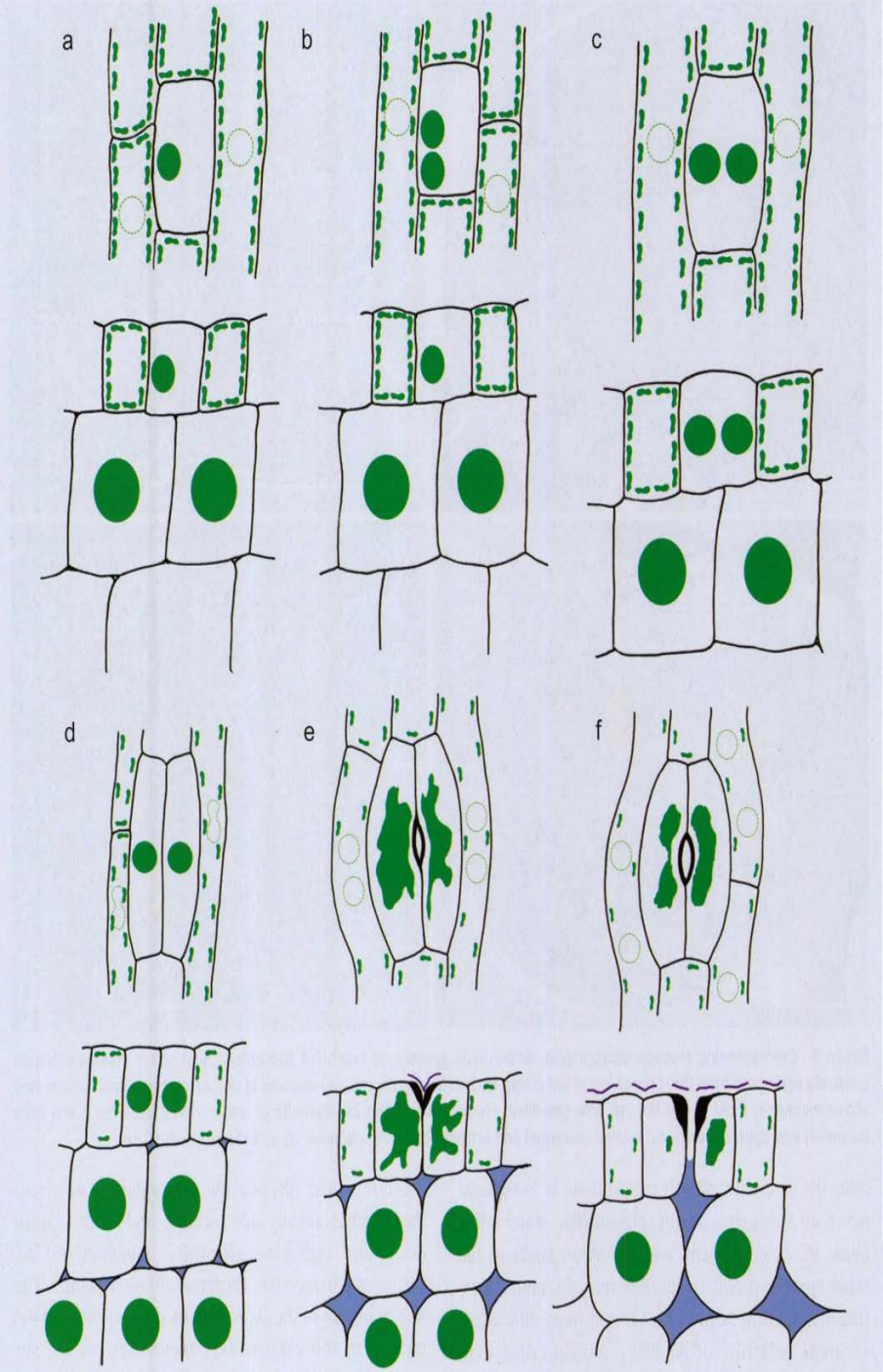


Figure 7 Cryo-scanning electron micrographs. *Anthoceros agrestis*. a) Fractured sporophyte, lower portion of – within involucre: all the intercellular spaces are liquid-filled. Stomata are unopened (arrowed) and spore mother cells (arrowed) (b) have yet to undergo meiotic division; c) young, open stoma; the subtending intercellular spaces are all filled with liquid (*). It is only after stomatal opening that the liquid in the ISs begins gradually to dry out (d–f) (arrows in d and f indicate gas-filled spaces). Scale bars: (a) 100 μm; (b–f) 50 μm.



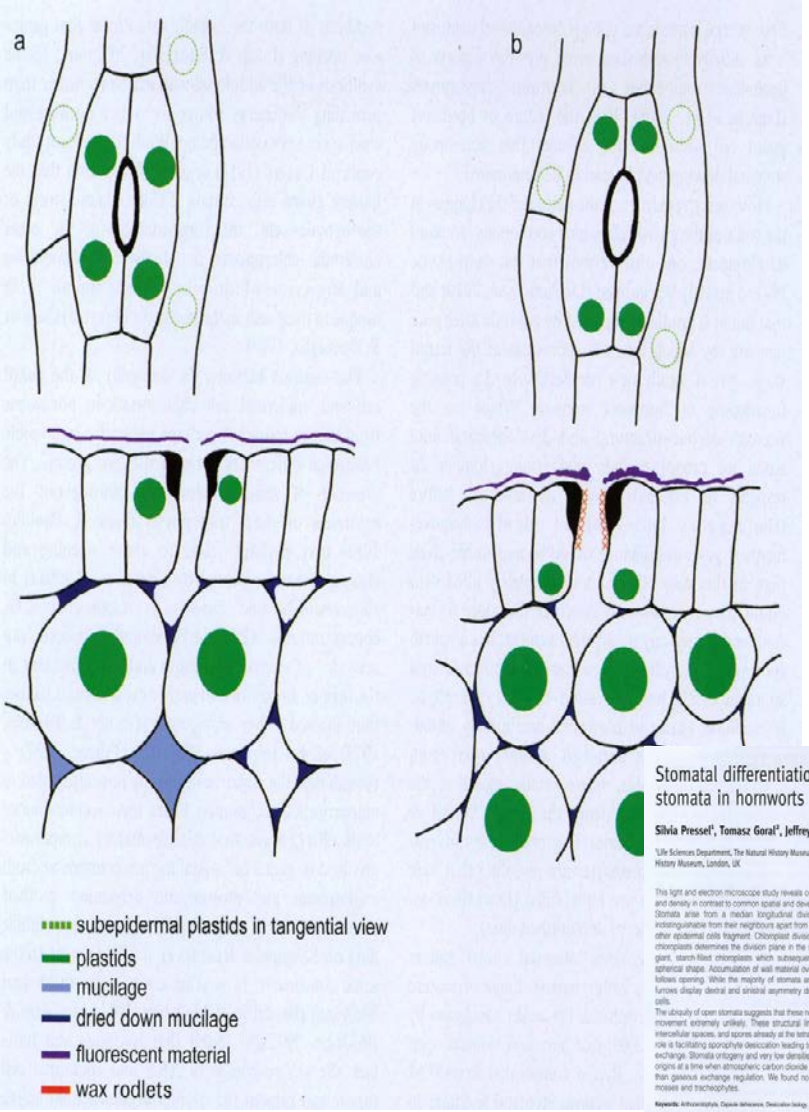


Figure 10 Schematic representation of stomatal ontogeny in hornworts; cont. from Fig. 9. a) Two spherical chloroplasts near the surface of each of the guard cells (Fig. 2g). The mucilage in the intercellular spaces below the epidermis has dried down to the cell corners but remains between the cells further inside the sporophytes (Fig. 7d, f); b) mature stoma with irregular deposits of fluorescent wall material covering the external surface (Figs. 5h, i; 6h, i); wax rodlets lining the pore (Fig. 6j) and chloroplasts lying along the inner walls of the guard cells (Fig. 2h–j). All the intercellular spaces are now gas-filled with dried-down mucilage along the cell junctions (Fig. 8a, c).

Figure 9 Schematic representation of stomatal ontogeny in hornworts; tangential views (top) and transverse sections (bottom). a) Nascent mother cells with a single spherical chloroplast (Fig. 1a); b) division of the mother cell chloroplast (Fig. 1 b–d); c) immediately before the longitudinal division of the mother cell the chloroplasts increase in size and migrate to lie side-by-side centrally (Fig. 1e); d) nascent stoma with each guard cell containing a single spherical chloroplast (Fig. 1f); the initial stage in aperture formation (Fig. 2a–c) coincides with division of the subepidermal chloroplasts and the almost complete disappearance of the fragmented epidermal cell chloroplasts. Huge pleiomorphic, starch-filled chloroplasts in the guard cells. Fluorescent additional wall material above the aperture (Fig. 5f, g). Mucilage-filled intercellular spaces (Fig. 7a, c); f) pore formation coinciding with division of the guard cell chloroplasts (Fig. 2d–f) and spread of fluorescent material over the external surface (Fig. 5h, i).

Stomatal differentiation and abnormal stomata in hornworts

Silvia Pressel[1], Tomasz Goral[2], Jeffrey G. Duckett[1]

[1]Life Sciences Department, The Natural History Museum, London, UK, [2]Imaging and Analysis Centre, The Natural History Museum, London, UK

This light and electron microscope study reveals considerable uniformity in hornwort stomata morphology and density in contrast to common spatial and developmental abnormalities in tracheophytes and mosses. Stomata arise from a median longitudinal division of sporophyte epidermal cells morphologically indistinguishable from their neighbours apart from the retention of a single chloroplast whilst those in the other epidermal cells fragment. Chloroplast division and side-by-side repositioning of the two daughter chloroplasts determines the division plane in the stomatal mother cell. The nascent guard cells contain giant, starch-filled chloroplasts which subsequently divide and, post aperture opening, regain their spherical shape. Accumulation of wall material over the guard cells and of wax rodlets lining the pores follows opening. While the majority of stomata are bilaterally symmetrical those lining the dehiscence furrows display dextral and sinistral asymmetry due to differential expansion of the adjacent epidermal cells.

The ubiquity of open stomata suggests that these never close with the maturational wall changes rendering movement extremely unlikely. These structural limitations, a liquid-filled stage in the ontogeny of the intercellular spaces, and spores already at the tetrad stage when stomata open, suggest that their primary role is facilitating sporophyte desiccation leading to dehiscence and spore dispersal rather than gaseous exchange. Stomata ontogeny and very low densities, like those in Devonian fossils, suggest either ancient origins at a time when atmospheric carbon dioxide levels were much greater than today or a function other than gaseous exchange regulation. We found no evidence for stomatal homology between hornworts, mosses and tracheophytes.

Keywords: Anthocerotophyta, Capsule dehiscence, Desiccation biology, Guard cells, Stomatal evolution

Introduction

Genetic and hormonal manipulation of stomatal density in flowering plants (Tal *et al.*, 1970; Martin & Stimart, 2003; Doheny-Adams *et al.*, 2012; Zhang *et al.*, 2012), together with investigations into the effects of carbon dioxide concentrations (McElwain & Chaloner, 1995; Woodward & Kelly, 1995; Beerling, 2007; Konrad *et al.*, 2008), sits at the forefront of current research on yield improvement and climate change. Alongside these experimental studies a wide variety of stomatal defects, affecting both guard cell and subsidiary cell morphology and vitality, have been reported from numerous vascular plants (Dehne, 1981; Takahashi, 1982; Inamdar & Patil, 1969; Inamdar *et al.*, 1969; Gopal & Shah, 1970; Inamdar *et al.*, 1970; Inamdar & Patil, 1976).

In contrast, there has never been a thorough investigation of stomatal abnormalities in bryophytes. Kashyap (1922) described several aborative structures and suggested links between bryophyte stomata and those in pteridophytes. Haberlandt (1886) and Paton (1957) reported the regular occurrence of stomata with 3 or 4 guard cells, which they regarded as 'freaks', in several groups of mosses. Paton and Pearce (Paton, 1957; Paton & Pearce, 1957) also recorded the occasional occurrence in mosses of two adjacent stomata at variance with the one cell spacing rule (Rudall *et al.*, 2013).

In hornworts, Campbell (1895) described the stomata as arising from epidermal cells that cease to elongate, become oval in shape and then divide longitudinally into two guard cells whose median walls subsequently split to form the pores. Whereas in many mosses the cells surrounding stomata can be distinguished from other epidermal cells by their radial arrangement (Paton, 1957), indicating that ontogeny depends on patterns of cell divisions extending beyond the guard cells, recalling many similar situations in angiosperms (Evert, 2006), in hornworts only a single epidermal cell is involved and the adjacent epidermal cells are unaffected.

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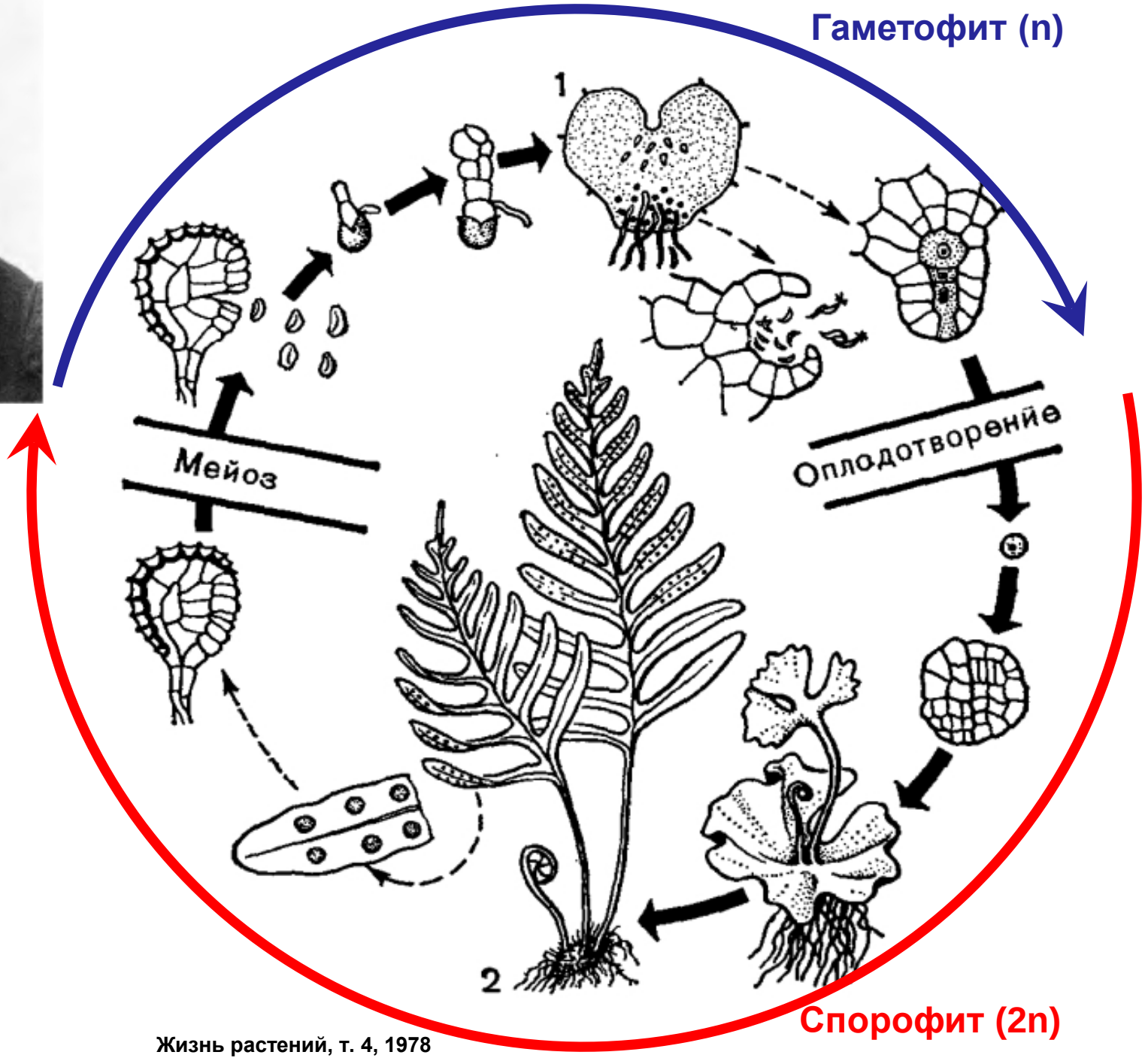
Wilhelm Hofmeister (1824-1877)

профессор Гейдельбергского и Тюбингенского университетов, начинал, идя по стопам отца, с того, что торговал музыкальными инструментами



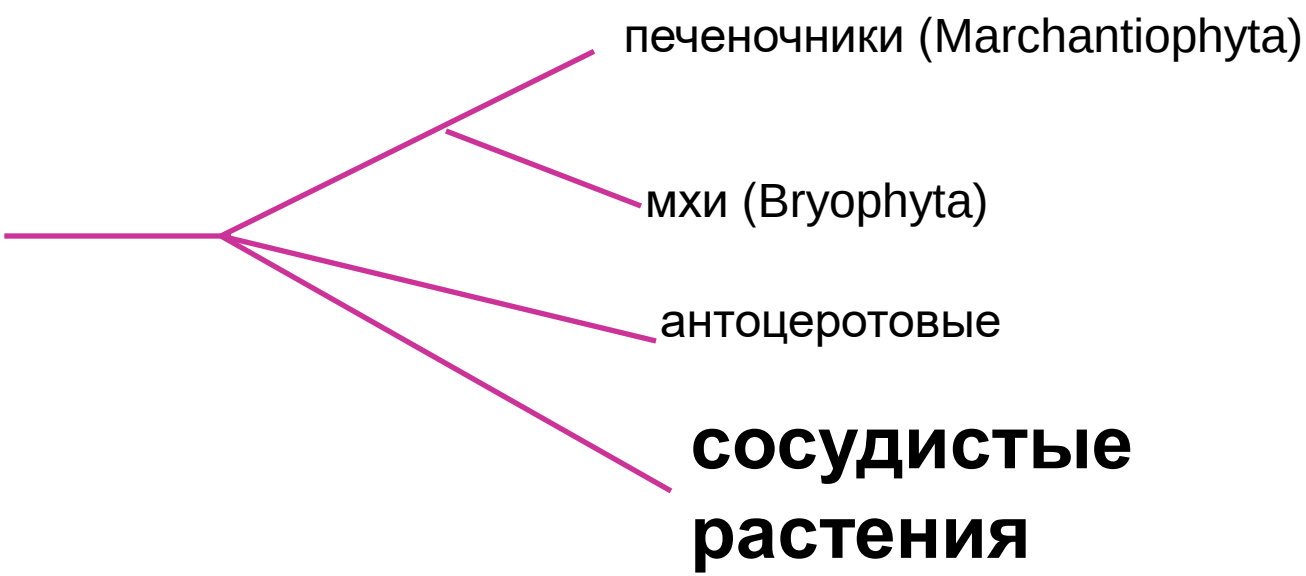
Жизнь растений, т. 4, 1978

Возможные родственные связи сосудистых растений

Сосудистые растения (Tracheophyta)

