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BUXBAUMIA: A MOSS PERISTOME WITHOUT A PERISTOMIAL FORMULA

BUXBAUMIA: МОХ С ПЕРИСТОМОМ БЕЗО ВСЯКОЙ ФОРМУЛЫ ПЕРИСТОМА

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Abstract

This study of peristome development in *Buxbaumia aphylla, B. minakatae* and *B. viridis* has revealed major differences from all other peristomate mosses. The fundamental square patterning, characteristic of moss peristome formation, is lacking in *Buxbaumia*. Endothecium and amphithecium are differentiated, but cells of the endothecium are arranged radially and are likely derivatives of a large tetrahedral central cell. Cells of the inner peristomial layer (IPL) are all offset against cells of the primary peristomial layer (PPL), in both transverse and longitudinal sections. At early stages, IPL cells are 1.2–2 times fewer than PPL cells; subsequently they become about equal in number. However, close to urn base additional anticlinal divisions result in IPL cells double in number to those in the adjacent PPL layer. The maximum number of cells in the PPL is 48 in *B. aphylla*, but the peristomial formula can be calculated only by counting of all cells in moderately regular cell rings around endothecium and dividing these by eight. However the absence in *Buxbaumia* of cell columns, as in other mosses, and the progressive increase in the cells in peristomial layers makes such a count too approximate and uncertain. The pleated cone in *Buxbaumia minakatae* and in the distal half of *B. aphylla* has about 24 folds, whereas closer to base the folds are more numerous, with up to 40 folds. The cone-shaped endostome points the close relationship to *Diphyscium*, and also their prostome structure is very similar. However *Diphyscium* sporophyte at early stages of development is narrow and its peristomial layers differentiate as in other mosses and have similar to haplolepideous mosses cell arrangement. Contrary, in *Buxbaumia* the urn is broader than long at this stage and IPL forms continuous subepidermal layer overarching semi-globose endothecium. Its development proceeds essentially by means of morphologically longitudinal / spatially almost radial cell divisions, but not periclinal ones as in *Diphyscium* and all other mosses. This mode of development explains the progressively increasing number of cell in IPL, and consequently also PPL and OPL. The sporophyte structure in *Buxbaumia* does not represent an archaic type, but seems to be extremely specialized.

Резюме

Изучено развитие перистома у *Buxbaumia aphylla, B. minakatae* и *B. viridis* и показано его принципиальное отличие от того, как оно происходит у все остальных мхов. Характерное крестообразное расположение клеток в спорофите на ранних стадиях его развития у *Buxbaumia* отсутствует. Эндотеций и амфитеций дифференцированы, но в эндотеции клетки располагаются радиально, будучи производными тетраэдрической клетки. Все клетки внутреннего перистомного слоя (ВПС) располагаются очередно клеткам первичного перистомного слоя (ППС), как это представлено и на поперечных, и на продольных срезах. На ранней стадии развития клетки ВПС оказываются в меньшем количестве (в 1.2–2 раза), чем клетки ППС; затем их число становится одинаковым, а ближе к основанию из-за антиклинальных делений в ВПС клеток в нем становится больше, чем в ППС. В ППС *B. aphylla* число клеток доходит до 48, однако перистомную формулу можно вычислить только разделив число клеток по всей окружности на 8; впрочем, это мало осмысленно, поскольку не отражает колонновидной структуры, которая отсутствует из-за отсутствия крестообразного расположения клеток, а также и из-за постепенного увеличения числа клеток в перистомных слоях к основанию перистома. Эндостом *Buxbaumia minakatae* и *B. aphylla* имеет вид складчатого конуса, б.ч. с 24 складками, хотя к основанию их число возрастает до 40.

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Строение эндостома *Buxbaumia* указывает на родство с *Diphyscium*, что подстверждается и сходным строением простома у этих групп. Вместе с тем, у *Diphyscium* развитие перистома происходит так же, как и у гаплолепидных мхов, тогда как у *Buxbaumia* на ранних стадиях развития урночка шире своей длины, и клетки ВПС образуют субэпидермальный слой, покрывающий полушаровидный эднотеций. Такое развитие ВПС идет за счет делений, хотя и являющихся морфологически продольными, но просиходят они в пространстве почти поперечно оси спорофита, в радиальном направлении, а не периклинально, как у *Diphyscium* и у всех остальных мхов. Такой характер развития и объясняет постепенное увеличение клеток в ВПС, а затем и в ППС и далее в наружном перистомном слое. Такое строение спорофита *Buxbaumia* вряд ли следует считать примитивным типом, скорее это высоко специализированное строение, связанное с предельной редукцией гаметофита.

KEYWORDS: Buxbaumiales, *Diphyscium*, development, evolution, sporophyte, reduction, specialisation, peristome, exostome

INTRODUCTION

Similarly to flower in angiosperms, peristome in mosses is one of the most important organs, regulating spore release and therefore responsible for species survival and dispersal. Nothing surprising is that it provides a rich source of characters important for building moss classification (Hedwig, 1801; Brotherus, 1924; Frey & Stech, 2009).

Recent molecular phylogenetic studies provided two opposite trends in reevaluation of peristome importance for moss classification. From one side, molecular data revealed that it was incorrect to use peristome reduction as a character of high value for separating two orders of pleurocarpous mosses, Isobryales and Hypnobryales, used in the system of Brotherus (1925) and followed by most bryologists of 20th century. It was shown that various cases of peristome reduction or modification were caused by the transition to epiphytism, which is a more frequent event in many moss lineages than it was thought before (Huttunen *et al.*, 2004, 2012). From the other side, the basic peristomial formulae appeared to be even more stable than it was thought before (Shaw *et al.*, 2011; Budke *et al*., 2007). It was shown that even some cases of enigmatic deviations in peristome structure, like in *Catoscopium* (Ignatov *et al.*, 2015) and *Pseudoditrichum* (Fedosov *et al.*, 2016) that have diplolepideous peristome but are resolved in the haplolepideous clade by molecular phylogenetic data, demonstrate only a variation of the same principal scheme of peristome development common for all haplolepideous mosses.

One case however remains difficult for interpretation. *Diphyscium foliosum* was exhaustively studied by Shaw *et al.* (1987), who showed that its peristome passes in its development through the stage with peristomial formula 4:2:3, which is typical for terminal groups in moss evolution. This peristomial formula is most typical for the subclass Dicranidae, also called haplolepideous mosses (Shaw *et al*., 2011). However, the peristomes of diplolepideous alternate mosses also pass thought this pattern at least sometimes (Blomquist & Robertson, 1941; Ignatov *et al*., 2015), although Shaw *et al*. (1989a) expressed doubts that this is really typical case in this group. At the same time, the basal part of arthrodontous mosses, constituted by five orders, the Gigaspermales, Funariales, Encalyptales, Disceliales, and Timmiales, either lack peristome at all, or its elements are opposite. As *Diphyscium* is definitely more basal in the molecular phylogenetic trees than mosses with diplolepideous opposite peristome (Newton *et al.*, 2000; Tsubota *et al*., 2004; Cox *et al*., 2010; Shaw *et al*., 2011; Ignatov *et al*., 2015), the possession of a highly developed peristomial formula in this order seems to be strange. Some attempts to find 4:2:3 pattern in Funaliales and similar groups (Schwartz, 1994) did not succeed, and additional studies of mosses with diplolepideous opposite peristomes (Budke *et al.*, 2007; Ignatov *et al*., 2018) also did not reveal 4:2:3 formula in Timmiales and Encalyptales, respectively.

The genus *Diphyscium* was treated for a long time as a member of Buxbaumiaceae. The endostome consisting of a pleated cone, known in both groups and nowhere else, is an important evidence for this. Some authors of 20th century either included *Diphyscium* in Buxbaumiaceae (Lawton, 1971) or considered two families, the Buxbaumiaceae and Diphysciaceae within one order Buxbaumiales (Lazarenko, 1955) or two families constituting one subclass Buxbaumiinae (Crum & Anderson, 1981).

The considerable difference between *Buxbaumia* and *Diphyscium* was suggested from both molecular and peristome development studies. They were invariably found in phylogenetic trees (based on different DNA regions and calculated by different methods) in the grade from nematodontous to arthrodontous peristomes, and their order was always the same: *Buxbaumia* branched off before *Diphyscium* (Newton *et al.*, 2000; Tsubota *et al*., 2004; Cox *et al*., 2010, Ignatov *et al*., 2015).

Peristome development in *Diphyscium* was of exhaustively studied by Shaw *et al.* (1987), showing, as already mentioned, the passing through the stage 4:2:3, common with haplolepideous mosses and at least sometimes by diplolepideous alternate mosses. Studies of *Buxbaumia* peristome were less detailed, although it was in the focus of studies by Philibert (1888), cited by Taylor (1962)' translation, and Edwards (1984). The homology of the pleated cone with endostome was revealed, although these authors provided different number of its folds: Philibert found an indefinite number (Taylor, 1962), 16-folded endostome in Buxbaumiaceae was reported by Schofield

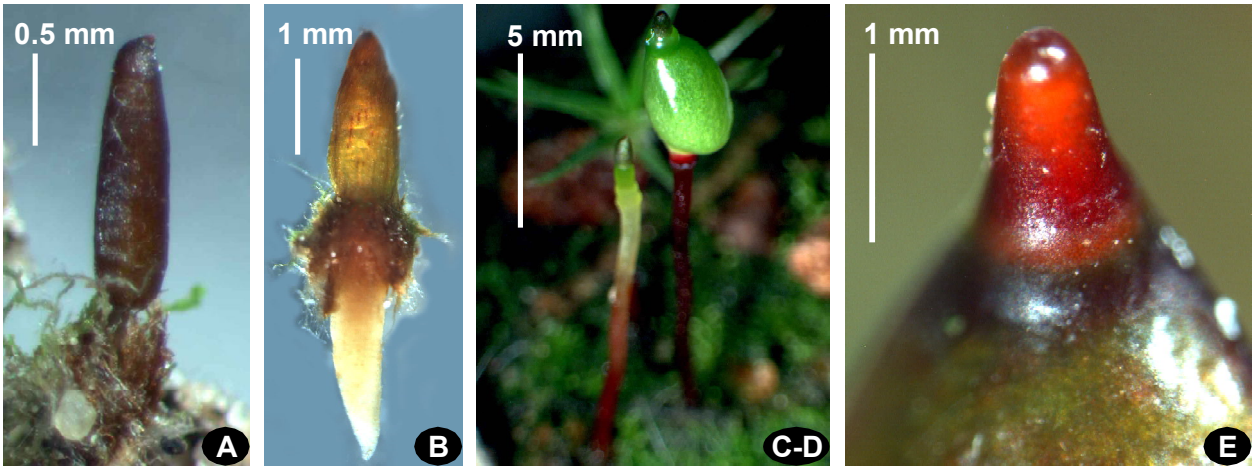

Fig. 1. *Buxbaumia aphylla* (living plants from Ryazan Province, Oksky State Reserve): stages of sporophyte development: A–B: sporophytes still covered with calyptrae; C–D: younger (left) and older (right) plants, calyptrae remain on operculum. E: operculum on the urn, shortly before falling off.