- преобладание спорофита в жизненном цикле
- обычно сложная гистологическая и морфологическая дифференциация спорофита, у современных форм обычно есть побеги и корни
- прочная кутикула; способность к синтезу суберина и лигнина (склереиды, волокна, *трахеальные элементы*).
- гаметофиты на теломном или талломном уровне организации
- архегонии погружены брюшком в ткань гаметофита (у продвинутых форм их нет)
- сперматозоиды исходно многожгутиковые (редко вторично 2-жгутиковые)
- за редкими исключениями, гомойогидрические растения

Возможные родственные связи сосудистых растений

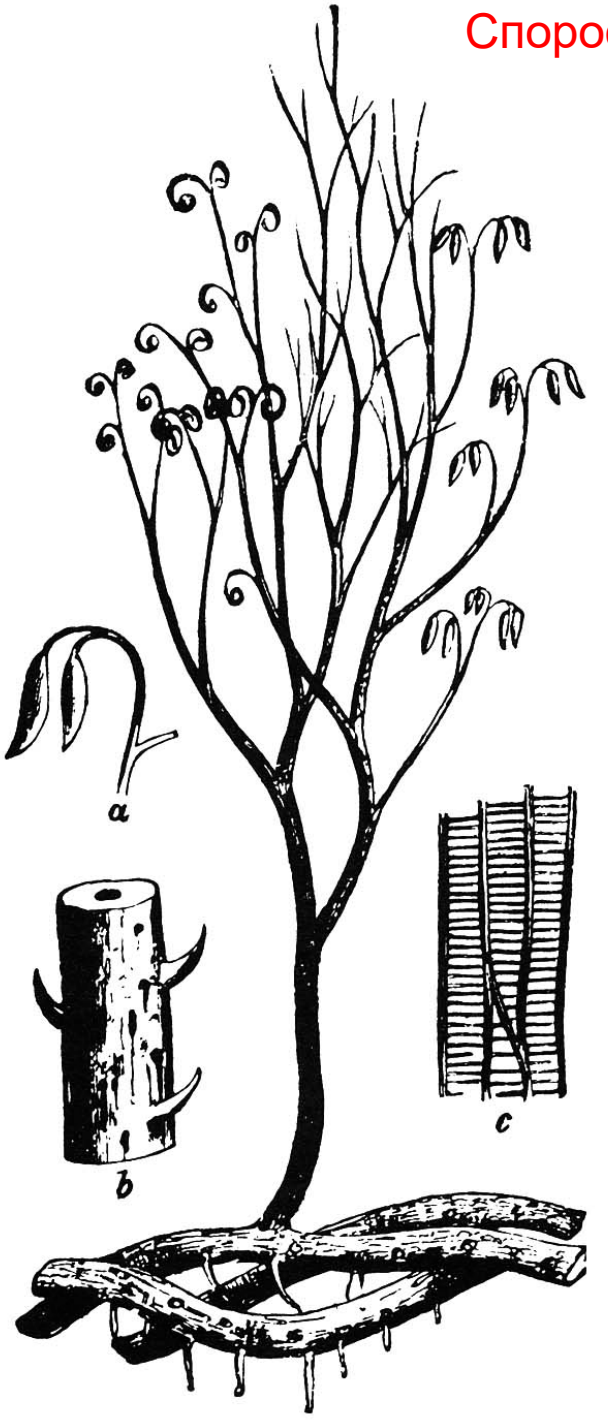


Сосудистые растения (Tracheophyta)

- преобладание спорофита в жизненном цикле
- обычно сложная гистологическая и морфологическая дифференциация спорофита, у современных форм обычно есть побеги и корни
- прочная кутикула; способность к синтезу суберина и лигнина (склереиды, волокна, *трахеальные элементы*).
- гаметофиты на теломном или талломном уровне организации
- архегонии погружены брюшком в ткань гаметофита (у продвинутых форм их нет)
- сперматозоиды исходно многожгутиковые (редко вторично 2-жгутиковые)
- за редкими исключениями, гомойогидрические растения

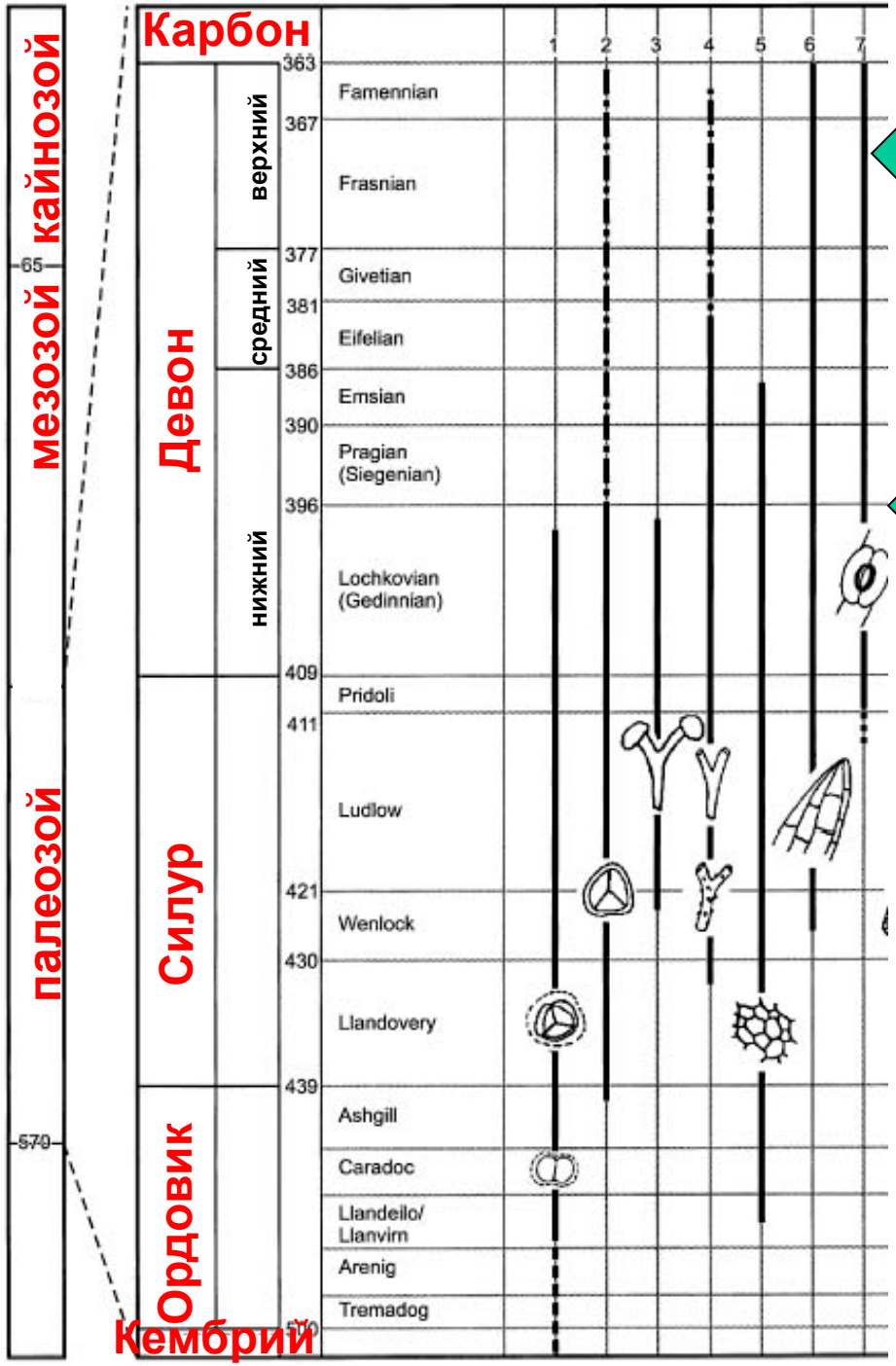
Sir John William Dawson
(1820-1899)
1859 - впервые описал древнейшие ископаемые растения, в том числе *Psilophyton princeps*
из отложений
Gaspe Bay,
Quebeck, Canada
Был креационистом, критиковал Дарвина с религиозных позиций

Спорофит!!!



«правильный»
Psilophyton dawsonii

из Kenrick, Crane (1997)

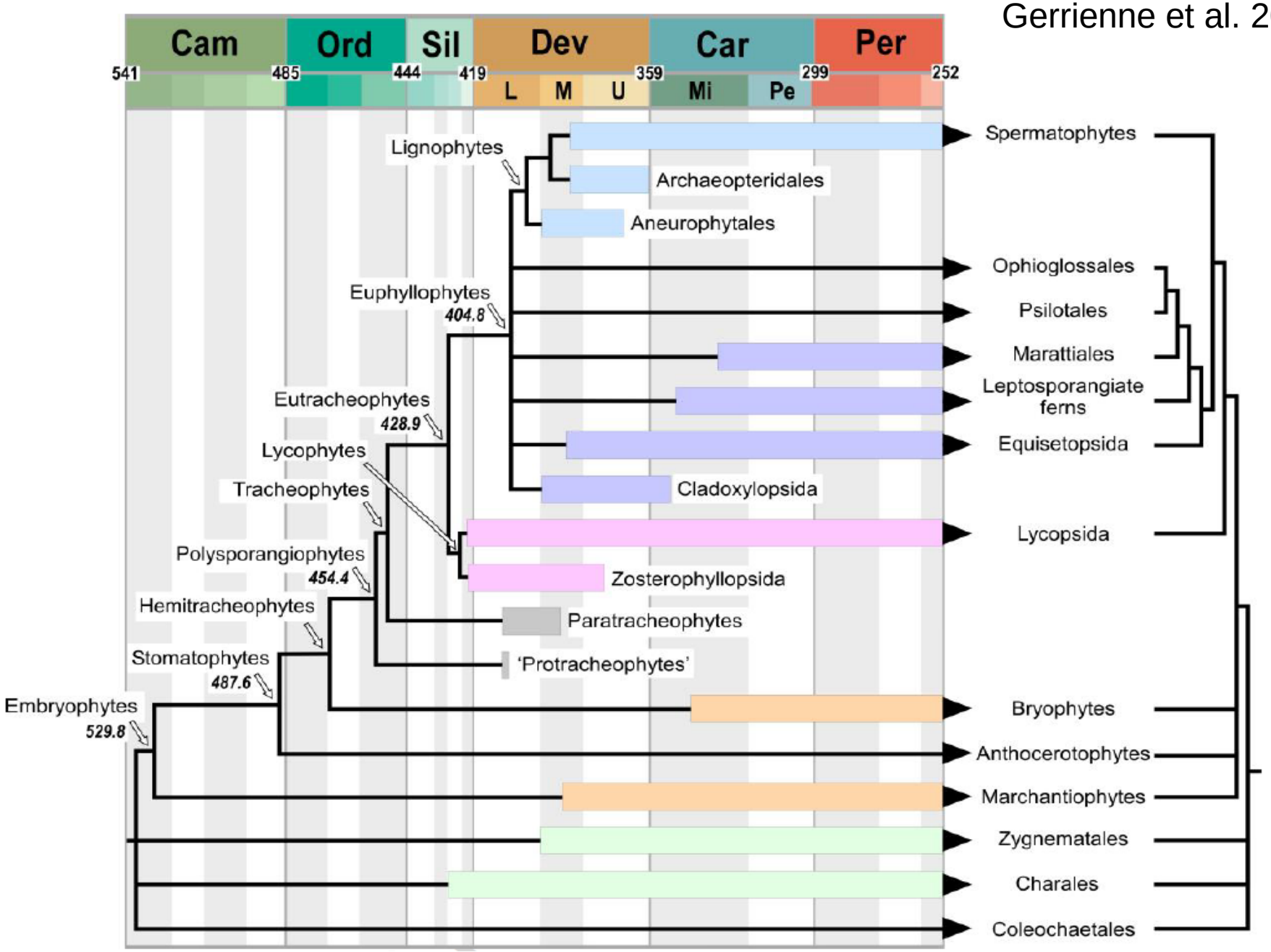


Традиционные представления о первых достоверных находках мохообразных.

Rhynie chert

(древнейшие сосудистые растения с полностью восстановленным жизненным циклом)

Gerrienne et al. 2016



Морфология

ДНК

Oldest known mosses discovered in Mississippian (late Visean) strata of Germany

Maren Hübers and Hans Kerp
Forschungsstelle für Paläobotanik, Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität Münster, Schlossplatz 9, 48143 Münster, Germany

ABSTRACT

The pre-Permian record of bryophytes is restricted to a very limited number of liverwort occurrences in Middle and Late Devonian and in Pennsylvanian strata, and a putative liverwort from the Middle Ordovician. The paucity of bryophytes, notably the apparent absence of mosses in the Carboniferous, is striking because this time interval is marked by the occurrence of extensive wetland environments that likely provided ideal habitats. We report three types of mosses from the Mississippian of eastern Germany that are the oldest unequivocal mosses known to date. Although the material is fragmentary, these finds show that mosses formed part of Carboniferous ecosystems. The moss remains were obtained by bulk maceration, a method that is not commonly used for studying Carboniferous floras. We anticipate that applying this method on material from other Carboniferous localities will show that mosses were more widespread in the late Paleozoic than previously thought.

GEOLOGICAL SETTING, AGE, AND METHODS

The mosses described here were collected from a roadcut of the A4 motorway near Chemnitz-Glösa, Saxony, Germany (50°52′34.67″N; 12°54′38.73″E), where an 80-m-thick succession of Mississippian sandstones, shales, and occasional coaly layers of the upper part of the Ortelsdorf Formation (Hainichen Subgroup, Hainichen Basin) is exposed (Schneider et al., 2005). The small Hainichen Basin (Fig. 1) is filled with alluvial plain, alluvial fan, and fan

Несомненные сосудистые растения известны из силура и массово встречаются в девоне.

Лишь очень немногочисленные печеночники известны из девона, а мхи вообще достоверно не обнаружены древнее карбона.

GEOLOGY, August 2012; v. 40; no. 8; p. 755–758;