(2007), while Edwards (1984) thought their number is 32. The structures outside OPL, the prostome, was discussed in detail by Edwards (1984).

The aim of this study was to provide more details for the early stages of peristome development in *Buxbaumia*, and to confirm its peristomial formula 8:4:4-8 in *B. aphylla* and 8:4:4 in *B. viridis* (Edwards, 1984), especially in order to understand if the similarity with *Diphyscium* is based on the similar developmental pattern, and if so, is it a way to discern the 4:2:3 pattern already in *Buxbaumia*, as a group split off the main trunk of the phylogenetic tree earlier than *Diphyscium*.

MATERIAL AND METHODS

Material. For peristome studies in *B. aphylla,* plants on various stages of development were taken (Fig 1A–D), and altogether 10 capsules were studied in transverse sections, and 5 in longitudinal ones. For *B. viridis* and *B. minakatae,* the material was more limited, with stages roughly corresponding to those shown in Fig. 1C.

Preparation and Microscopy. The material used for microtome sectioning was collected in the field, fixed shortly after collecting in 2.5% glutaraldehyde in 0.05M PBS. Further steps were done after several weeks or few months. Specimens were post-fixed with 1% osmium tetroxide in PBS, pH 6.8, for 6 hours. Then material was dehydrated through an ascending ethanol-acetone series to 100% acetone. After that samples were embedded in araldite 6005 medium, according to the manufacturer's protocol. Sections were cut 2 μm thick with glass knives, put on glass slides without mounting medium, stained with 0.01% berberine or its combination with DAPI and scanned under LSCM Olympus FV-1000 based on Olympus BX61, using 473 nm or combination of 405 and 473 nm lasers. Z-stacks of several scans were usually obtained and presented here. Some fresh material was simply cut with razor blade into rather thick sections and observed under LCSM.

For transmission electron microscopy (TEM) observations, we took capsules at stage C (Fig. 1), where peristome zone was about 100–200 μm long. Material for TEM observation was taken from the same araldite embeddings. The search of appropriate position was made by the same 2 μm thick cuts, studied under the light microscope. A Leica UC-5 Ultracut-R (Leica Microsystems) ultramicrotome with a diamond knife was used to make ultrathin sections (ca. 50 nm). The sections were examined with a JEM-1011 TEM (Jeol, Japan) at accelerating voltage of 80 kV, with a CCD GATAN ES500W, in the Laboratory of electron microscopy at the Biological faculty of Lomonosov Moscow State University.

Scanning electron microscope (SEM) observations of peristome structure were done with the SEM Jeol 6380 for specimens coated by gold without additional preparation.

RESULTS

Buxbaumia aphylla

Sporophyte on the earliest studied stage of development is shown in **Fig. 2A**; it is composed mostly of the foot, which is 3–5 times longer than the capsule. Young capsule is well delimited by a ringlike fissure. The capsule is ca. 230 μm in diameter at base and its length is about the same. Its wider proximal part is formed by homogeneous cells, except for well differentiated epidermis, while in its distal conic part, 230 μm long, the peristomial / sporogeneous layers are apparent (Fig. 2). One especially conspicuous layer consists of rectangular cells that form an arc in distal ca. 50 μm of the capsule. These cells are 8–14 μm thick (in radial direction) and 15–20 μm long, while some have old cell wall outlines of 30–35 μm long, with thin cell wall of recent transverse division, subdividing it into mostly more or less equal halves.

This layer is the second from the surface in uppermost region of 1–4 cells wide, while in most of its length it is the third one, as cell outwards it are already periclinally divided and thinner (=younger) cell walls are observed within them. The transverse cell walls of epidermal cells and of cells of conspicuously differentiated layer of rectangular cells are offset, as seen in longitudinal section (Fig. 2). The trans-

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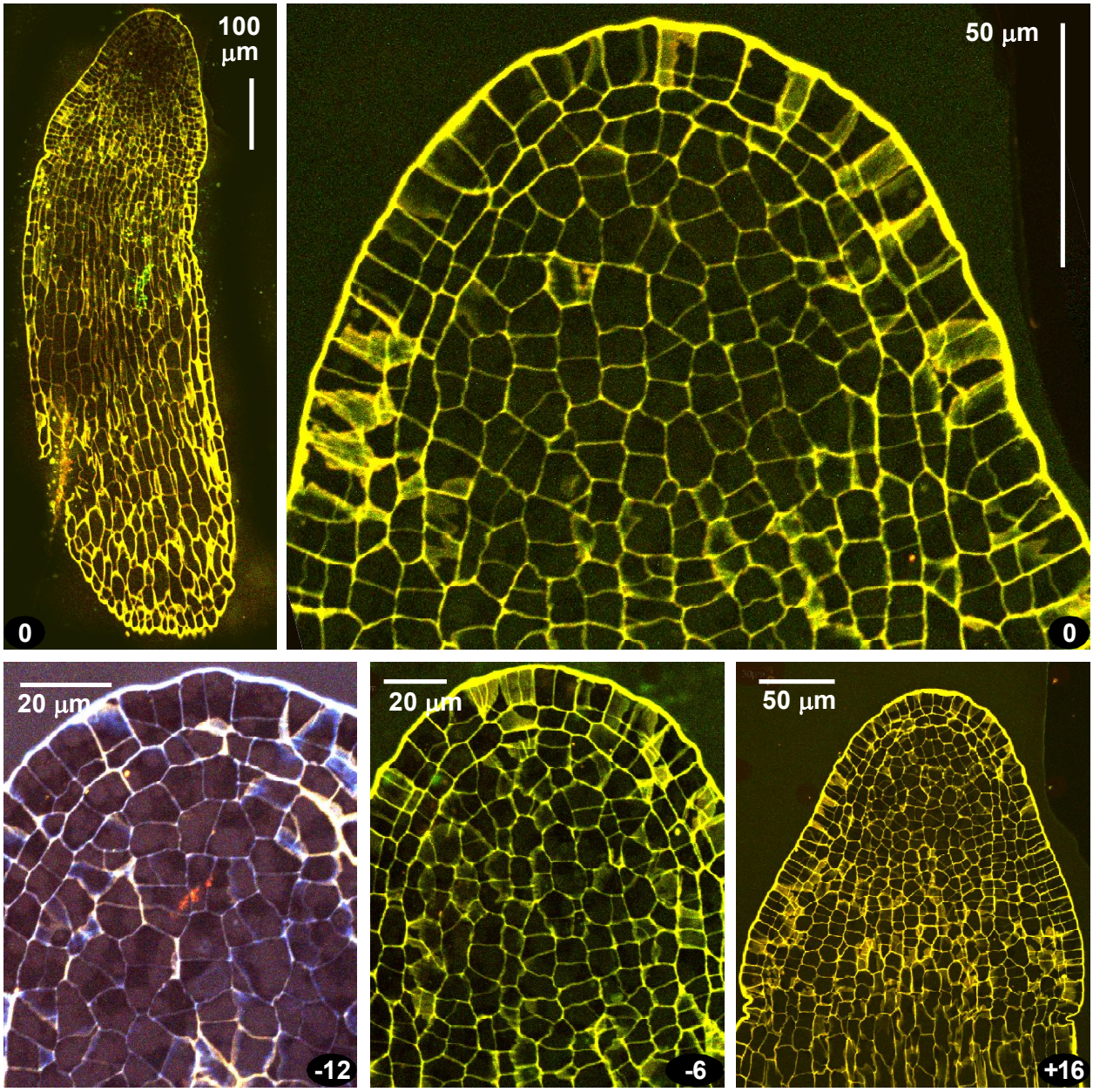
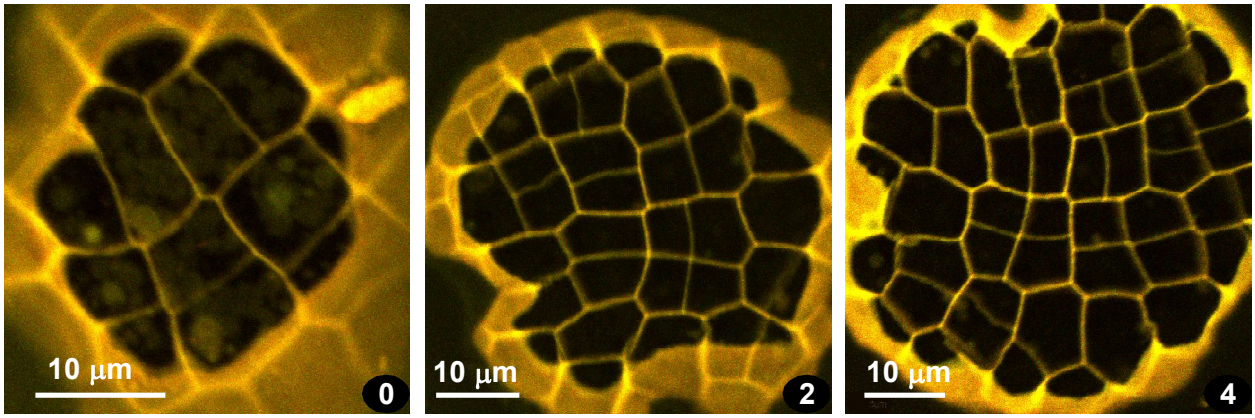


Fig. 2 (above), LCSM. *Buxbaumia aphylla*: longitudinal sections of sporophyte, showing in addition to median section (0) also neighboring ones from both sides, showing variation. Numbers indicate the distance from the median section, in μm.

Fig. 3a (below, beginning of the series shown also on next page), LCSM. *Buxbaumia aphylla*: transverse sections of young capsule. Numbers indicate the distance from the uppermost section in μm.



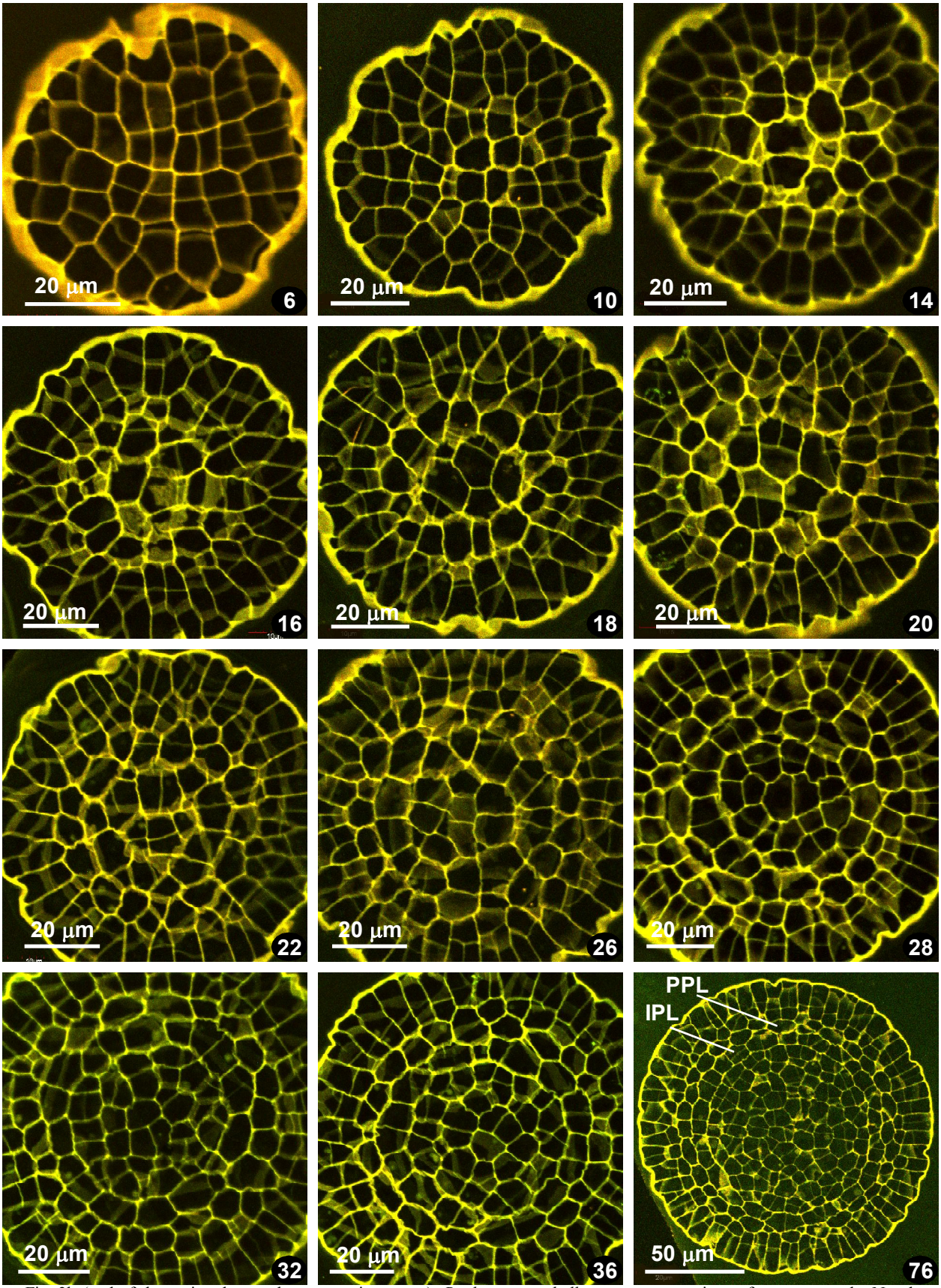


Fig. 3b (end of the series shown also on previous page): *Buxbaumia aphylla*: transverse sections of young capsule. Numbers indicate the distance from the uppermost section in µm. The homology of peristomial layers becomes apparent from the comparison with similar structures in Fig. 5. Note large irregularly radially arranged cells at about the top of endothecium, Figs. 3-14 – 3-20 (cf. with Fig. 11-0).

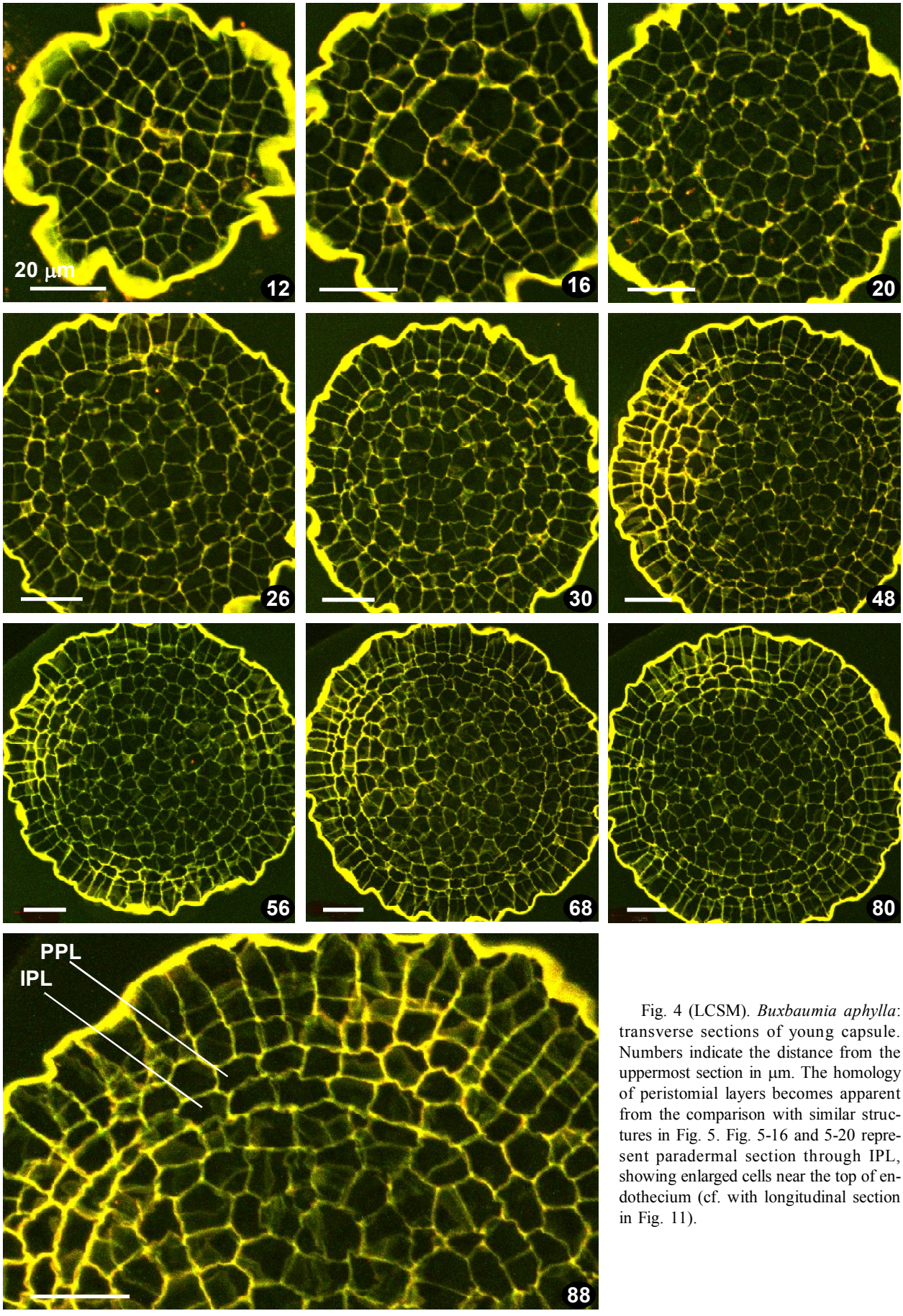


Fig. 4 (LCSM). *Buxbaumia aphylla*: transverse sections of young capsule. Numbers indicate the distance from the uppermost section in μm. The homology of peristomial layers becomes apparent from the comparison with similar structures in Fig. 5. Fig. 5-16 and 5-20 represent paradermal section through IPL, showing enlarged cells near the top of endothecium (cf. with longitudinal section in Fig. 11).