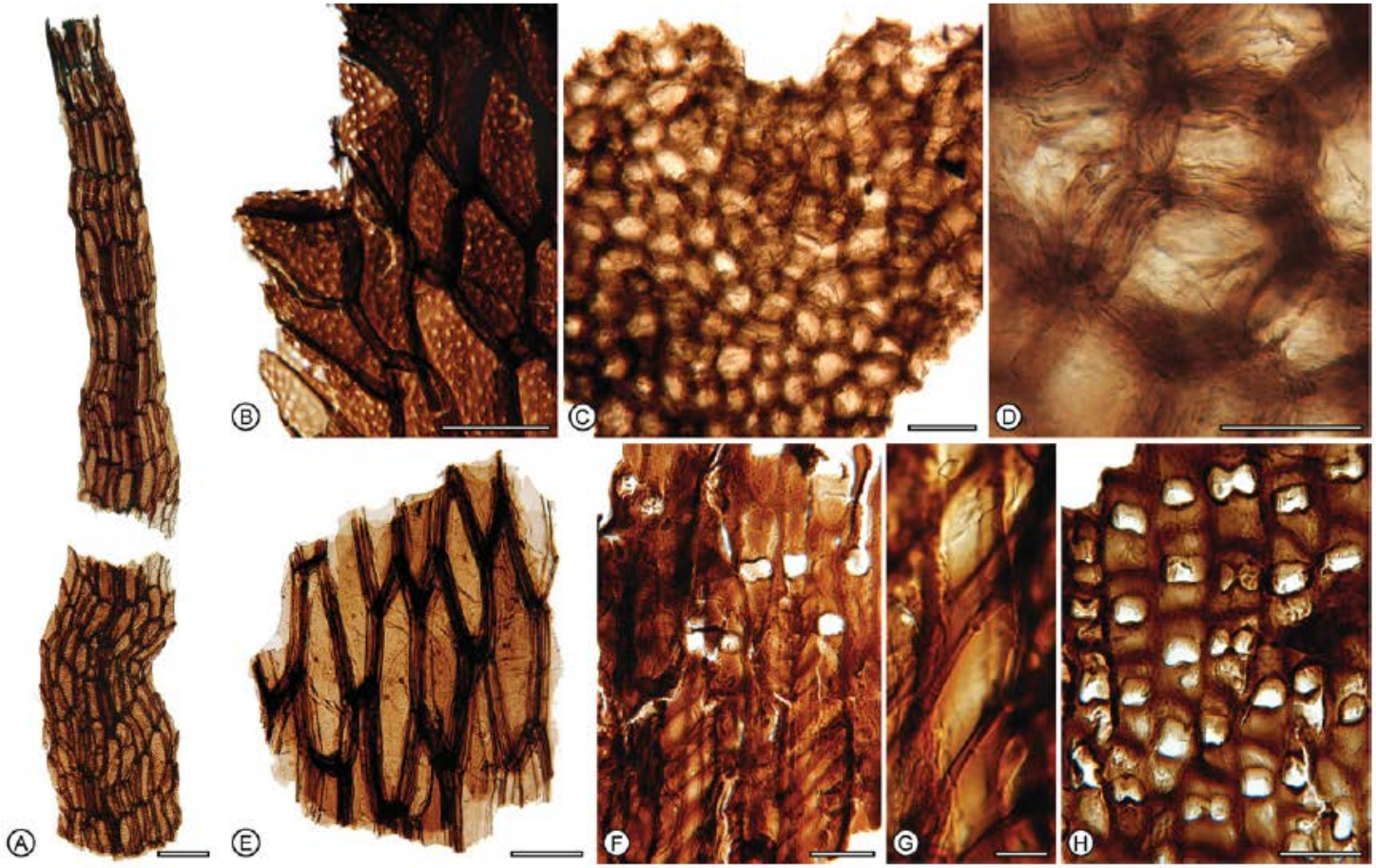
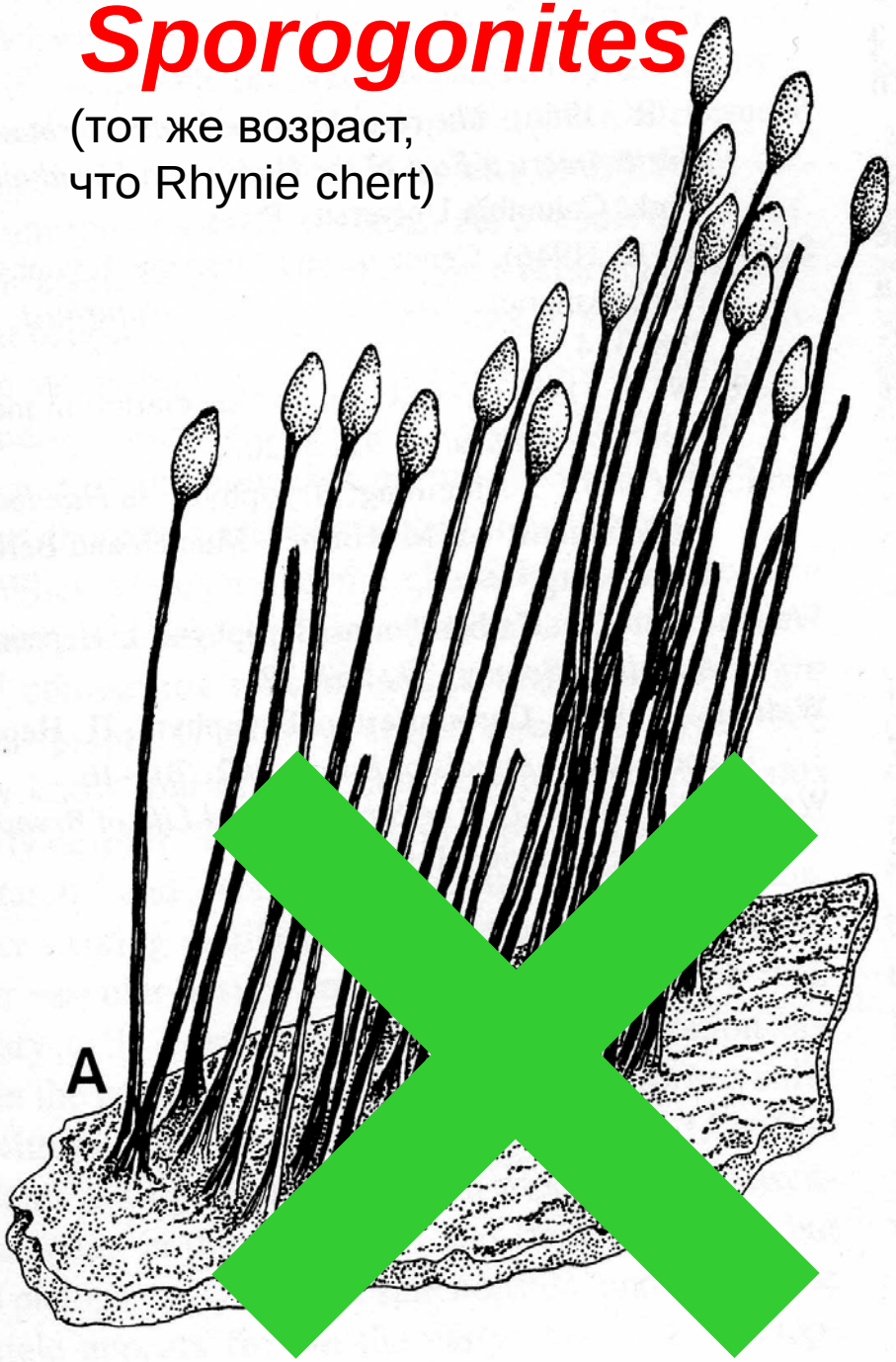


Figure 3. Mosses from Visean of Glösa. A: Type I. Almost complete leaf (KS27–074); scale bar = 100 µm. B: Type I fragment (KS27–031); scale bar = 50 µm. C: Type II. Overview showing network formed by darker cells and fenestrae with lighter colored cells (KSgrPr-068); scale bar = 100 µm. D: Detail of C showing elongate cells forming network; scale bar = 50 µm. E: Type II. Bistratose fragment with more elongate cells (KS11–090); scale bar = 100 µm. F: Type III. Elongate cells with pores and fibrils (KS11–029); scale bar = 30 µm. G: Type III. Detail of F (fibrils), scale bar = 10 µm. H: Type III. Another form with short cells with pores (KS27–048); scale bar = 50 µm.

Sporogonites

(тот же возраст,
что Rhynie chert)



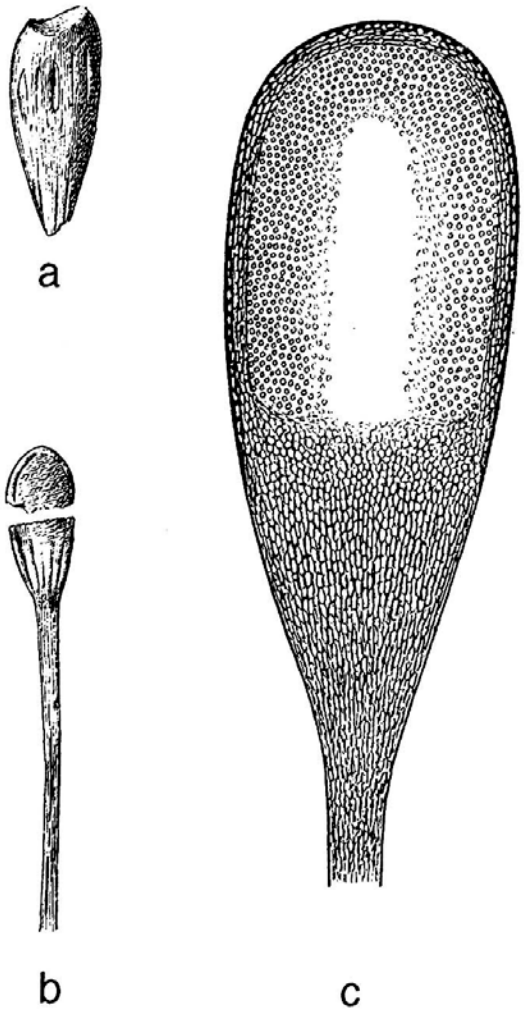


FIGURE 4.18. *Sporogonites exuberans*. Drawings reproduced from Halle 1936a (Figure 1), with permission. (**a**) Sporangium (capsule) fragment showing five short vertical slits (dehiscence features?) on the outer surface (×2). (**b**) Sporangium terminal on slender axis (×2). (**c**) Partial reconstruction of sporangium showing parts of interior and exterior (×7). Spore sac surrounds a central sterile region (columella?).

споры древнейших известных ископаемых высших растений

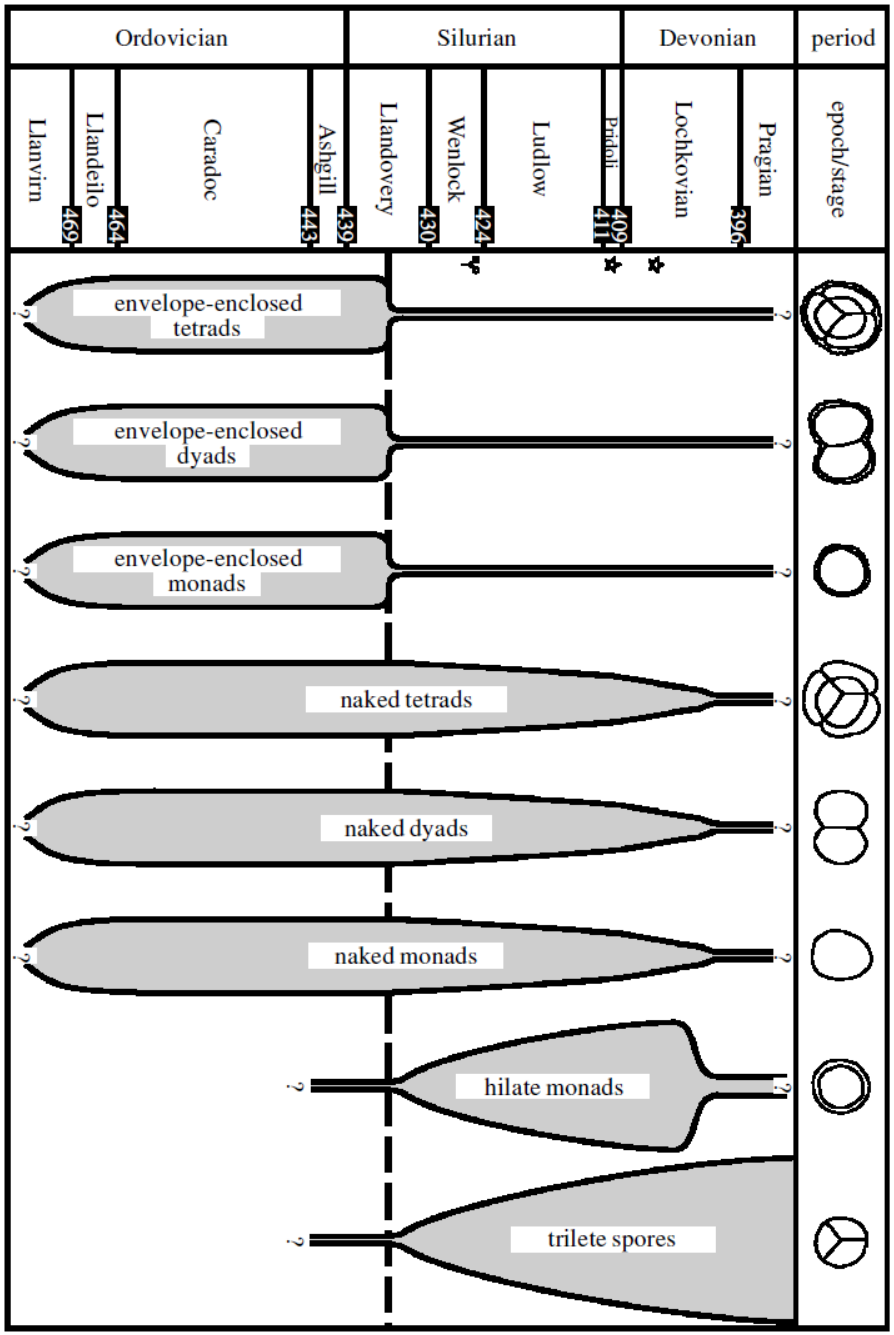


Figure 1. Stratigraphical range chart for early land plant spore morphotypes. Time-scale from Harland *et al.* (1989). Regarding annotation adjacent to the stratigraphic column: the small '*Cooksonia*' indicates the age of the earliest unequivocal land plant megafossils, the asterisks indicate the age of important plant mesofossil assemblages (i.e. Ludford Lane-Pridoli; North Brown Clee Hill-Lochkovian). The dashed time-line indicates the position of the major change in the nature of dispersed spore assemblages in the Llandovery. The width of range bars provides a very basic indication of relative abundance to illustrate gross changes in abundance through time. Note that range bar width has no quantitative implications. The taper and question marks at the base of range bars extending into the Llanvirn indicate the age of the earliest known spore assemblages and do not necessarily coincide with their first appearance, nor necessarily with changes in abundance.

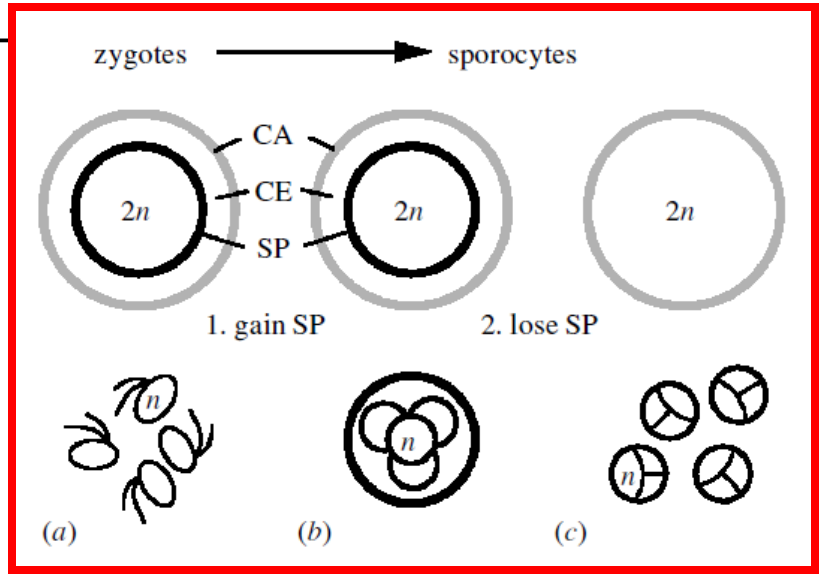
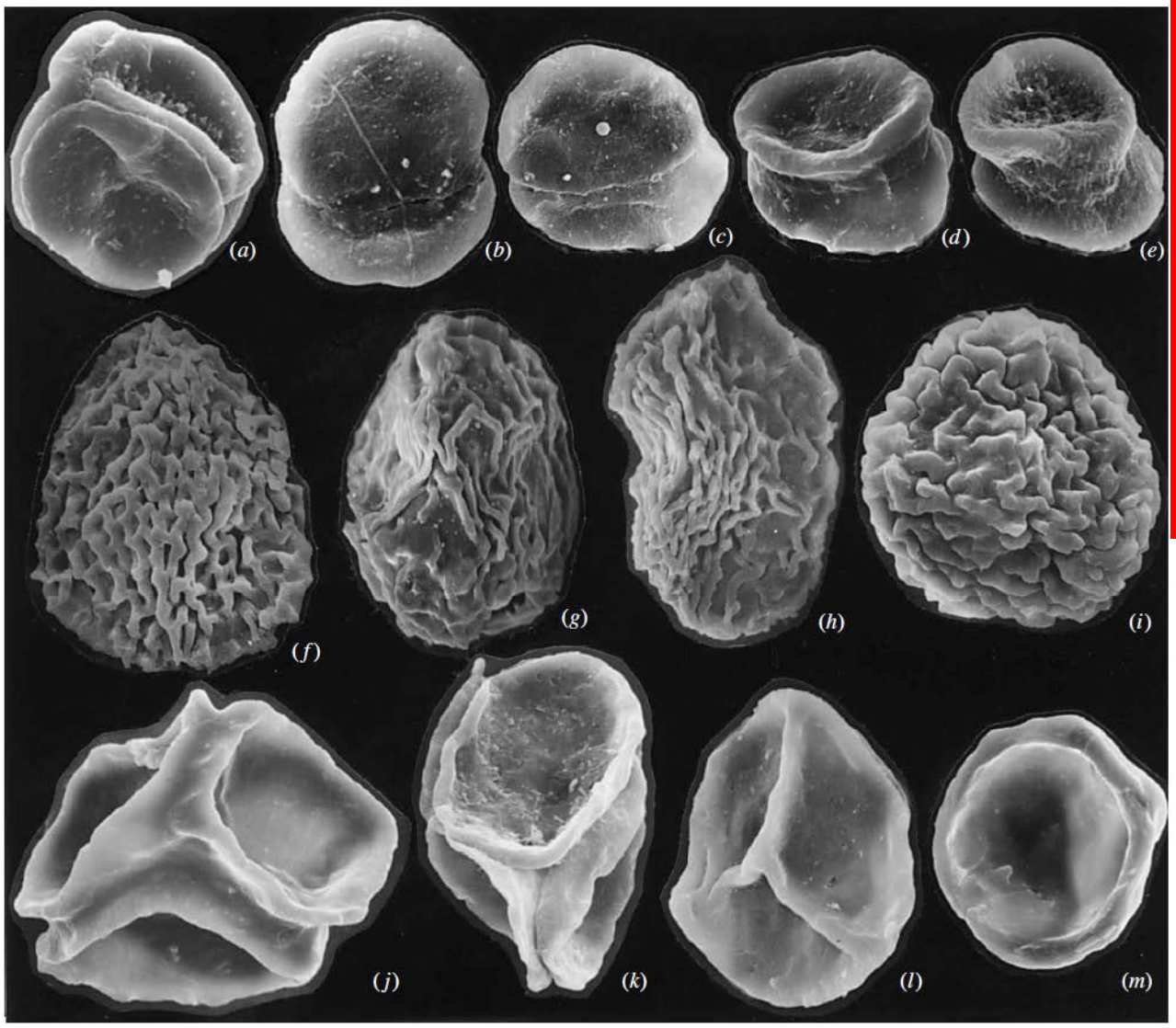


Figure 6. Hypothetical transformations involved in the origin of walled, non-flagellate spores, as they occur in modern embryophytes by gain of sporopollenin (SP) in spore walls (1), then loss of sporopollenin from sporocyte walls (2). (*a*) The extant charophycean *Coleochaete* produces zygotes having callosic (CA), cellulosic (CE) and SP layers, within which develop flagellate, non-walled meiospores. (*b*) A hypothetical intermediate stage in which diploid sporocytes (that are homologous to charophycean zygotes) have resistant walls, and produce walled, non-flagellate meiospores. Persistence of the resistant sporocyte wall forms an envelope around meiospore tetrads, preventing their dissociation. (*c*) Sporopollenin-walled, dissociated meiospores as they occur in most embryophytes.