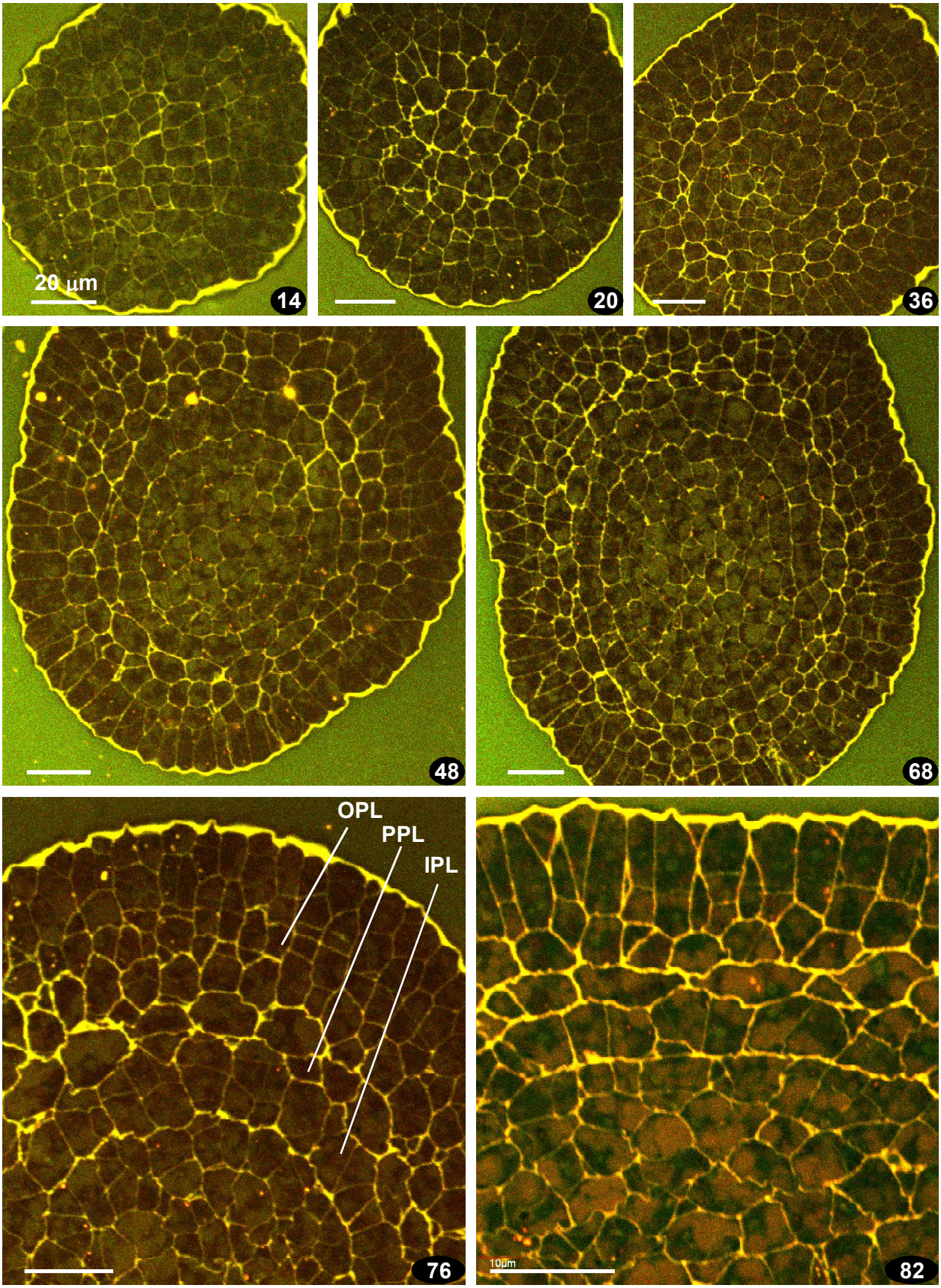
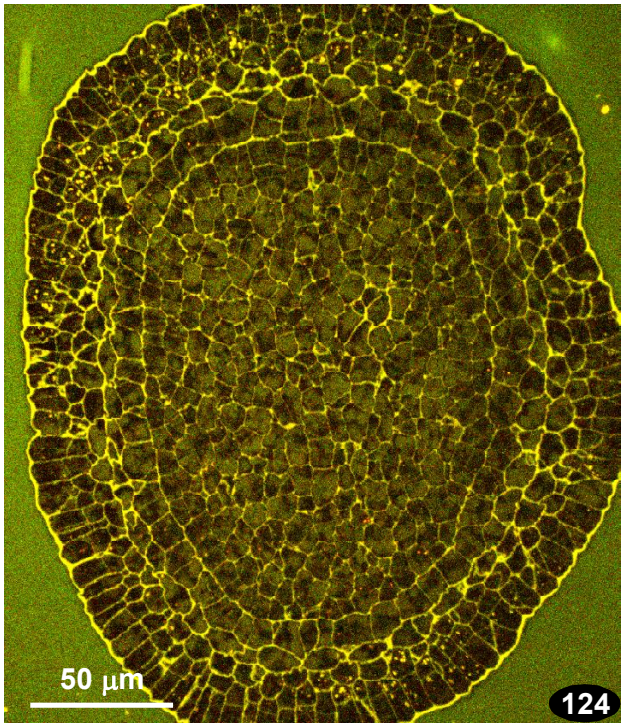


Fig. 5 (LCSM) (the series continued also on the next page). *Buxbaumia aphylla*: transverse sections of young capsule. Numbers indicate the distance from the uppermost section in µm. In the basal portion of peristome number of PPL cells is 48; IPL cells undergo numerous anticlinal divisions (Figы. 5-124, 5-170).


50 μm
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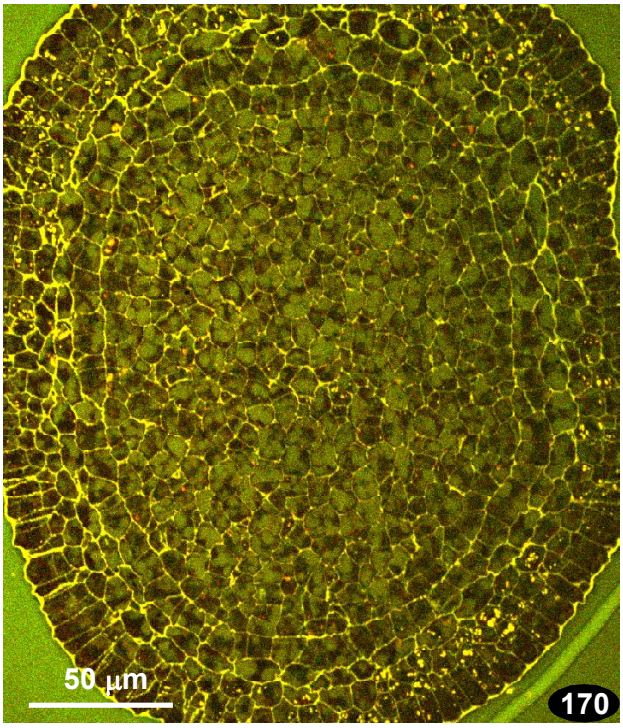
50 μm
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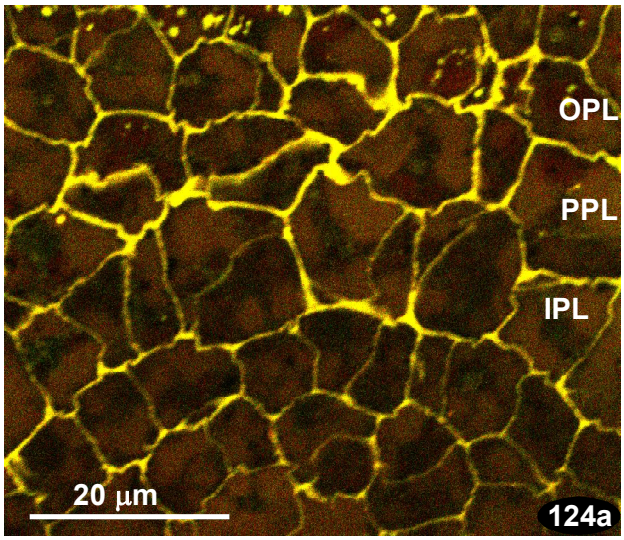
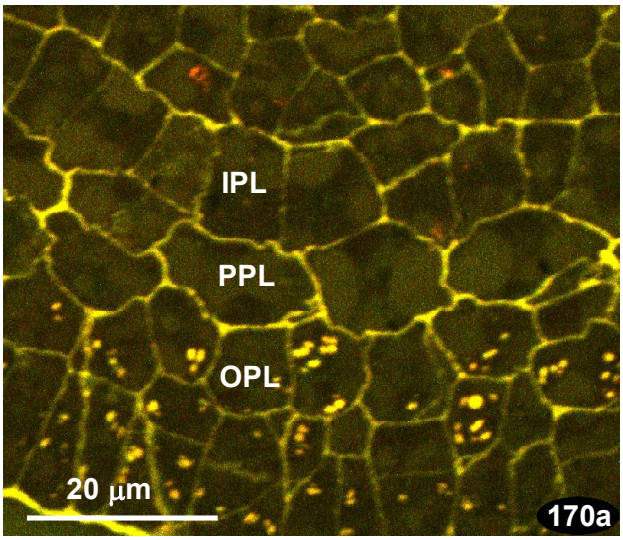
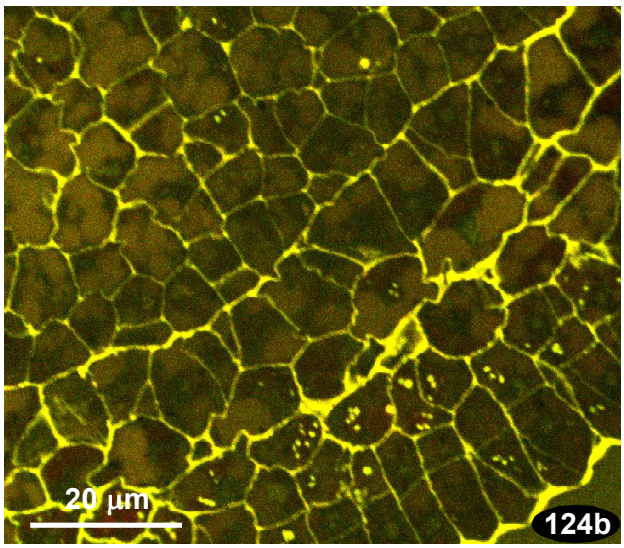

OPL
PPL
IPL
20 μm
124a


IPL
PPL
OPL
20 μm
170a


20 μm
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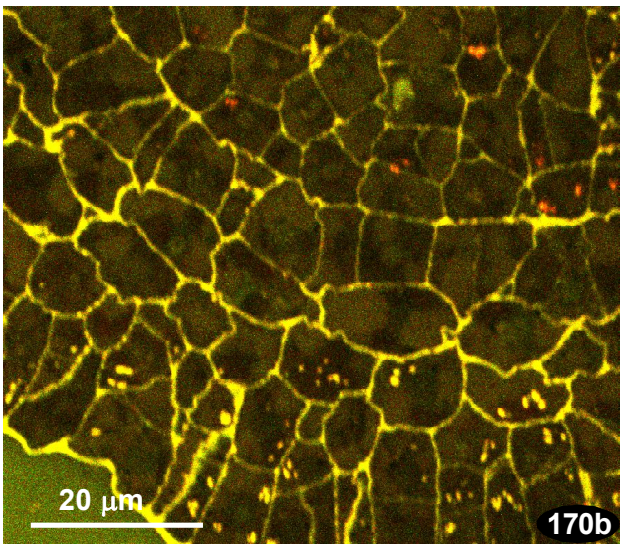
20 μm
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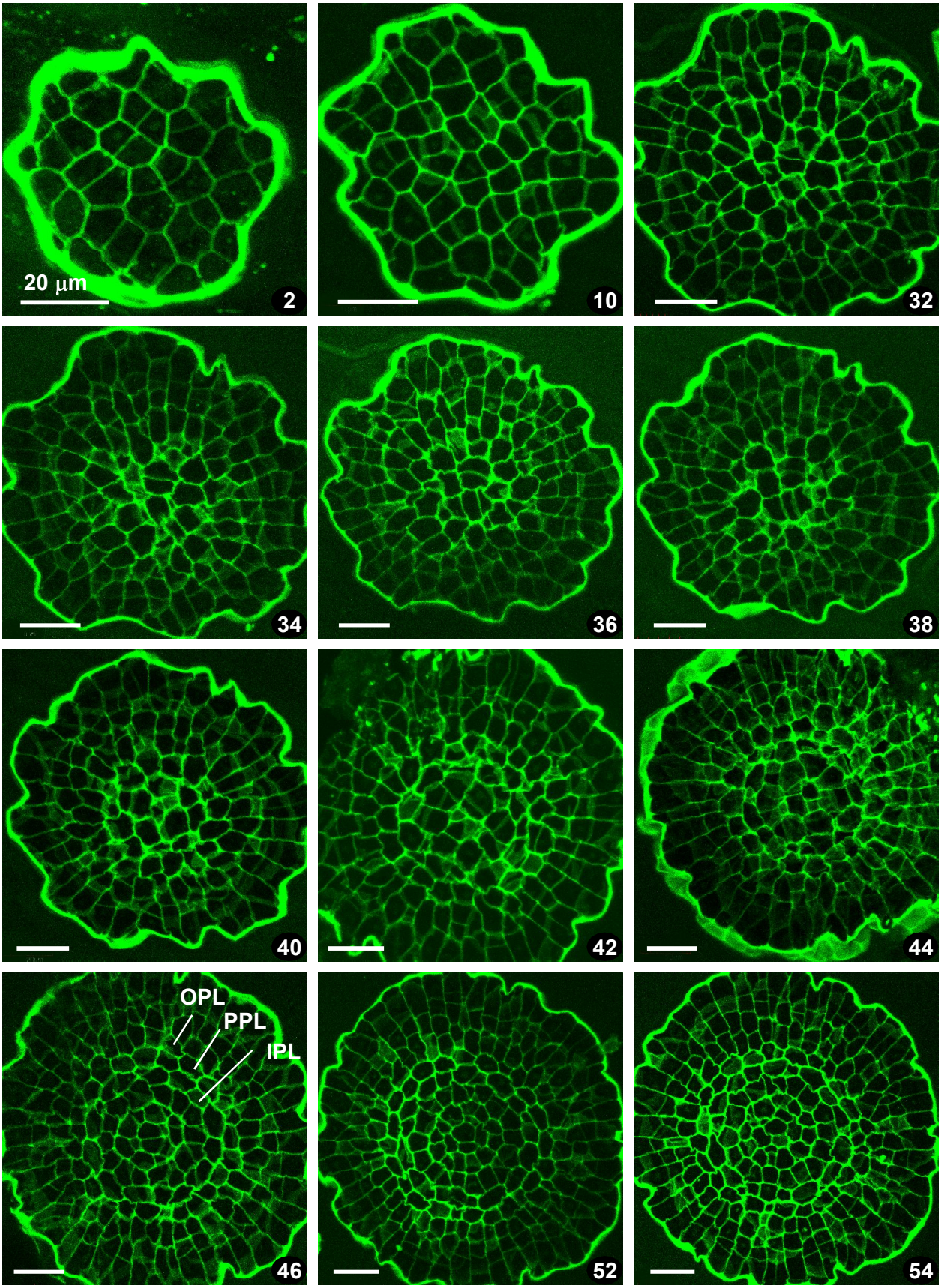


Fig. 6a (LCSM) (series shown also on the next page). *Buxbaumia aphylla*: transverse sections of young capsule, showing cell arrangement in concentric rings. Numbers indicate the distance from the uppermost section in μm.

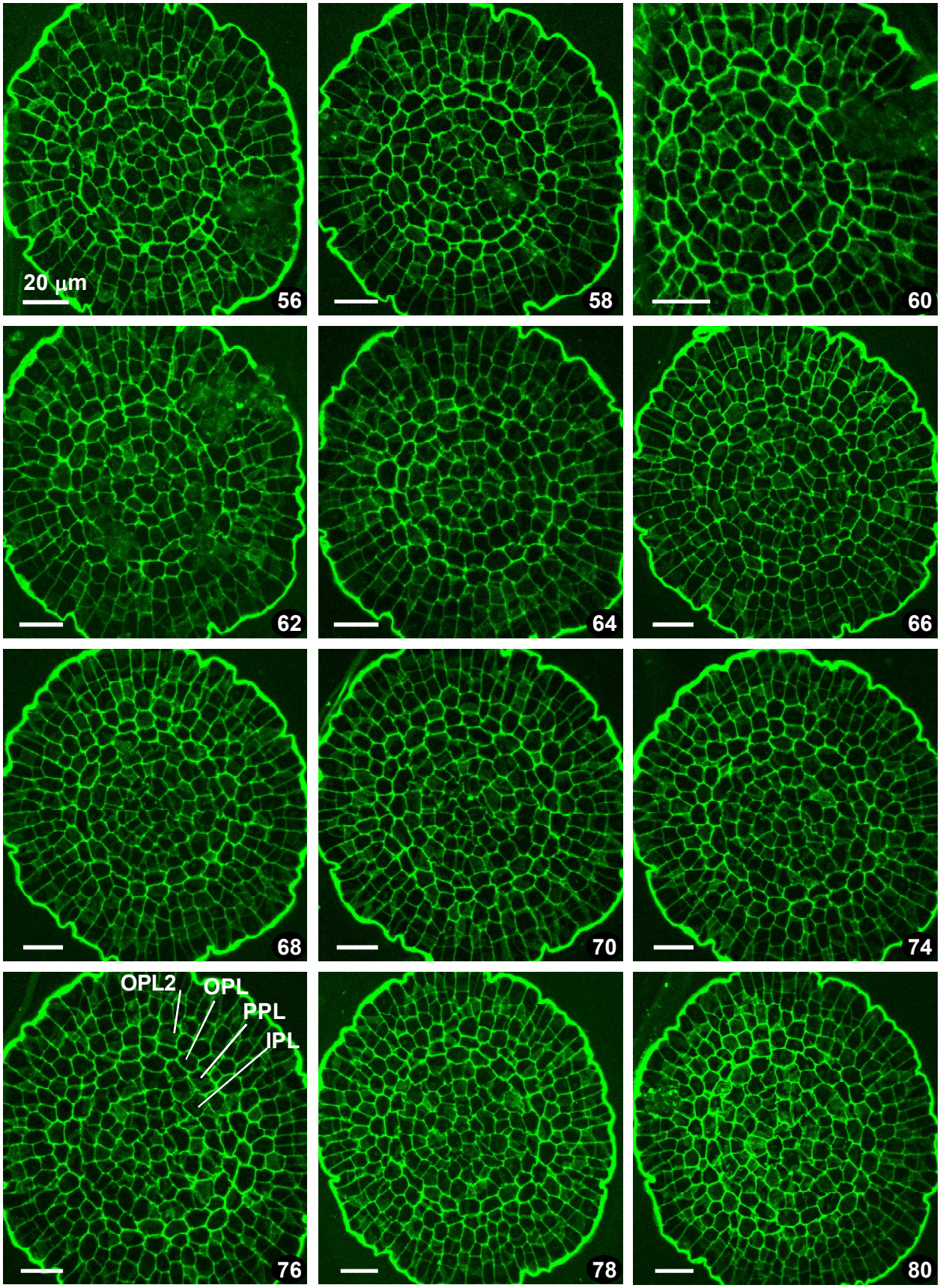


Fig. 6b (LCSM) (series shown also on the previous page). *Buxbaumia aphylla*: transverse sections of young capsule, showing cell arrangement in concentric rings. Numbers indicate the distance from the uppermost section in µm.