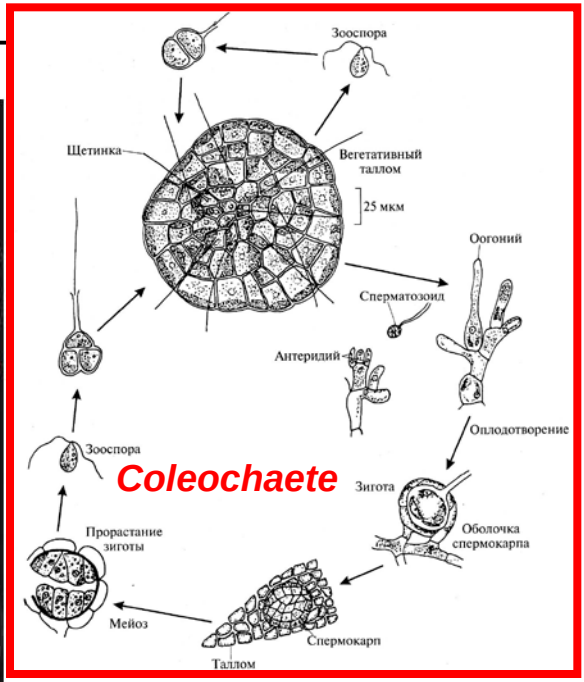


Figure 3. SEM images of dispersed early land plant spores. (*a–i*) From the type area for the Caradoc, Shropshire, England (Caradoc, Late Ordovician) (Wellman 1996); (*j–m*) from the Silurian inliers along the southern margin of the Midland Valley of Scotland (early Wenlock, Late Silurian) (Wellman & Richardson 1993). (*a*) Naked, unfused, permanent tetrad (× 2000); (*b*,*c*) naked, unfused, permanent dyad (× 1500); (*d*,*e*) naked, fused, permanent dyad (× 1500); (*f–h*) envelope-enclosed permanent ?dyad (× 1500); (*i*) envelope-enclosed permanent ?monad (× 1500); (*j*) naked, fused, permanent tetrad (× 1210); (*k*) loose tetrad (× 1070); (*l*) laevigate trilete spore (× 1380); (*m*) laevigate hilate monad (× 1230).

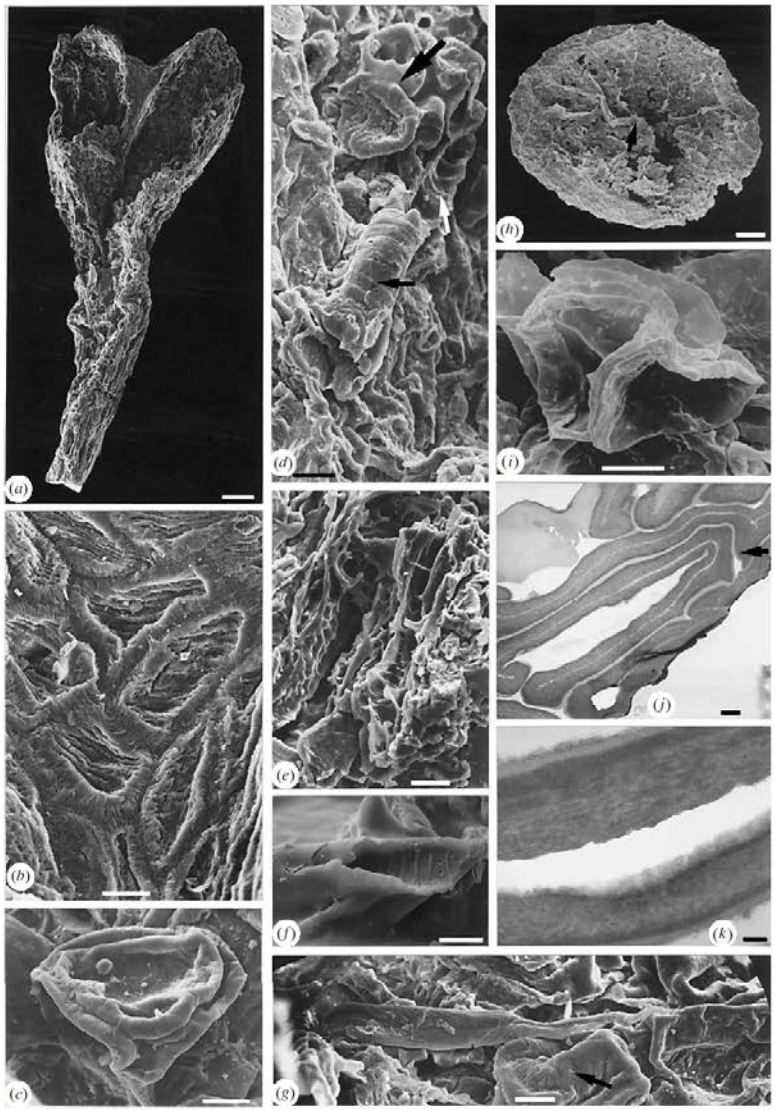


Figure 2. (*a–k*) North Brown Clee Hill specimens, Shropshire. Lochkovian, Lower Devonian. (*a–e,g*) SEMs: *Grisellatheca salopensis*. NMW94.76G.1. (*a*) Entire specimen with bifurcating terminal region. Scale bar = 100 µm. (*b*) Surface at bifurcation. Scale bar = 10 µm. (*c*) *In situ* tetrad with laevigate surface; *?Cheilotetras*. Scale bar = 10 µm. (*d*) 'Banded' tube in fertile region (small arrows) and remains of spore tetrad (large arrow). Scale bar = 10 µm. (*e*) Longitudinal elements with irregular thickenings from centre of axis. Scale bar = 10 µm. (*g*) Possible elater. Arrow indicates spore tetrad. Scale bar = 10 µm. (*f*) 'Banded' tube attached by amorphous material to surface of a *Tortilicaulis* sporangium. NMW96.5G.9. Scale bar = 10 µm. (*h–k*) ?Cuticle enclosed flattened spore mass. NMW98.23G.3. (*h*) SEM: intact specimen. Arrow indicates possible attachment site. Scale bar = 100 µm. (*i*) SEM: isolated tetrad. Scale bar = 5 µm. (*j,k*) TEMs. (*j*) Part of a tetrad. Arrow indicates possible apertural fold. Note sections through sporangial covering (top left) are of same optical density as outer layer surrounding each spore. Scale bar = 500 nm. (*k*) Trilayered exospore. Lightest layer to outside. Scale bar = 100 nm.

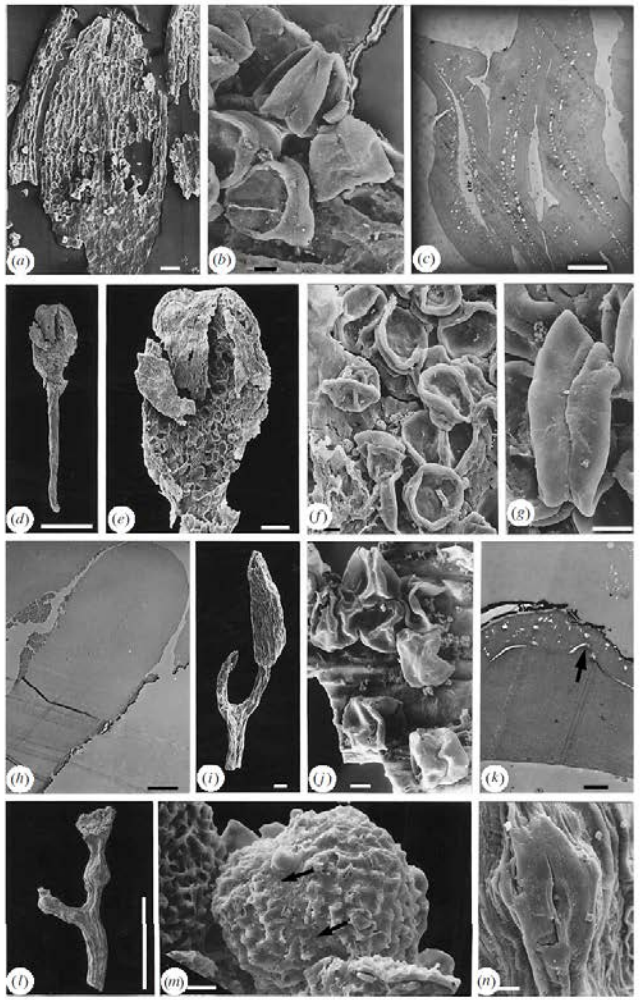


Figure 4. *In situ* permanent dyads. All North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian. (*a–c*) Sporangial cuticle with adhering laevigate dyads. NMW97.42G.1. (*a*) SEM: central cuticle probably representing one complete valve. Scale bar = 100 µm. (*b*) SEM: cluster of probably naked dyads with deeply invaginated distal surfaces. Scale bar = 10 µm. (*c*) TEM: walls of several spores. Note row of voids close to lumen in otherwise homogeneous exospore. Scale bar = 250 nm. (*d–h*) *Cullulitheca richardsonii*. NMW96.11G.6. (*d*) SEM: entire specimen. Scale bar = 500 µm. (*e*) SEM: sporangium enlarged. Scale bar = 100 µm. (*f*) SEM: *in situ* laevigate dyads with distal invaginations. Scale bar = 10 µm. (*g*) SEM: single dyad showing contact feature. Scale bar = 10 µm. (*h*) TEM: homogeneous exospore with some attached extra-exosporal material. Scale bar = 1 µm. (*i,j*) SEMs: *Fusitheca fanningiae*. NMW97.42G.4. (*i*) Intact specimen. Scale bar = 100 µm. (*j*) Laevigate dyads attached to inside of sporangial wall. Scale bar = 10 µm. (*k-n*) Naked bifurcating axis with vestiges of a terminal sporangium. NMW99.19G.1 (courtesy of K. Habgood). (*k*) TEM: homogeneous exospore and envelope with voids. Arrow indicates ornament on spore. Dark line is gold coating. Scale bar = 500 nm. (*l*) SEM: intact specimen. Swelling on axis is probably a taphonomic artefact. Scale bar = 1 mm. (*m*) SEM: single tetrad with envelope. Arrows indicate position of contact between spores. Scale bar = 10 µm. (*n*) SEM: stoma. Scale bar = 10 µm.

Permanent spore dyads are not 'a thing of the past': on their occurrence in the liverwort *Haplomitrium* (Haplomitriopsida)

KAREN S. RENZAGLIA[1]*, BARBARA CRANDALL-STOTLER[1], SILVIA PRE
JEFFREY G. DUCKETT[2], SCOTT SCHUETTE[3] and PAUL K. STROTHER[4]

Botanical Journal of the Linnean Society, 2015,

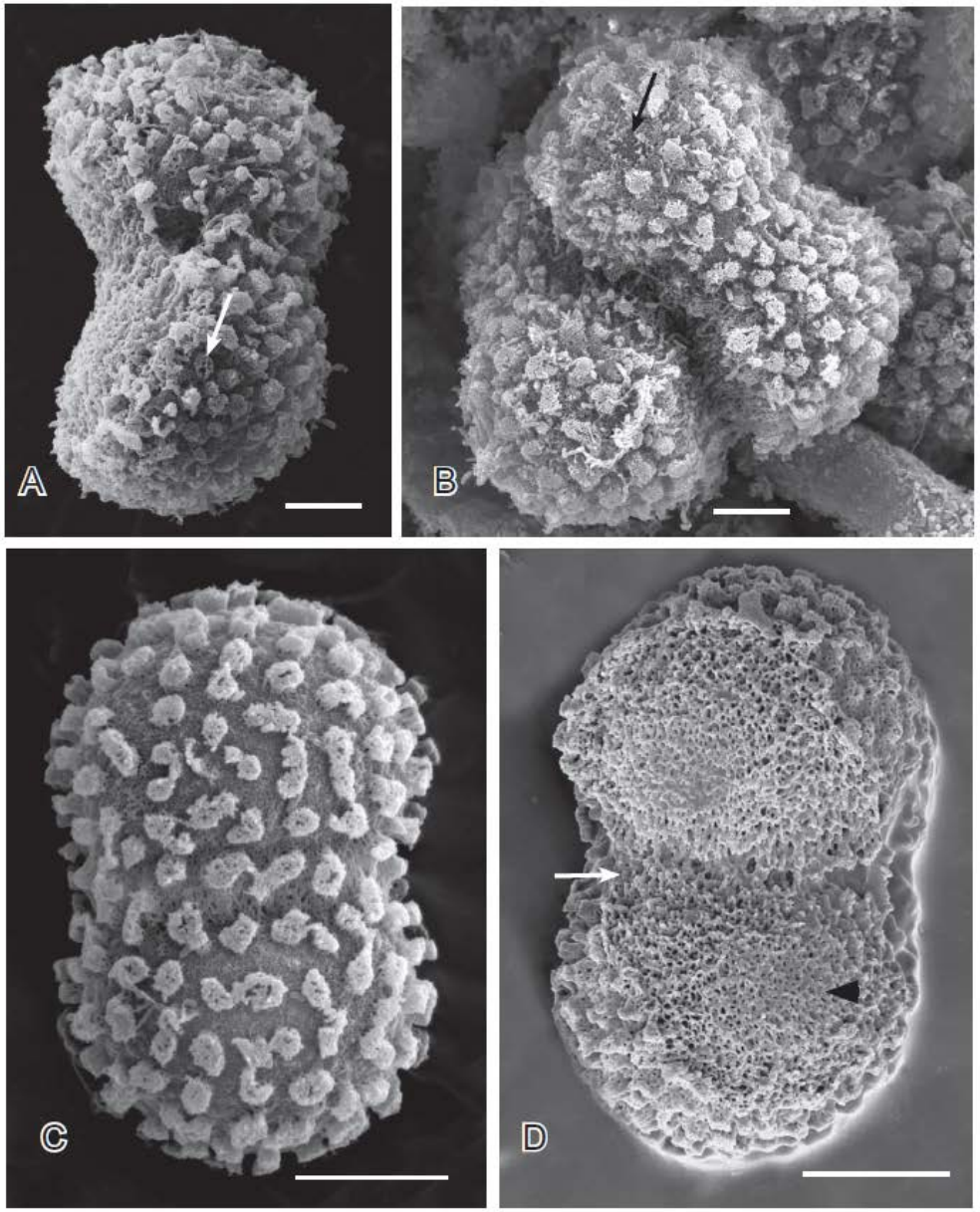


Figure 2. Scanning electron micrographs of dyads and a tetrad of the two populations of *Haplomitrium gibbsiae*. A, Chilean dyad in side view showing flattened proximal and rounded distal surfaces. Tubercles with caps decorate the distal surface with small holes on the wall between. Arrow indicates cap that detached during specimen preparation. B, Chilean tetrad showing dyad arrangement. Arrow indicates entire tubercle that detached during specimen preparation. C, Distal surface of New Zealand dyad showing tubercles that are continuous across spore boundaries. D, Flattened proximal surface of New Zealand dyad with reticulate sculptoderm and small irregular upright rods. Arrow indicates exine elements connecting the two spores and arrowhead points to dense central reticulum of exine elements. Bars, 10 µm.

Семейство Cooksoniaceae

Это семейство мы не можем отнести ни к одному из трех отделов современных сосудистых растений

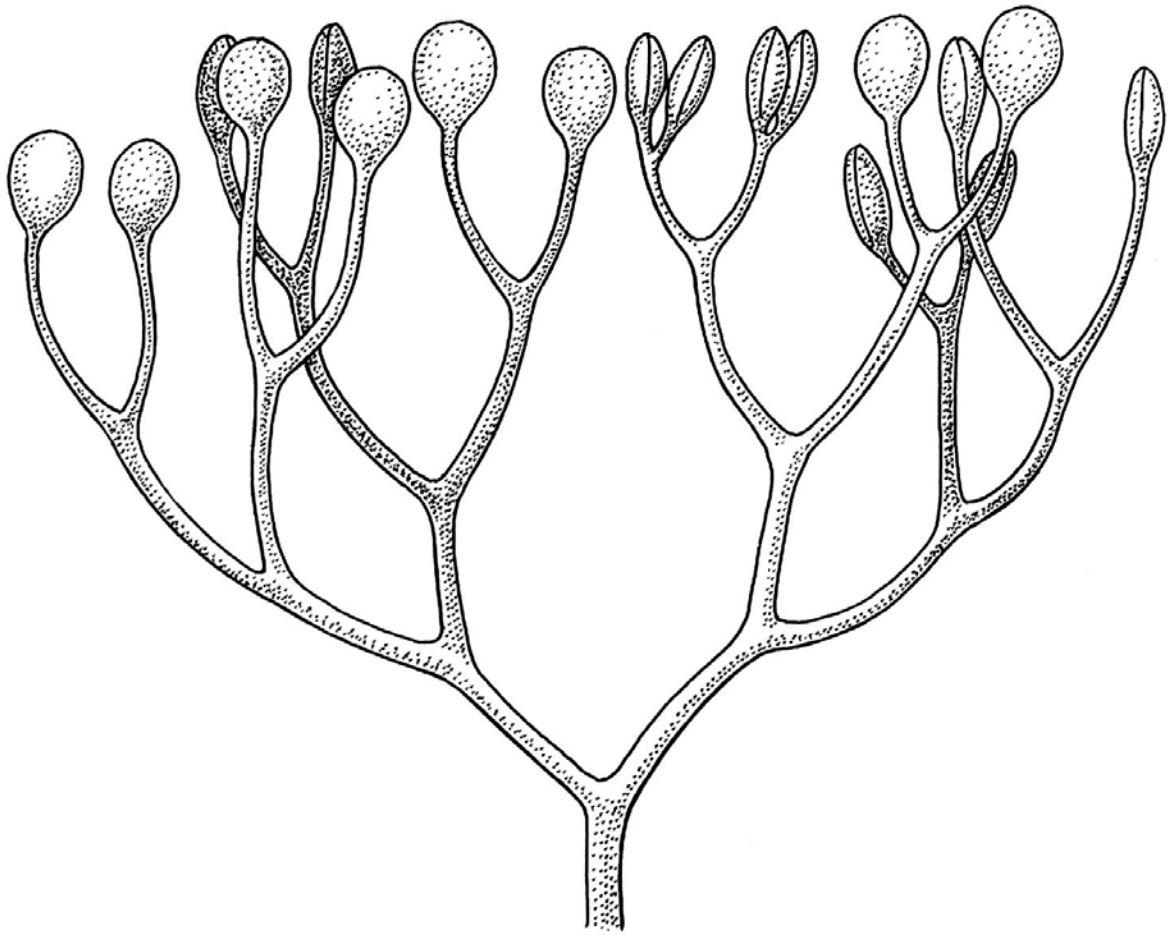
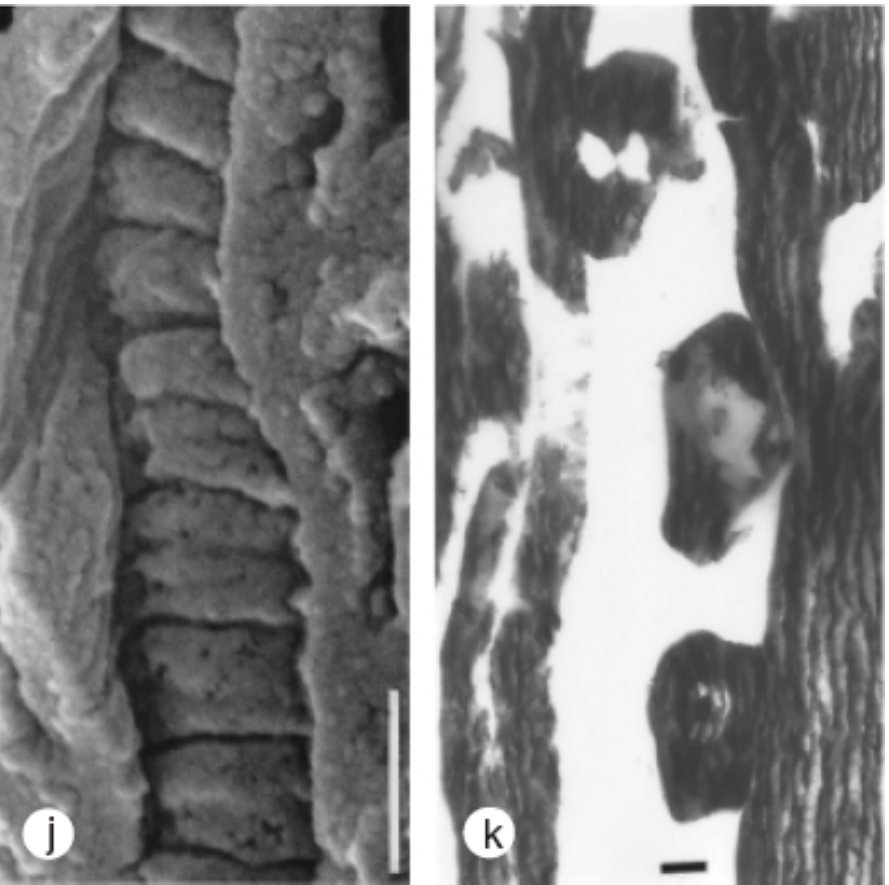
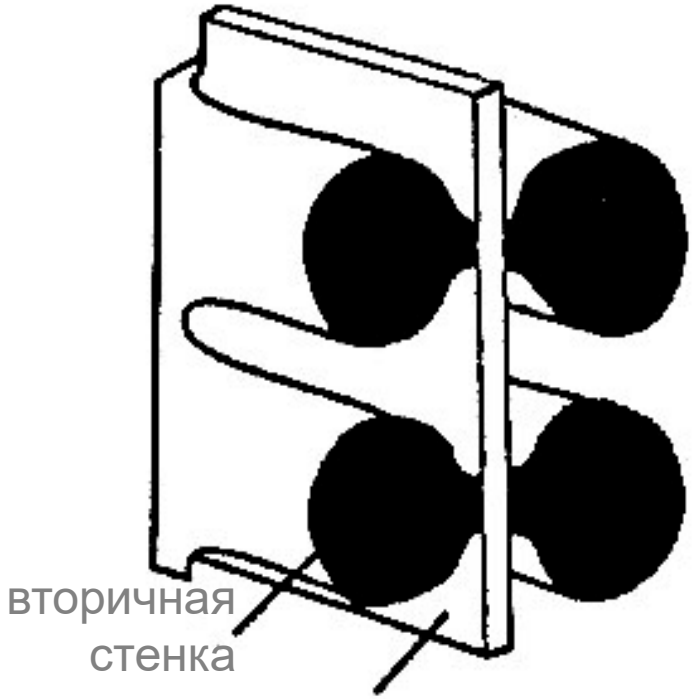


FIGURE 4.10. Reconstruction of distal parts of *Uskiella spargens* showing terminal spatulate sporangia with distal isovalvate dehiscence on isotomous branching axes (×1). Redrawn from Shute and Edwards 1989, Figure 71.

Семейство *Cooksoniaceae*

тонкое строение стенок трахеид





Тонкое строение трахеид – примерно как у современных сосудистых растений, но больше толщина первичной

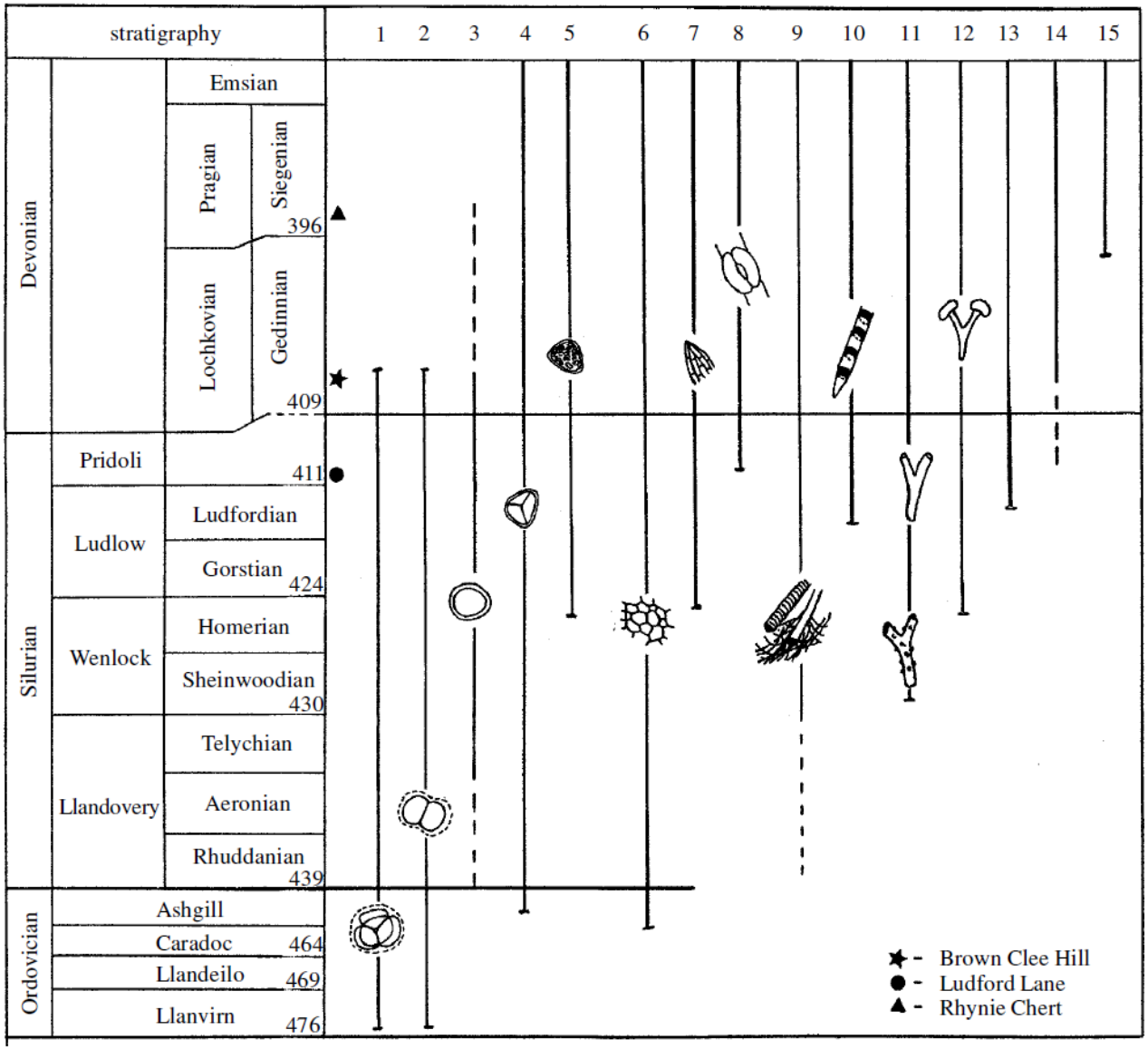


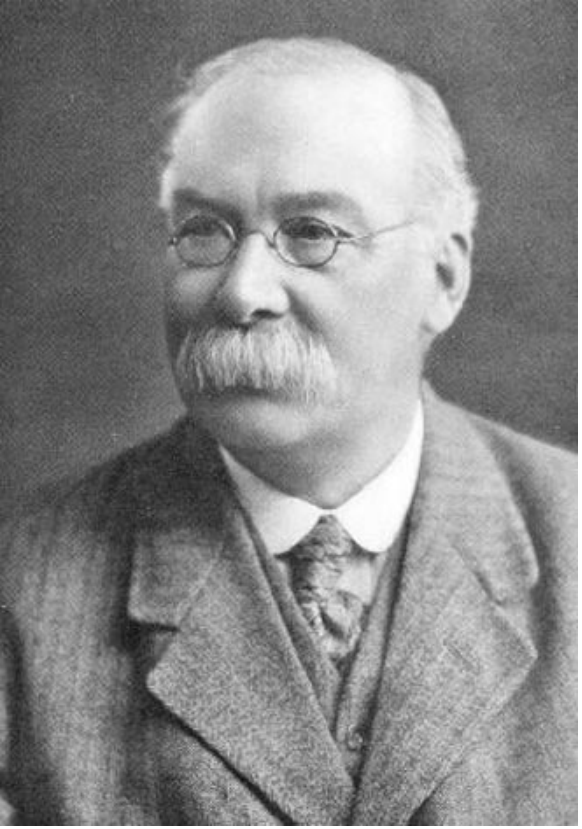
Figure 1. Stratigraphic ranges of fossils mentioned in text. 1, permanent (obligate) tetrads ± envelope; 2, permanent dyads ± envelope; 3, hilate monads; 4, trilete laevigate monads; 5, ornamented trilete monads; 6, cuticular sheets (cf. *Nematothallus*); 7, sporangial cuticles; 8, stomata; 9, associations of tubes, solid line only indicates presence of banded tubes; 10, tracheids; 11, bifurcating axes of ?tracheophyte type; 12, *Cooksonia*/Rhyniopsida; 13, Lycophytina sensu lato; 14, zosterophylls; 15, Trimerophytina.

http://www.uni-muenster.de/GeoPalaeontologie/Palaeo/Palbot/erhynie.html
http://www.abdn.ac.uk/rhynie/intro.htm

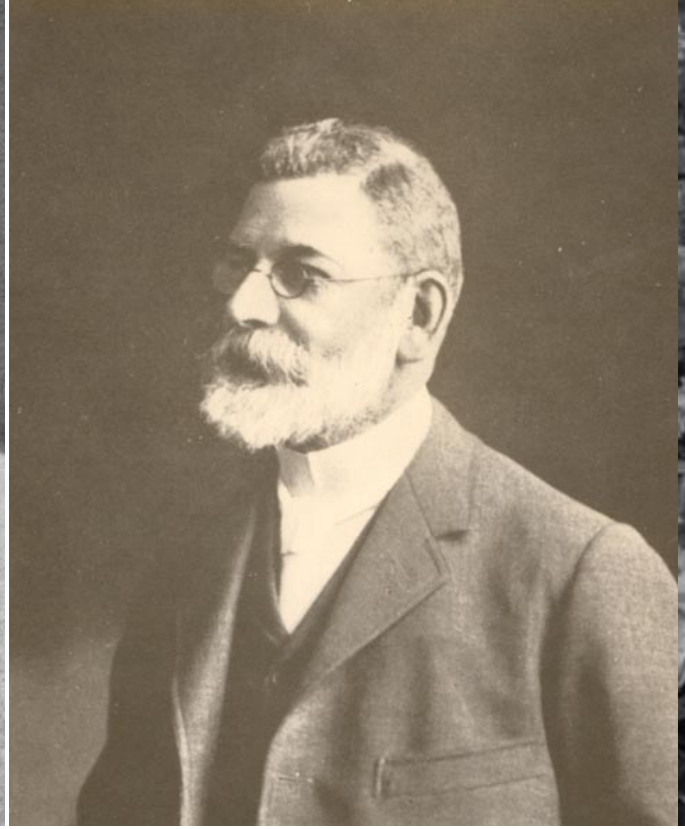
Rhynie

Rhynie chert (400 млн лет)

Современный аналог: Yellowstone National Park



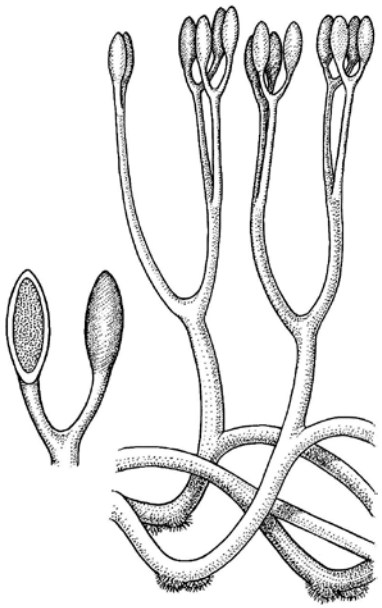
The Rhynie chert was discovered in 1912 by
Dr William Mackie,
a medical practitioner from the town of Elgin to the north of Rhynie



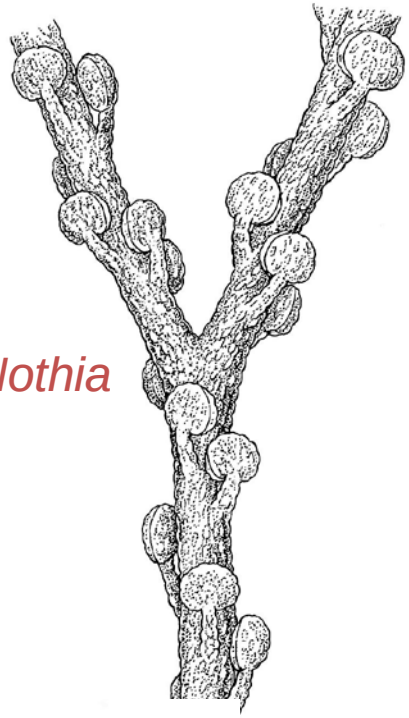
Dr Robert Kidston
Вместе с Henry Lang первыми научно описали ископаемые в 1917

Dr Geoffrey Lyon возродил интерес к материалу из Rhynie в 1950 гг. и описал прорастание спор, положив начало пониманию жизненного цикла ископаемых

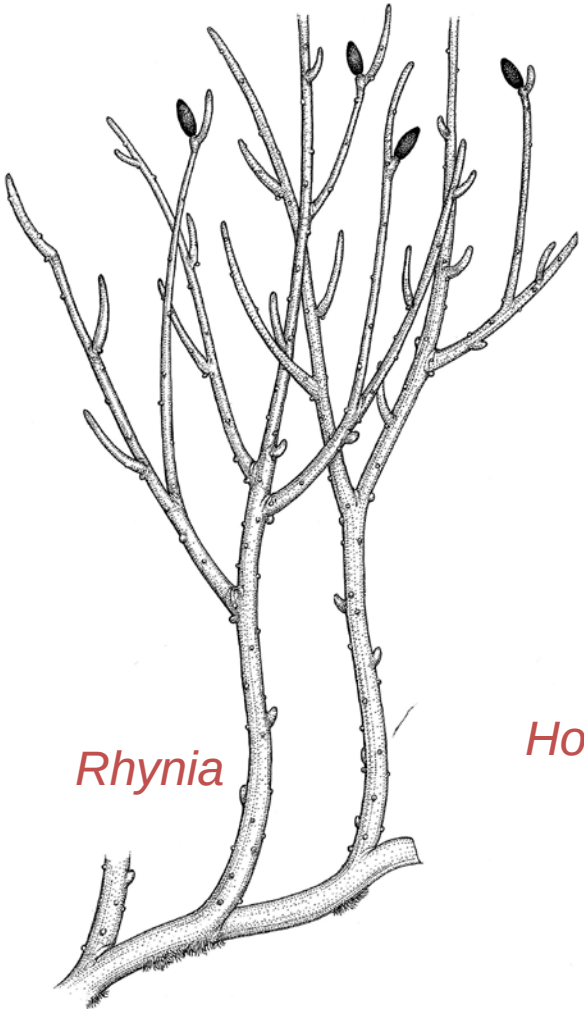
из Kenrick, Crane (1997)



Aglaophyton

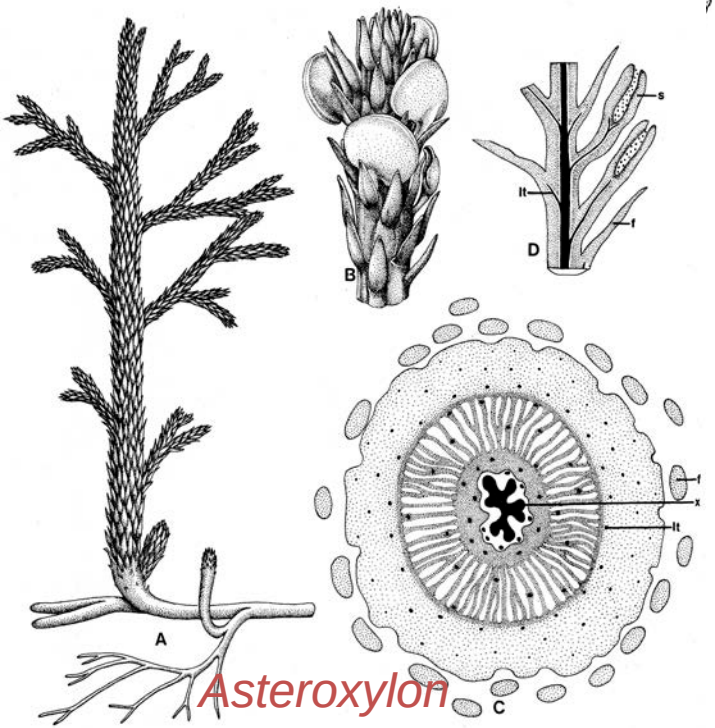


Nothia



Rhynia

Horneophyton

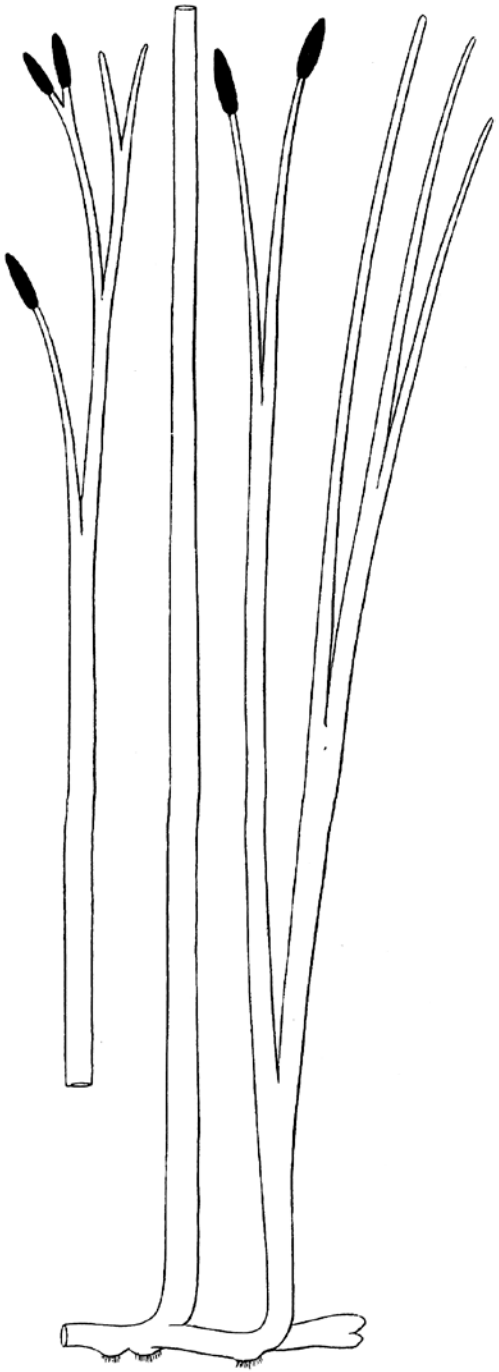


Asteroxylon

Это только *некоторые* из растений, найденных в Rhynie chert.