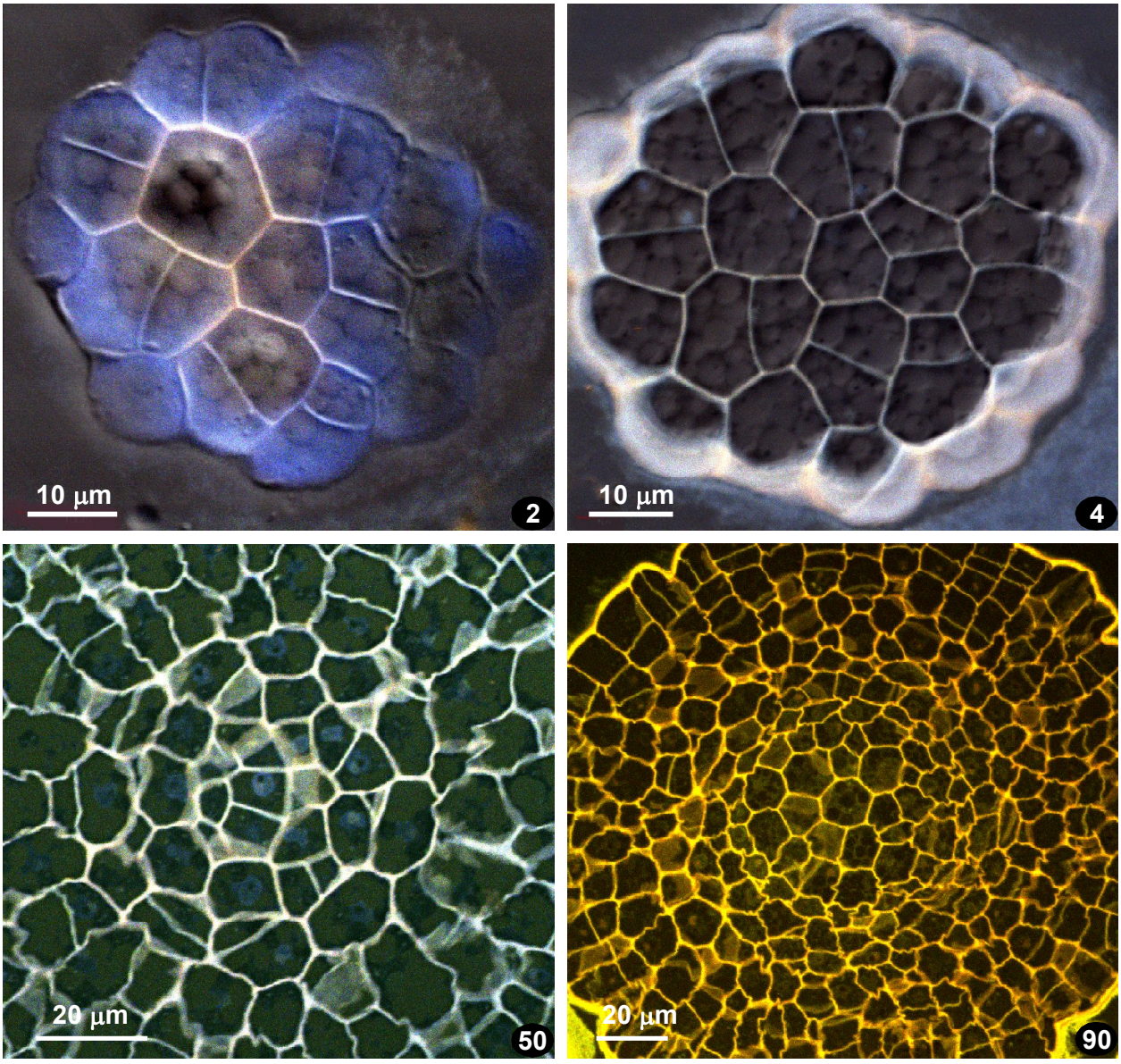


Fig. 7 (LCSM). *Buxbaumia aphylla*: transverse sections of young capsule. Uppermost cells are arranged in a rosette-like pattern. At 50 μm from the apex, note a triangular arrangement of 12 cells (cf. with Fig. 8, showing another series). At 90 μm from the apex cells in IPL are 12, and in PPL 24. Numbers indicate the distance from the uppermost section in μm.

verse cell walls of layers outwards of conspicuously differentiated layer (i.e. "two-layered epidermis" are aligned, which clearly corresponds to the fact that their periclinal cell walls are still much thinner than other cell walls.

The conspicuously differentiated layer at the distance ca. 50 μm from the sporophyte apex jounts to multilayered subepidermal tissue, indicating propably the end of peristome area, although the continuation of more or less definite layers extend downwards to about another 50 μm. The group of cells "under the arc" is more or less delimited at about the same level. These cells are large, ca. 20 μm, polygonal, and often with thin (=young) cell walls, dividing them. In the central part of this group divisions are longitudinal, indicating the recent elongation of this part of capsule, whereas the most distal cell in this group has thinner cell walls, indicating its division rather perpendicular to the axis of the sporophyte, although considering that cells deriving from it are following the arc to peristomial layers, the direction of these divisions should be considered transverse, i.e. further developing longitudinal cell rows.

The complete series of 2 μm sections shows similar shape of this part, becoming more acute from the central section (denoted in Fig. 2 as "2-0"). Fig. 2-16, i.e. showing section at 16 μm from the central one, is clearly more fast tapered to the apex. The central part can be assumed as such by apical epidermal cells that are still not divided periclinally, unlike most other epidermal cells.

Inwards from the conspicuously differentiated layer, cells are not forming especially regular layers, but they abruptly differ by numerous oblique and unequal cell divisions.

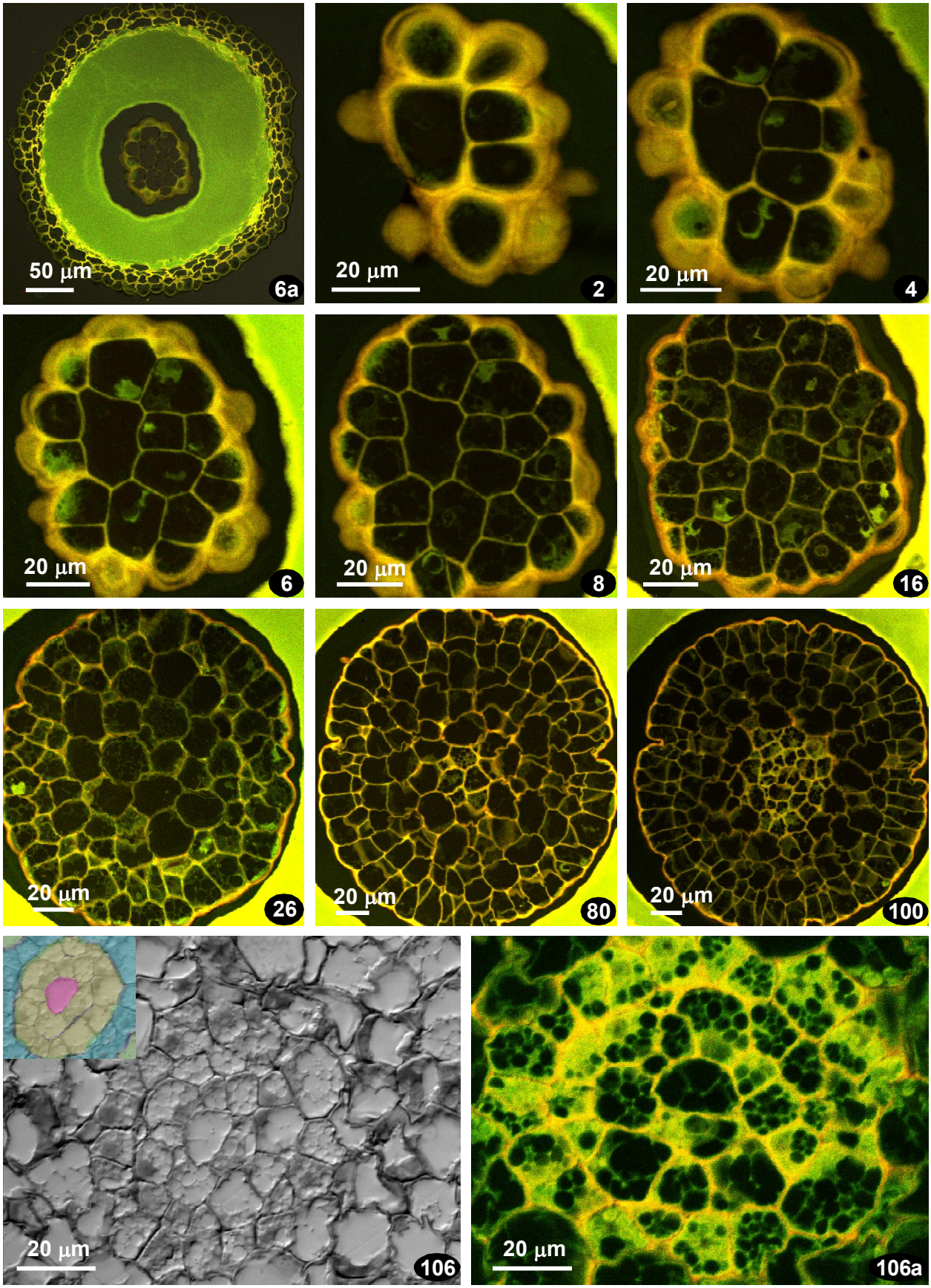


Fig. 8 (LCSM). *Buxbaumia aphylla*: transverse sections of young capsule. Fig. 9-106 provides DIC image in pseudotransmitting channel, with insertion of central cell in false colors: 12 cells in the outer layer of endothecium (green) are surrounded by ca. 18 cells of IPL (blue), the latter partly having strongly wavy cell walls (cf. also Fig. 7-90). Numbers indicate the distance from the uppermost section in µm.