Некоторые (не изображенные здесь) растения из Райни описаны только в последние годы!

Все найденные здесь высшие растения – сосудистые. Мохообразных нет!



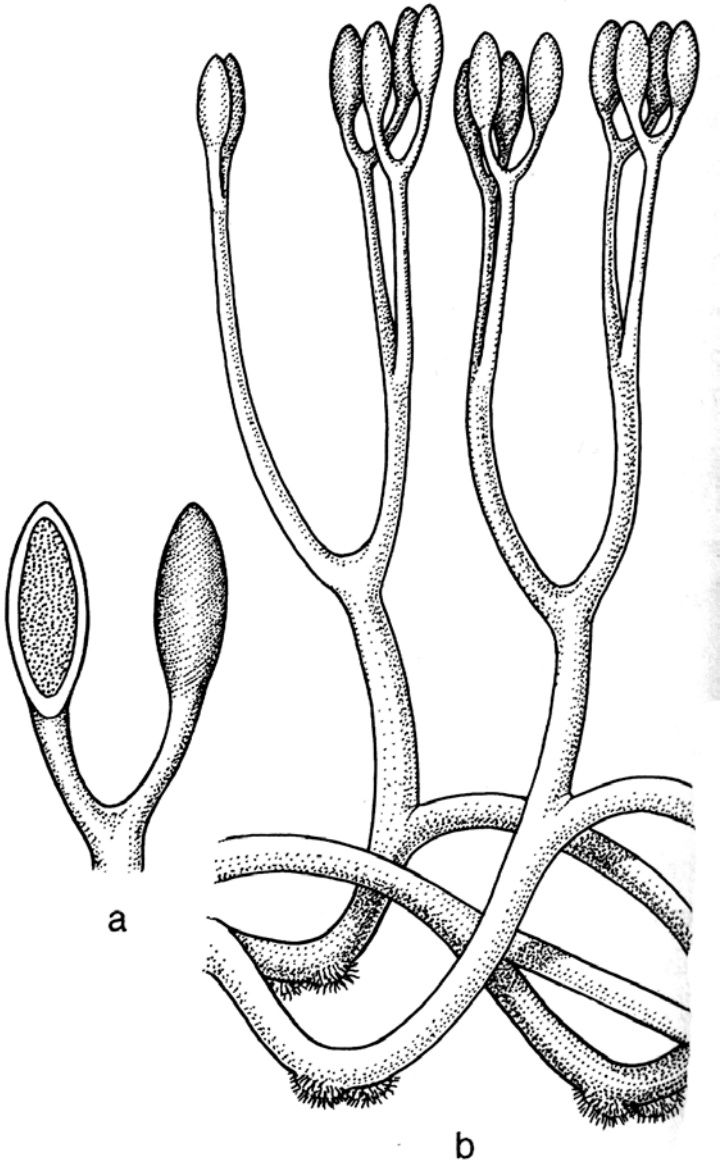
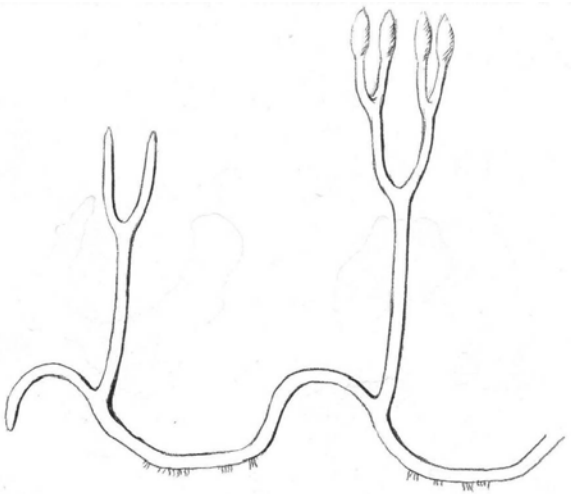


FIGURE 4.7. *Aglaophyton (Rhynia) major.* Drawings based on D. S. Edwards 1986, Figure 57, and Kidston and Lang 1921, Plate 1. (**a**) Details of sporangium, including view of interior; no columella present (×3). (**b**) Reconstruction of habit: terminal, fusiform sporangia; rhizomatous axes with clusters of unicellular rhizoids (×0.8).

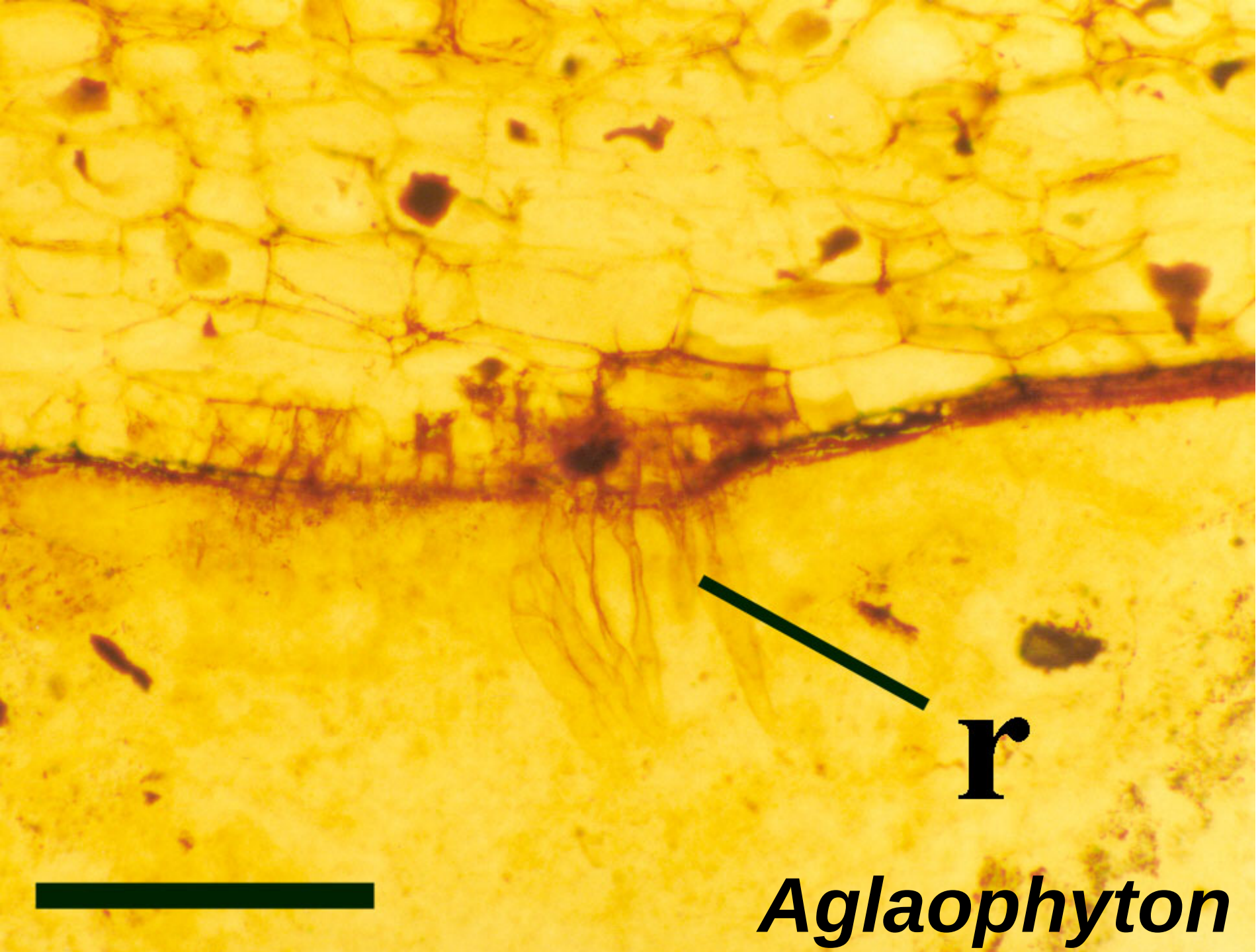
Aglaophyton major

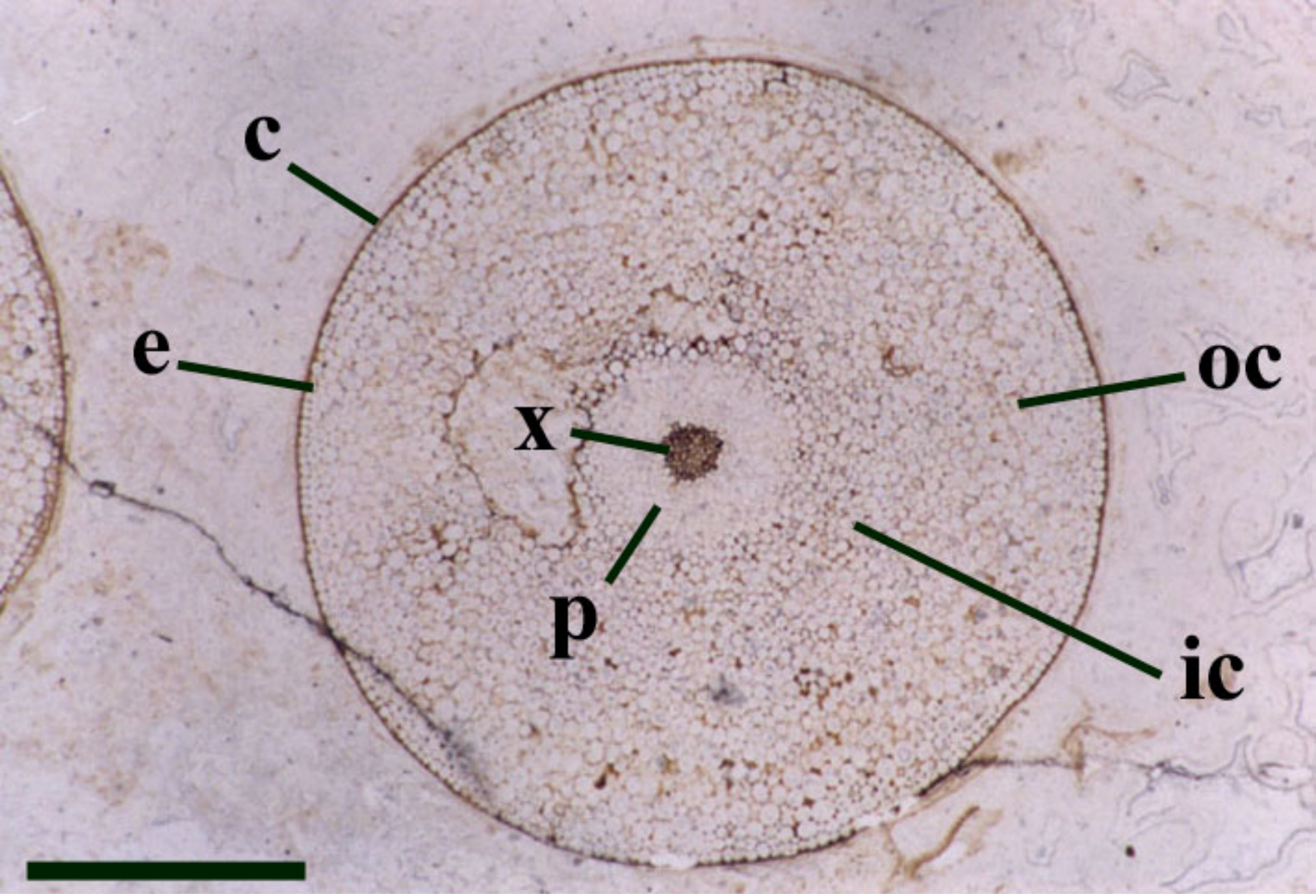
высота – не более 30 см



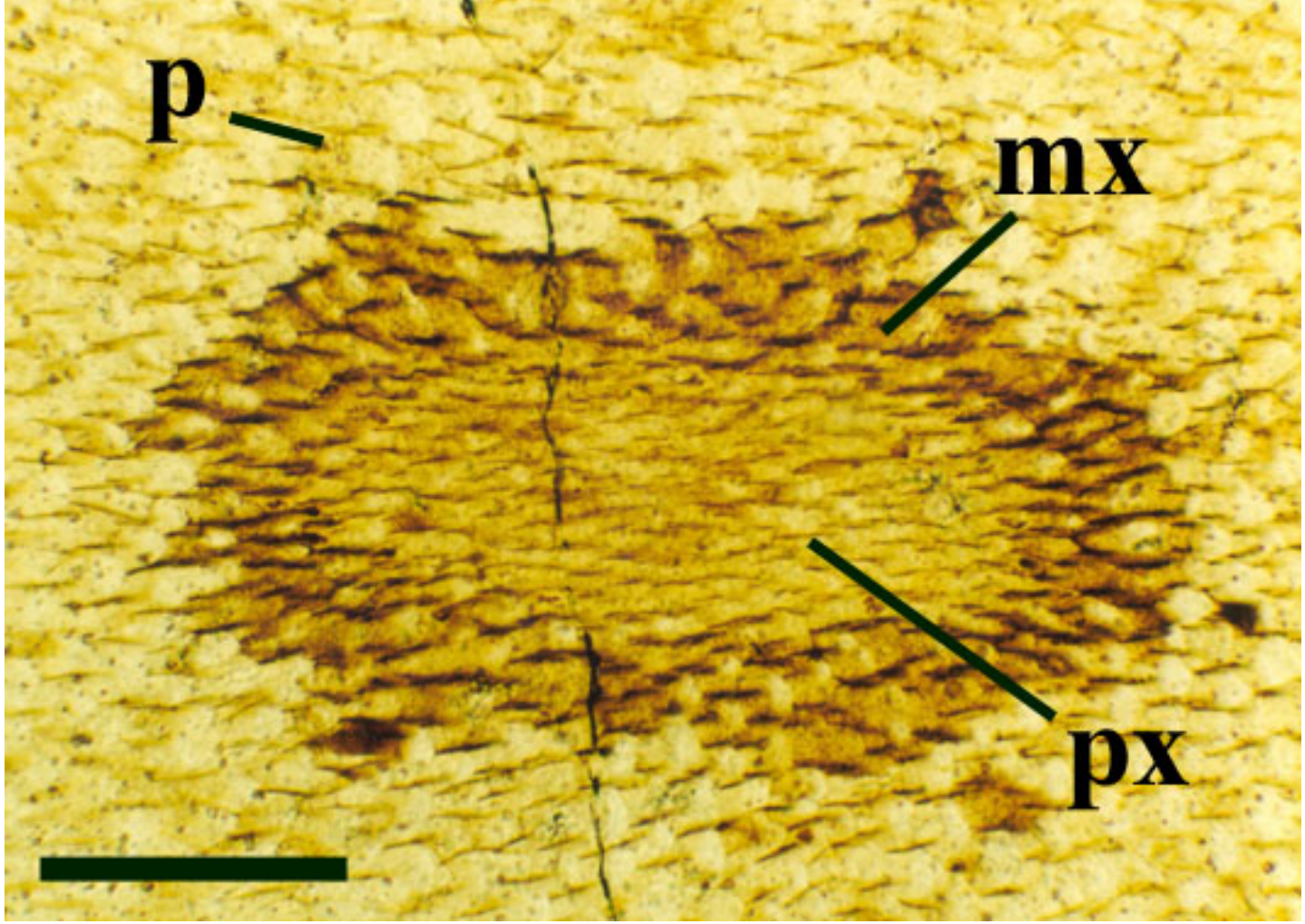

Aglaophyton


Aglaophyton

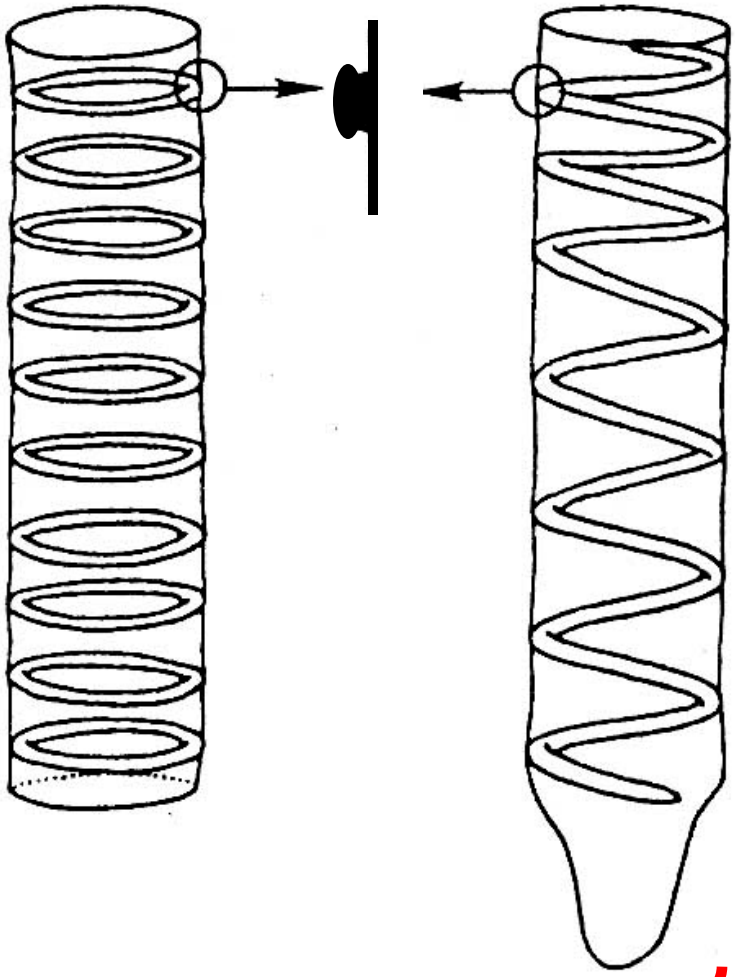

r
Aglaophyton



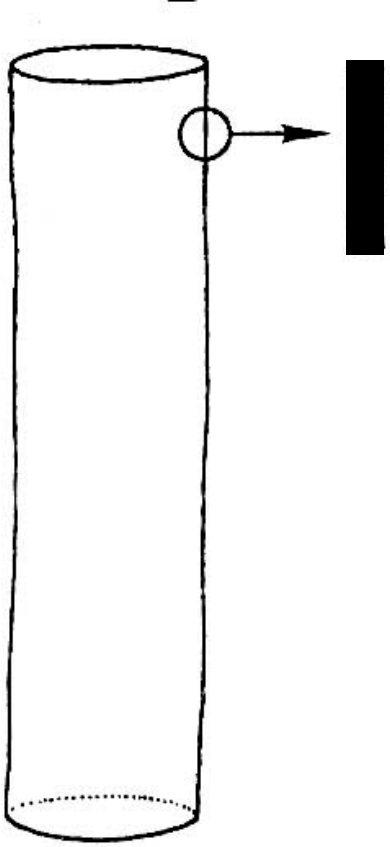
Aglaophyton



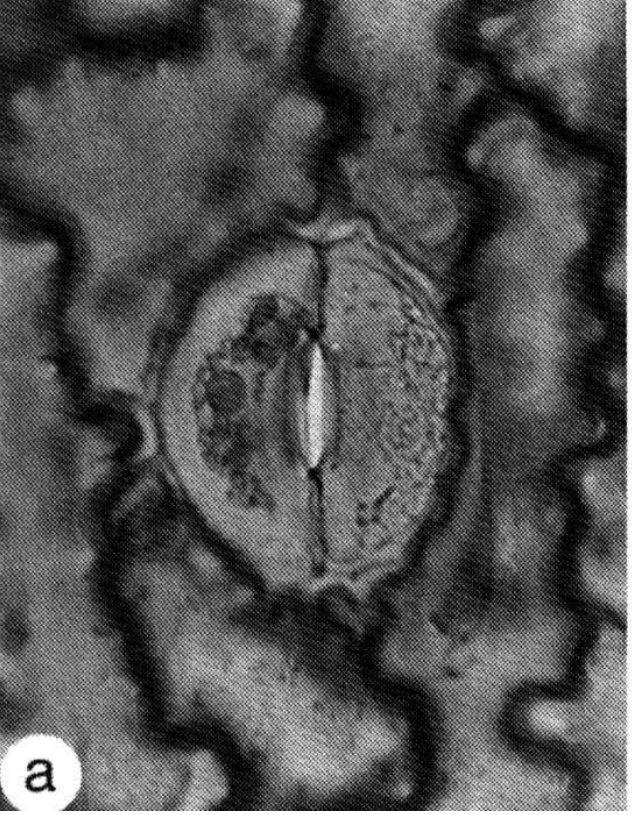
Aglaophyton major



кольчатая и спиральная
трахеиды сосудистых растений

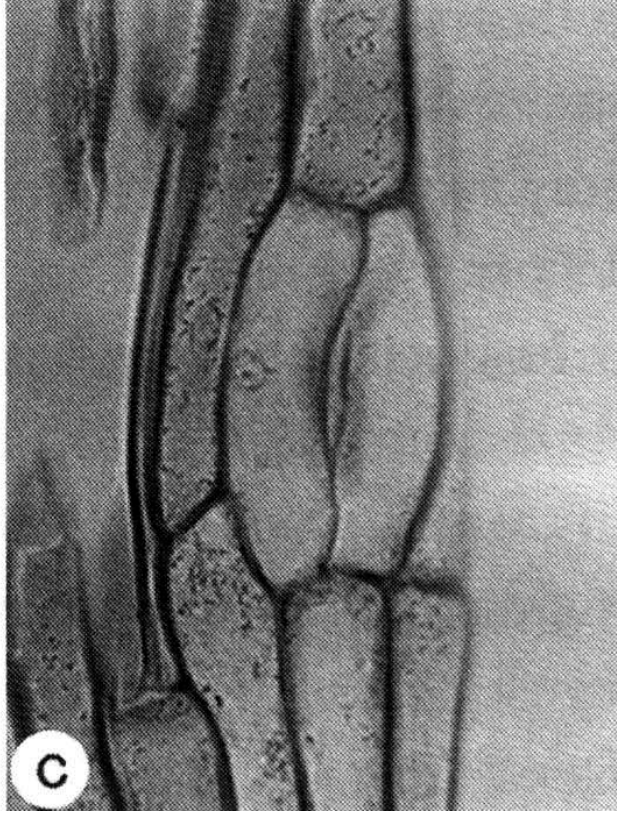


гидроиды мохообразных

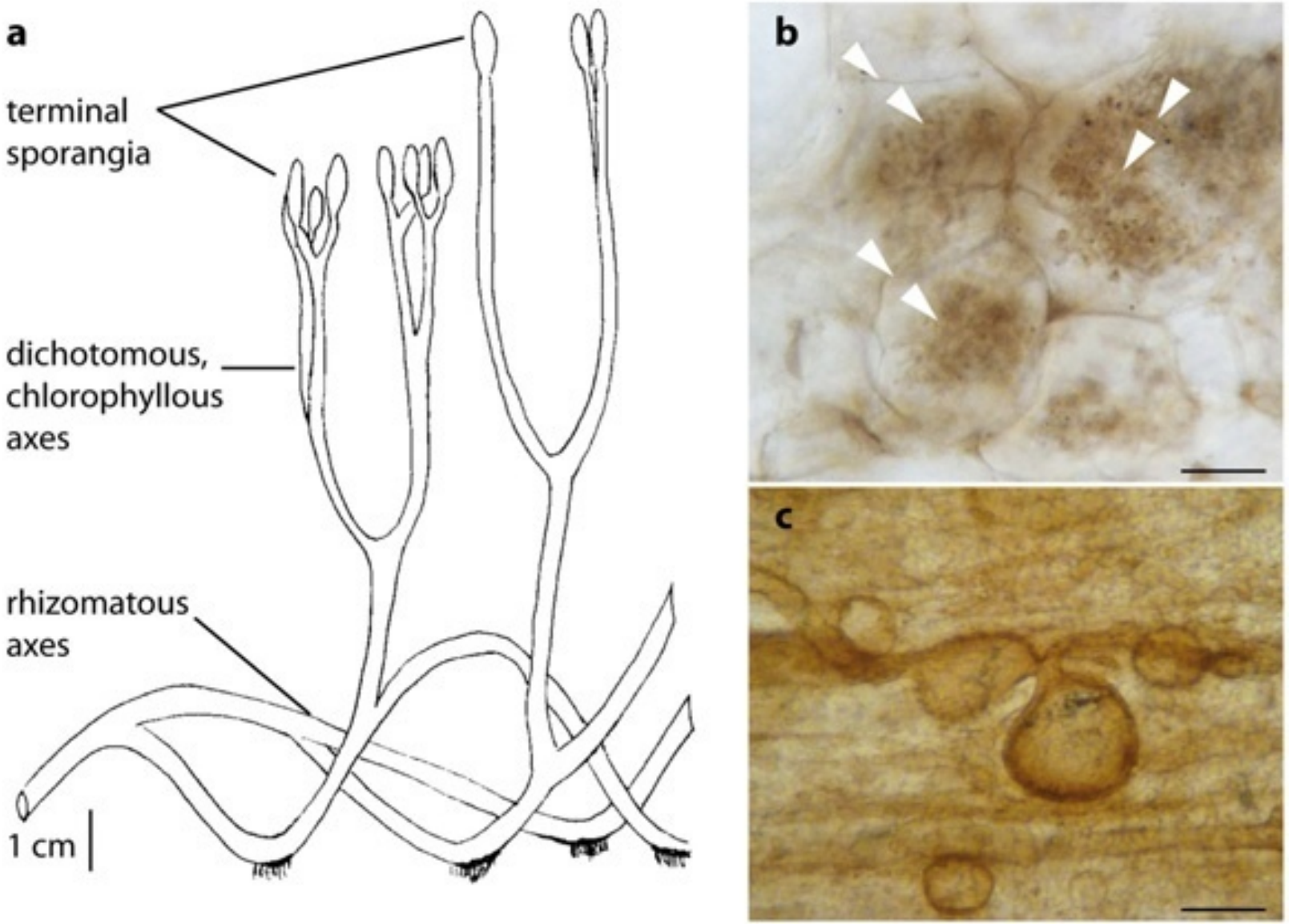


Lycopodium

Aglaophyton

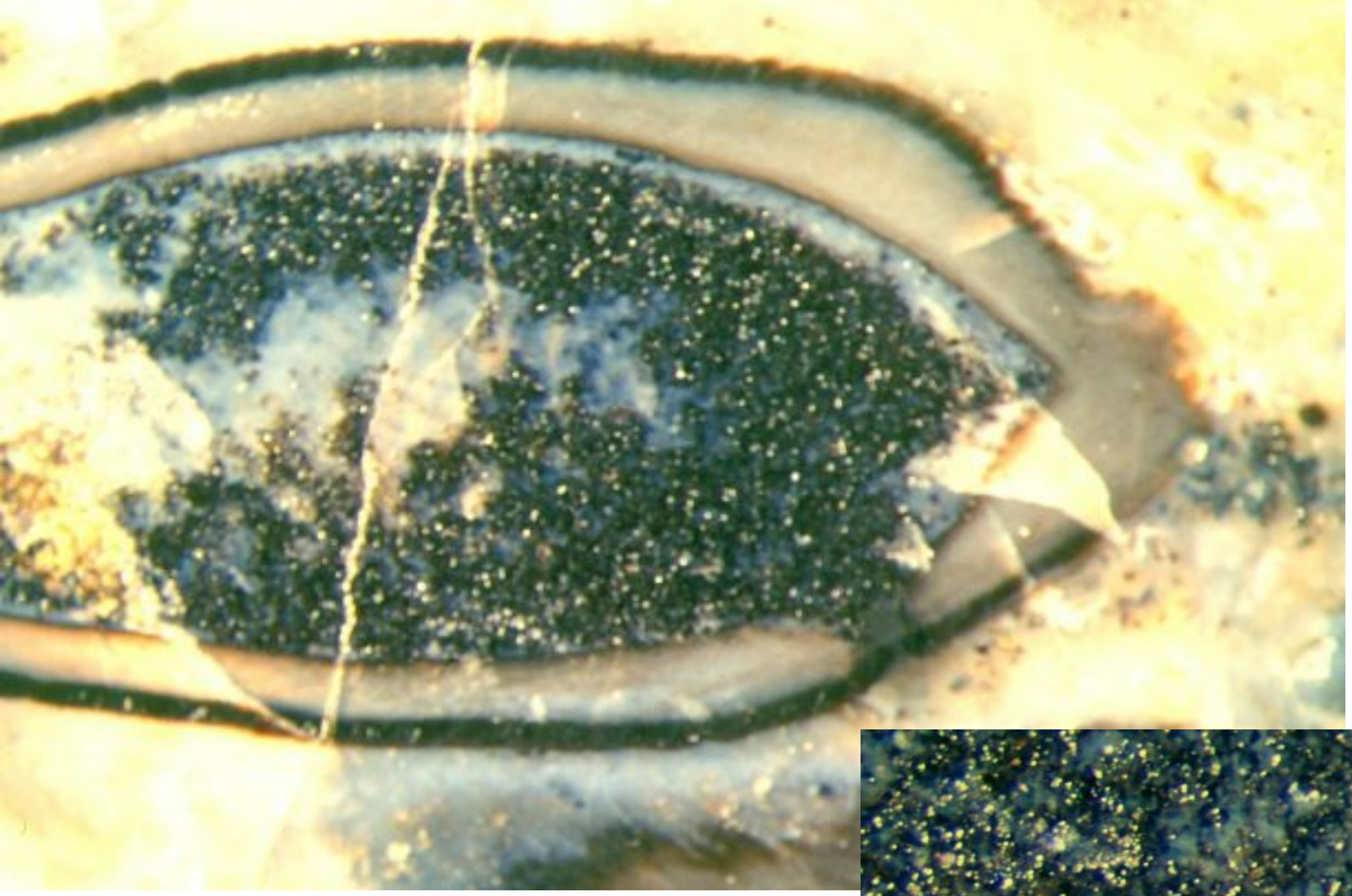


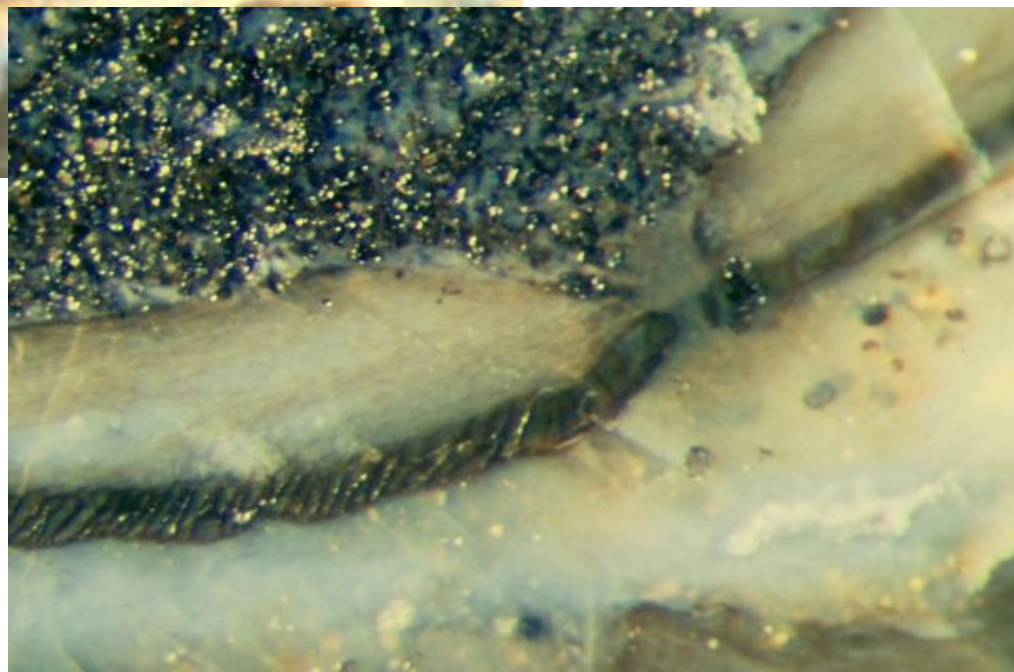
Anthoceros



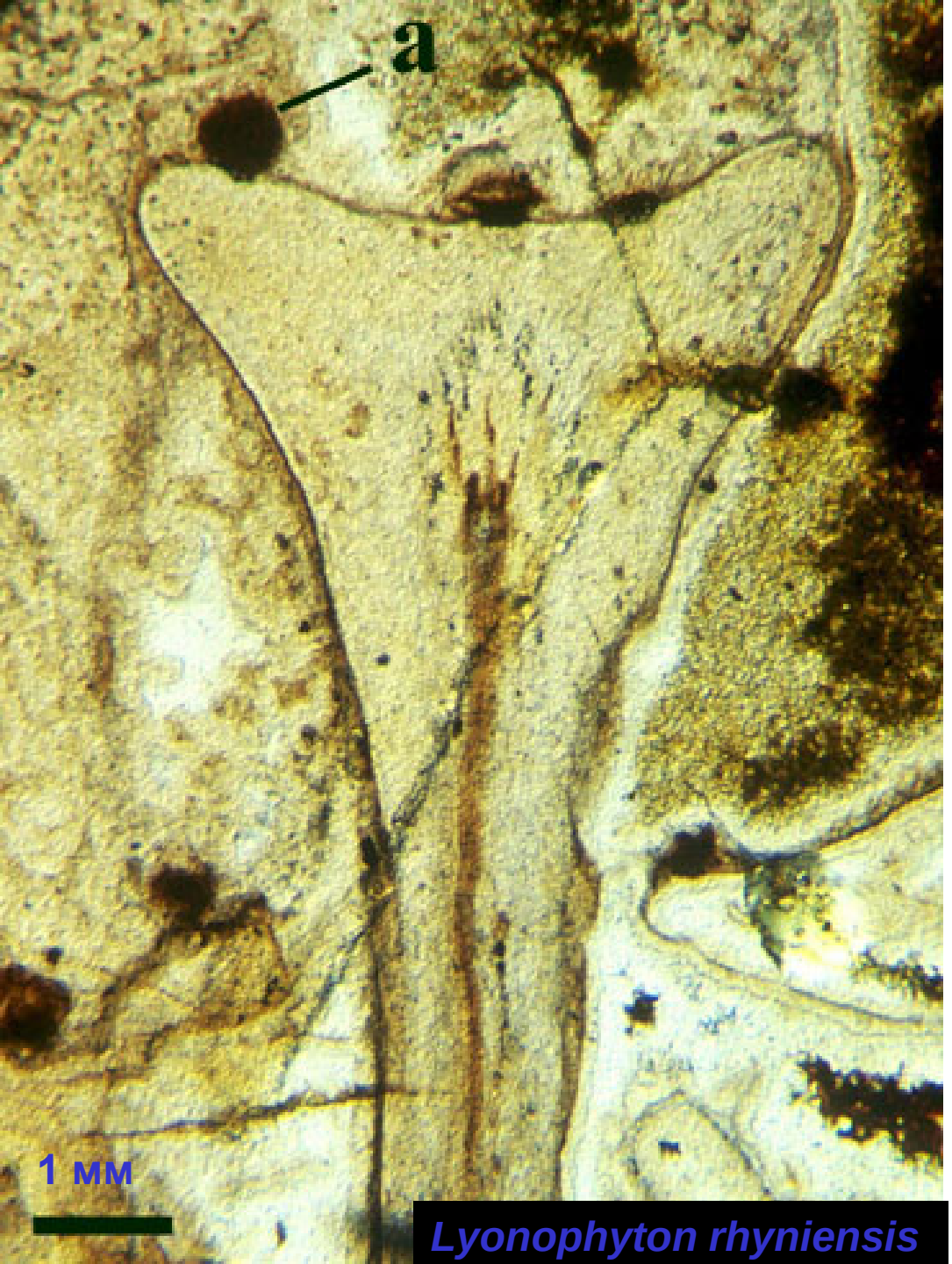
Arbuscular mycorrhizal colonization by Glomeromycetes (paramycorrhizae) in aerial and rhizomatous axes of the Rhynie chert plant Aglaophyton major. (a) General shape of the plant. (b) Colonized cortical cells of A. major showing intracellular arbuscules (white arrows) in turgid cells (photo courtesy of H. Kerp). (c) Hyphae and vesicles in the cortex of an aerial axe of A. major (photo C. Strullu-Derrien). Scale bars: (b) = 20 m; (c) = 40 m.
Selosse, Strullu-Derrien (2015).