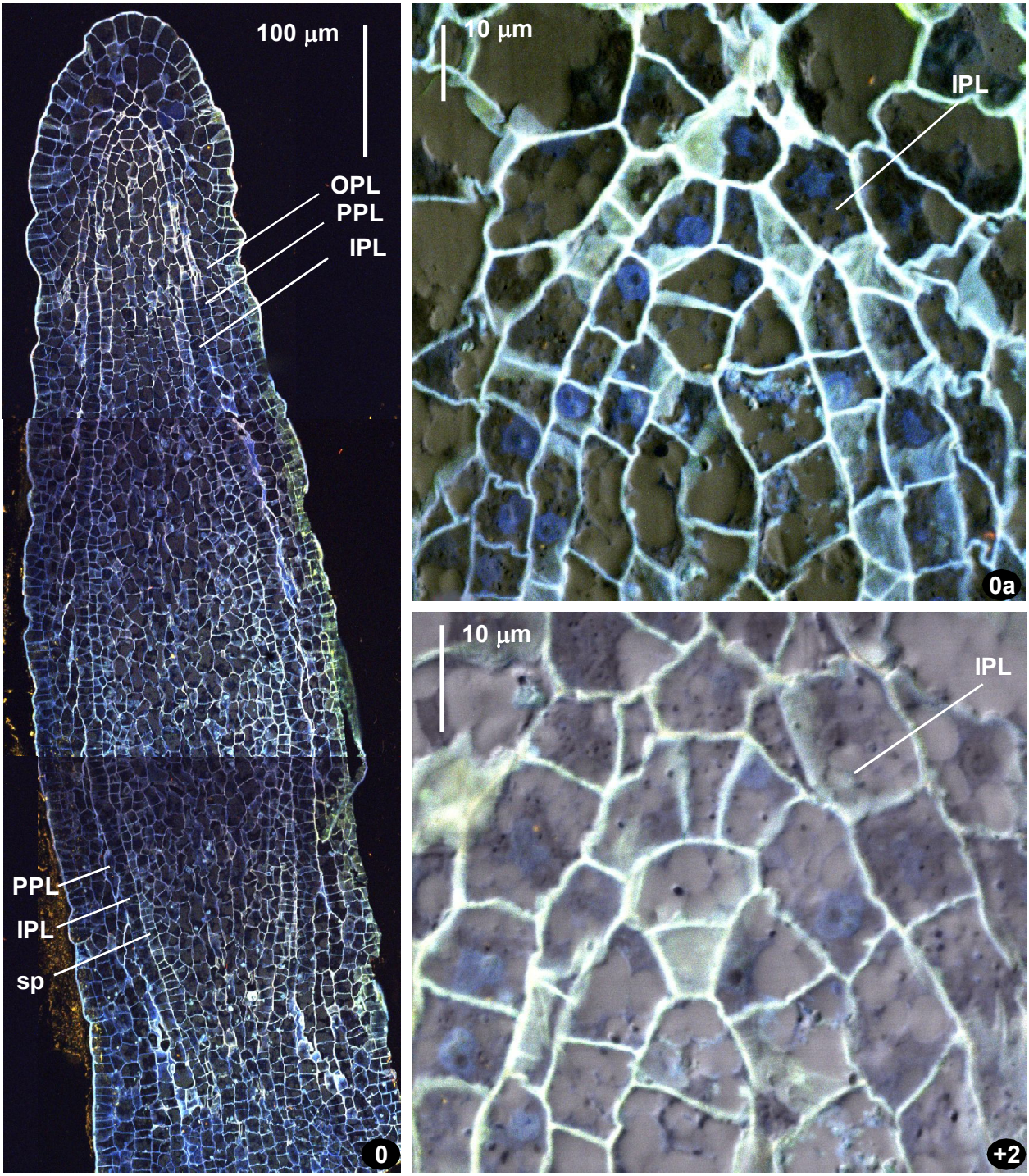


Fig. 9 (LCSM). *Buxbaumia aphylla*: longitudinal sections of young capsule, showing peristomial layers, including their continuations beyond the part where peristome is forming (IPL, PPL and OPL), and outermost layer of endothecium, developing later in sporogenic tissue (sp). Subapical endothecial cell of tetrahedral shape is close-uped (two nearby 2 μm' secions are shown).

* * *

The series in transverasal sections shown in **Fig. 3** is slightly younger than stage in Fig. 2, judging from sporophyte diameter at the level where conspicuously differentiated layers become apparent. The fundamental square pattern is seen at the level of uppermost cell, while already at the level of ca. 10–12 μm below the surface (Fig. 3-14), the square transforms into somewhat irregular pattern where at different levels are recognizable either (1) triradial pattern (cf. Figs. 3-18, 3-20), or (2) large cell surrounded by six cells (Figs. 3-14, 3-26). Uppermost cells are 5–8 μm, forming a rather regular squares, whereas later they elongate to rectangles, which arrangement in somewhat T-shaped, as the elongation of two of them is directed perpendicular to two others (Figs. 3-4, 3-6). Subepidermal cells below are large, to 12 μm, likely corre-

sponding to cells of conspicuously differentiated layer as in Fig. 2. A cell pattern in concentric ring appears in Fig. 3-18 and 3-22, but it becomes unequivocally distinct only since the level of Fig. 3-28. Below this level, rings are clearly seen in all the sections up to Fig. 3-76, and at ca. 80 μm from the apex regular cell arrangement disappear. Since level of 3-32 two rings are seen. The number of cells in them are somewhat difficult to count since some cells are recently divided, while some are in a such position that their affiliation to one or another row is questionable. In any case, an approximate count in Fig. 3-32 gives about 16 cells in the inner layer and about 24 in the outer one. In Fig. 3-76, the lowermost with apparent rings, there are about 24 cells the inner layer and 32 in the outer one.

Series in **Fig. 4 s**hows approximately the same pattern as in Fig. 3, but the plant was slightly larger, with differentiated peristomial layers extending to 100 μm form the apex. The large conspicuous cells appear at 20 μm from the apex, where a ring of 12 cells in inner layer and ca. 20 cells in outer layer occur (Fig. 4-20), then number of cells increases to 20/26 (Fig. 4-26) and 32/42 (Fig. 4-80).

Series in **Fig. 5** represents the plant only slightly longer that in Fig. 4, but it achieves a largest number of cells in peristomial layers. At 170 μm from the apex, their number in the outer circle reaches 48, while in the inner one cells are more numerous, but it is virtually impossible to count them with confidence, as many have imperfect and oblique anticlinal cell walls, and some are hardly discernible. At earlier stages, the number on cells in the inner circle is about 16, and in the outer one about 20 (Fig. 5-36). Close to peristome base, the cell of outer and inner layers achieve the shape common for cells in the primary peristomial layer (PPL) and inner peristomial layer (IPL) in other arthrodontous mosses. The cells of PPL have thicker cell walls, and mostly lack further anticlinal cell divisions, which is a common case in IPL near peristome base (Shaw *et al*., 1989b; Ignatov *et al*., 2018). The outer peristomial layer (OPL) is apparent in sections of this series, and noteworthy, the number of OPL cells is approximately double of the number of cells in PPL (Fig. 5-76), which is a typical pattern in arthrodontous peristomes.

Fig. 6 comprises a rather common variant (not all of them shown) of *Buxbaumia aphylla* sporophyte structure at the stage shown in Fig. 1C or a

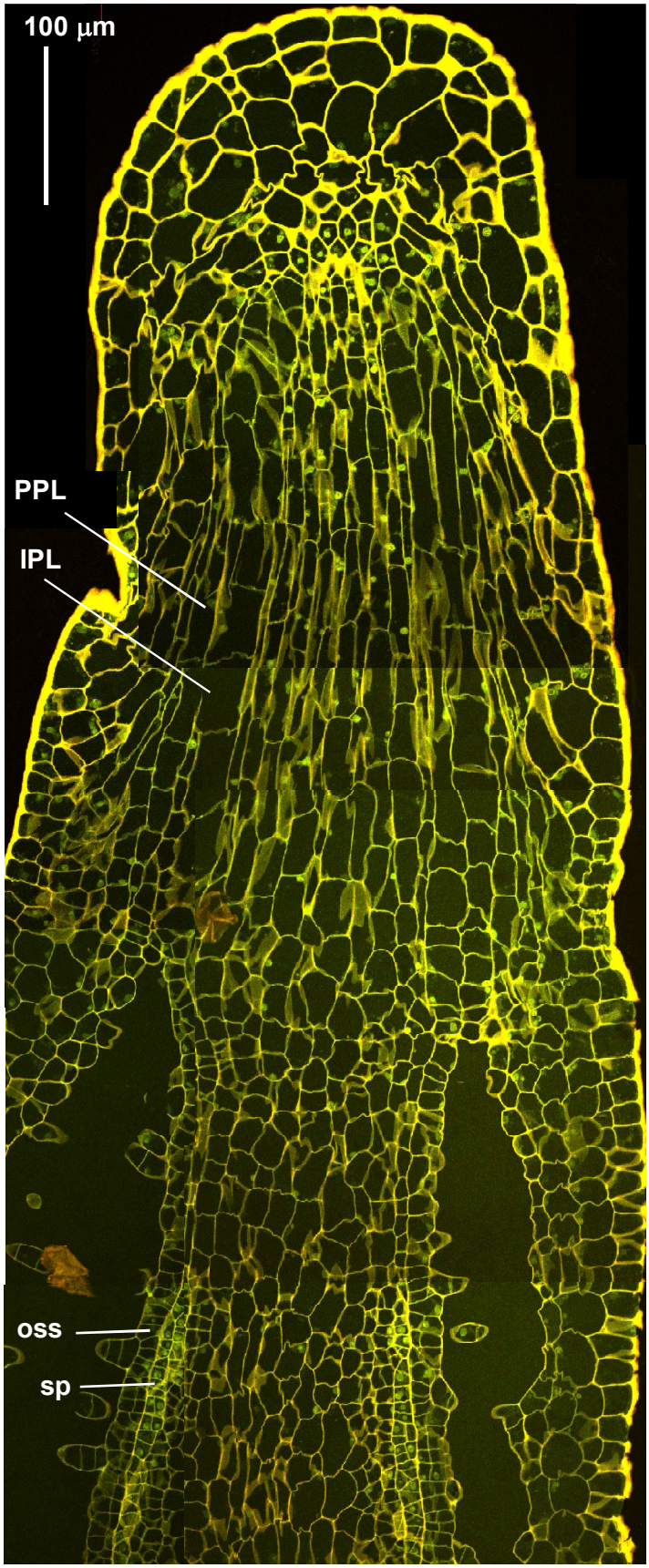


Fig. 10a (LCSM). *Buxbaumia aphylla*: longitudinal sections of moderately young capsule, showing peristomial layers (IPL, PPL), sporogeneous tissue (sp) and outer spore sac (oss). Section is made at 22 μm from median one in Fig. 10b, thus lacking subterminal endothecial cell, and showing cells near endothecium end especially rich in chloroplasts and presumably continuing divisions (cf. Figs. 11–12).