Aglaophyton:
Поперечный срез вскрывшегося спорангия с налегающими друг на друга краями

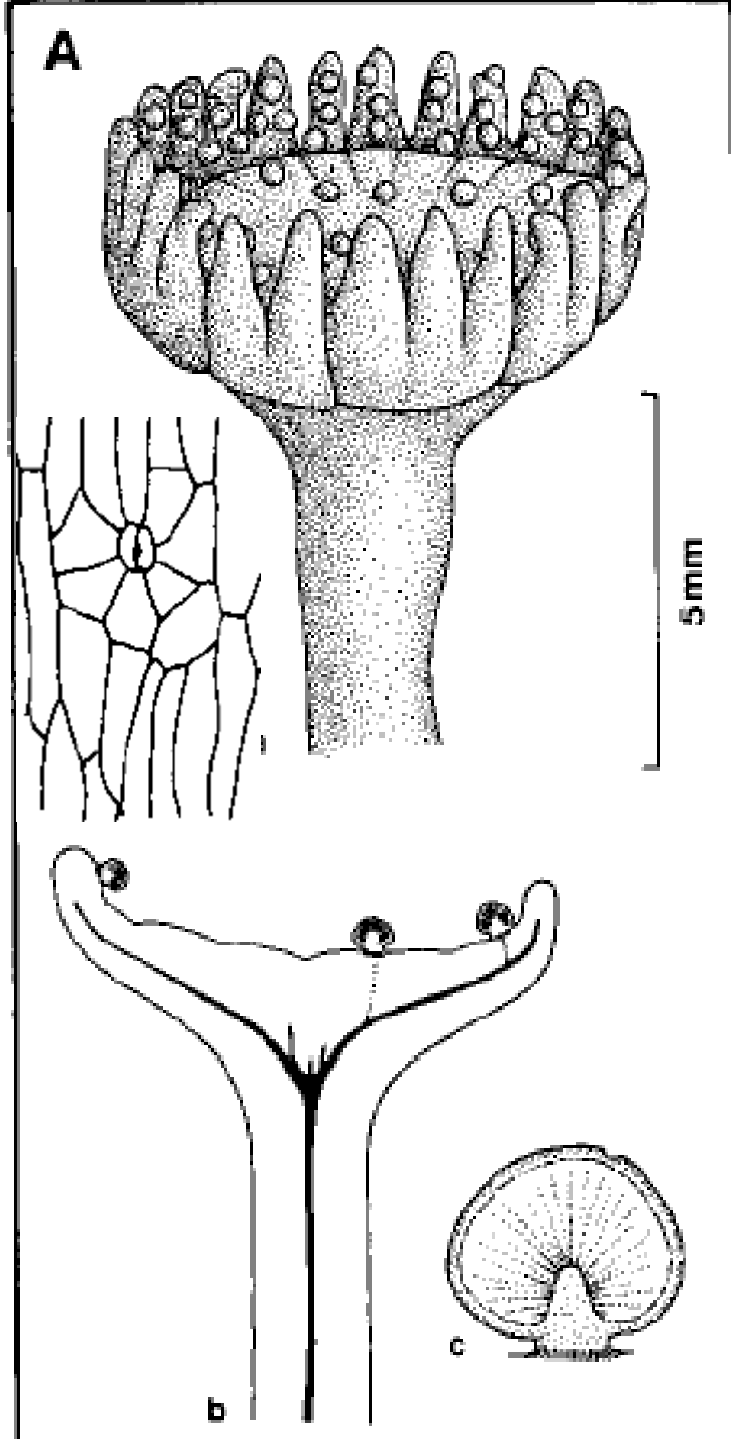


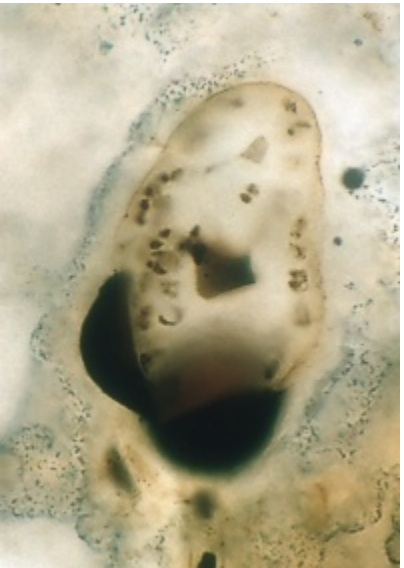


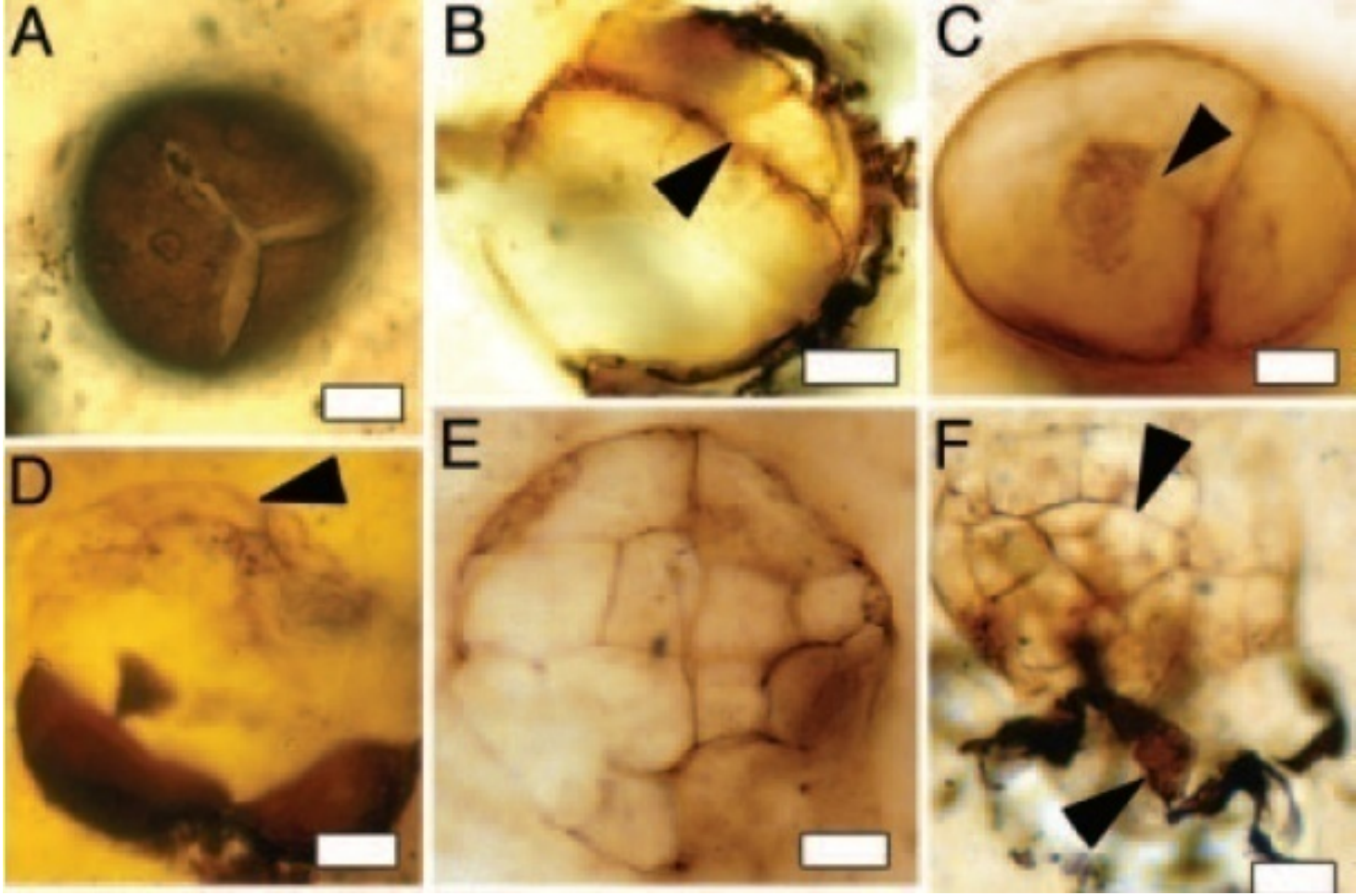
Aglaophyton:
Продольный срез спорангия с отверстием, прогрызенным неизвестным фитофагом



Lyonophyton rhyniensis

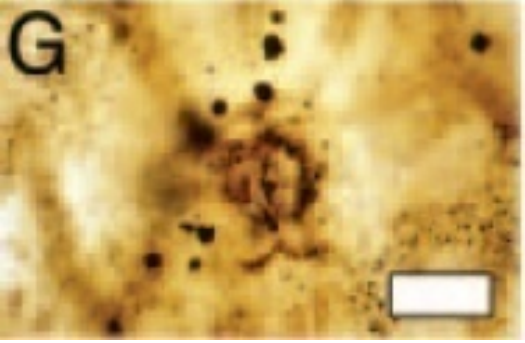




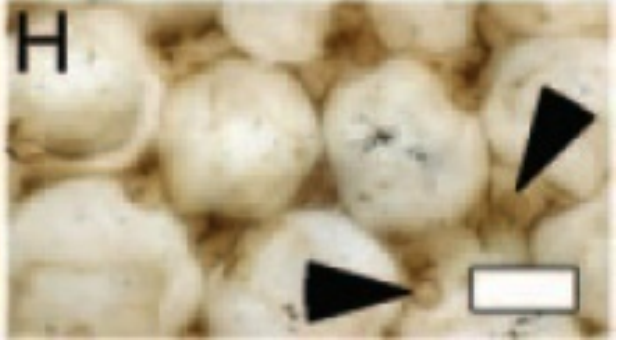


Lyonophyton = гаметофит *Aglaophyton*: прорастание споры и ранние стадии развития гаметофита

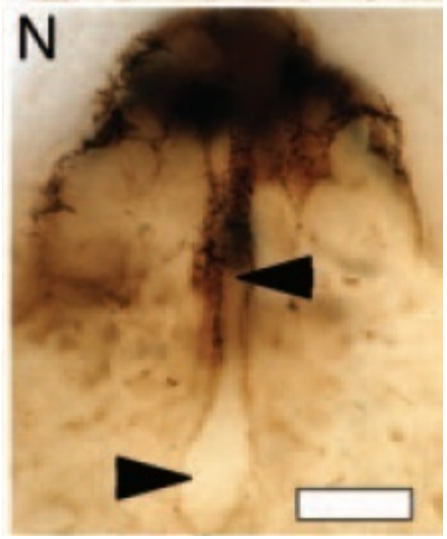
Lyonophyton
(= гаметофит
Aglaophyton)



устьице

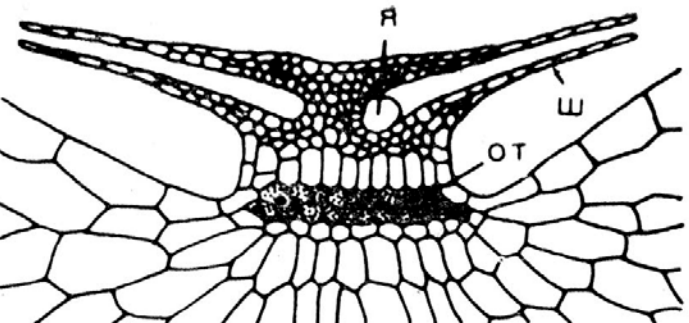


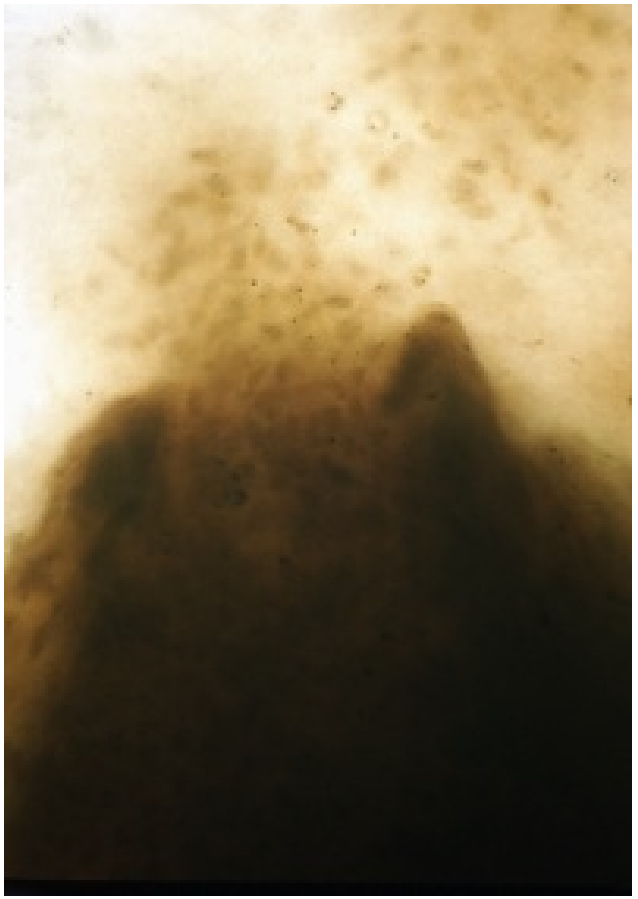
гифы гриба в паренхиме



архегоний

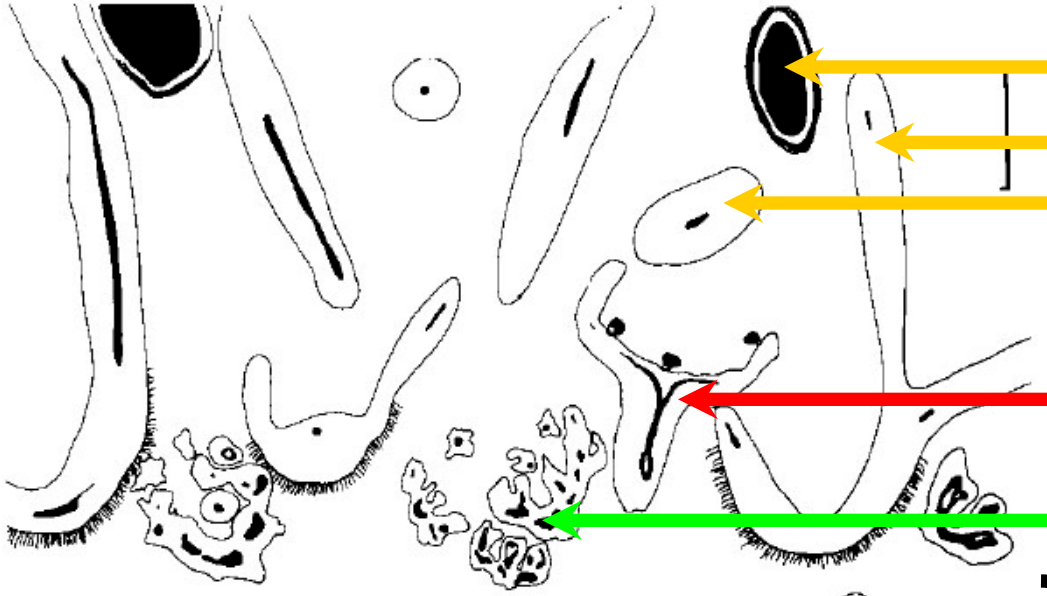
антеридий





выход сперматозоидов

Fig. 1. Life history of *A. major*/*L. rhyniensis* showing stages in the development of the dimorphic gametophytes. The mature sporophyte (lower left) bears sporangia with spores of two types. Blue spores develop into mature antheridiophores; orange spores develop into archegoniophores.



Aglaophyton

Lyonophyton
(гаметофит Aglaophyton)

Langiophyton
(гаметофит Horneophyton)

отмершие остатки
Asteroxylon (древнейшее плауновидное)