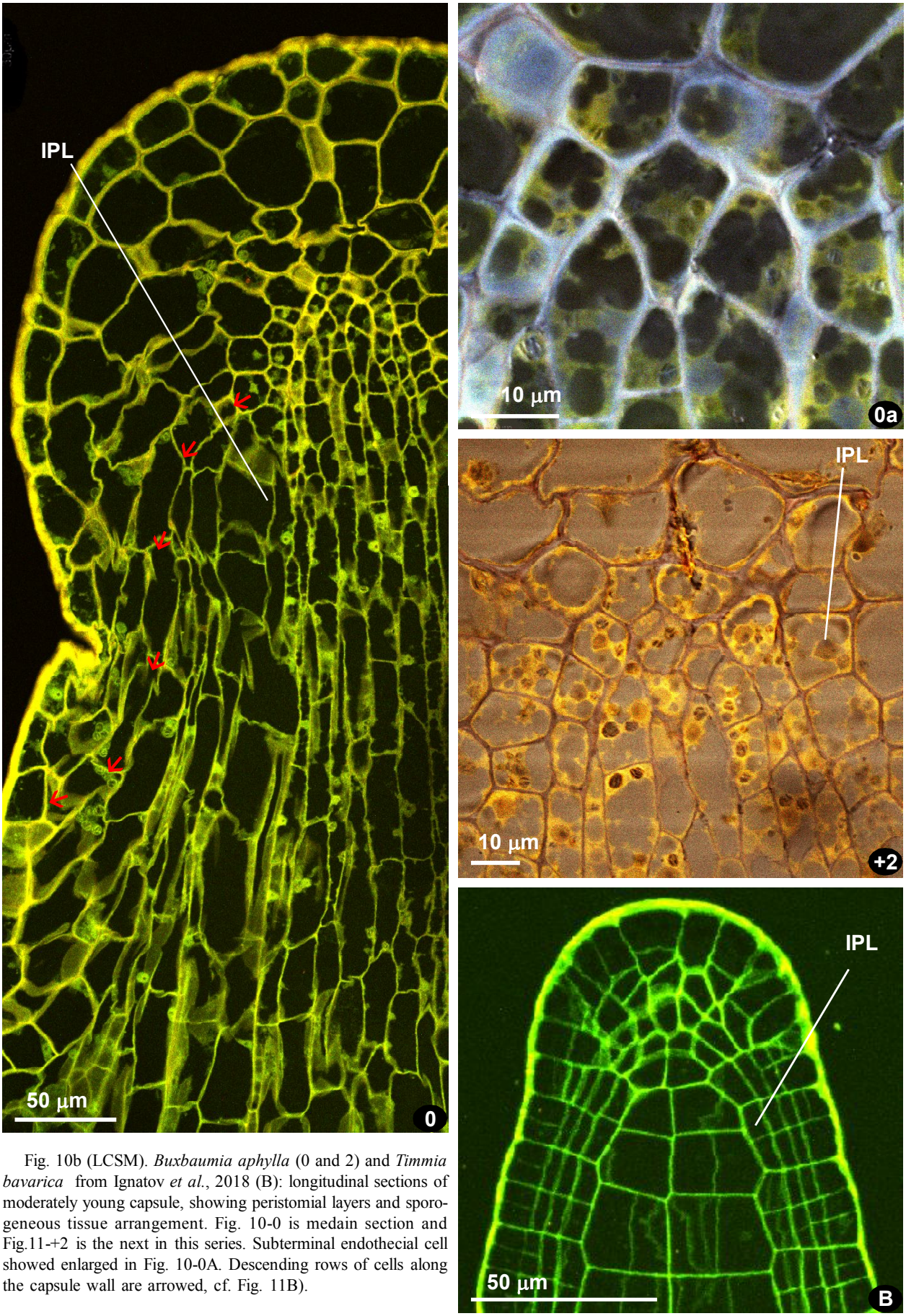


Fig. 10b (LCSM). *Buxbaumia aphylla* (0 and 2) and *Timmia bavarica* from Ignatov *et al.*, 2018 (B): longitudinal sections of moderately young capsule, showing peristomial layers and sporogeneous tissue arrangement. Fig. 10-0 is medain section and Fig.11-+2 is the next in this series. Subterminal endothecial cell showed enlarged in Fig. 10-0A. Descending rows of cells along the capsule wall are arrowed, cf. Fig. 11B).

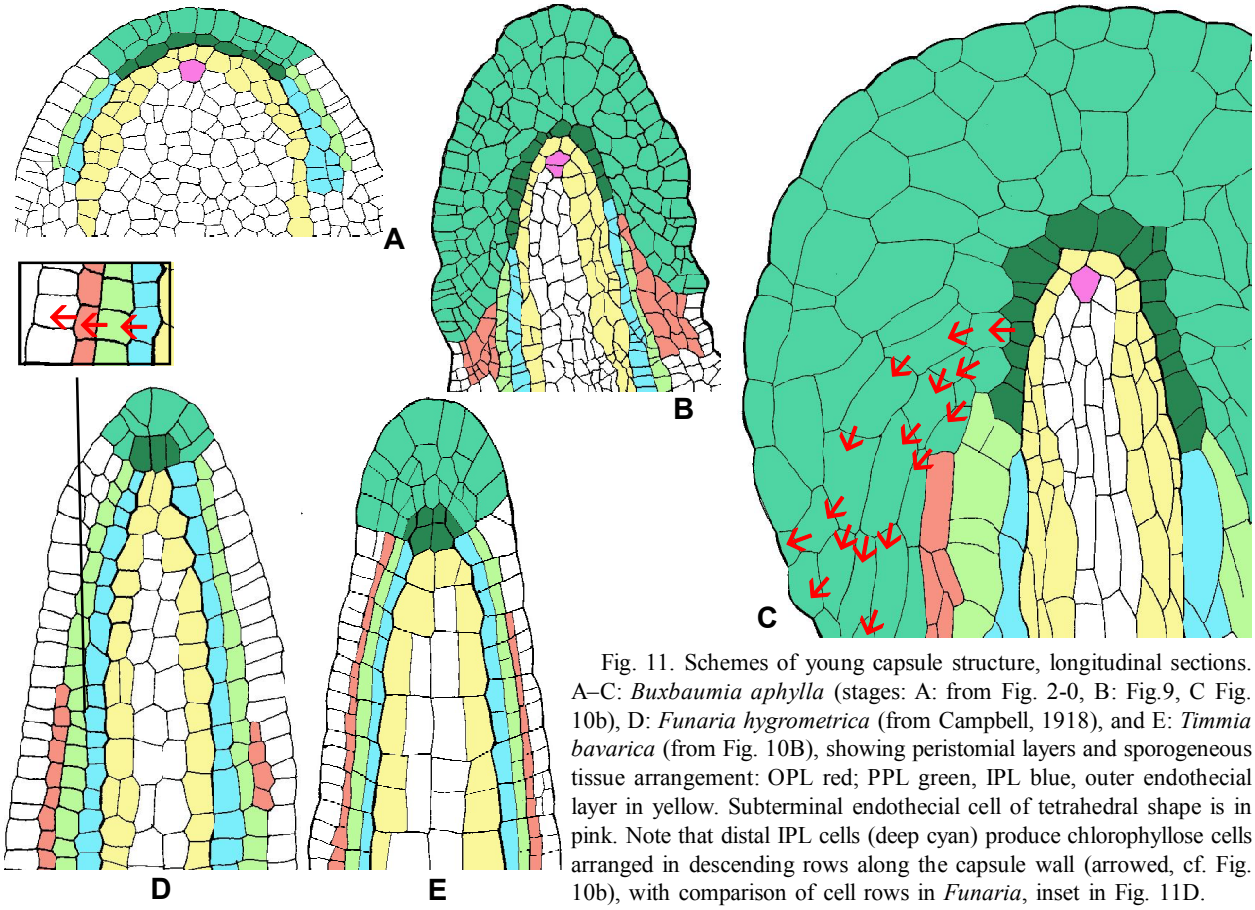


Fig. 11. Schemes of young capsule structure, longitudinal sections. A–C: *Buxbaumia aphylla* (stages: A: from Fig. 2-0, B: Fig.9, C Fig. 10b), D: *Funaria hygrometrica* (from Campbell, 1918), and E: *Timmia bavarica* (from Fig. 10B), showing peristomial layers and sporogeneous tissue arrangement: OPL red; PPL green, IPL blue, outer endothecial layer in yellow. Subterminal endothecial cell of tetrahedral shape is in pink. Note that distal IPL cells (deep cyan) produce chlorophyllose cells arranged in descending rows along the capsule wall (arrowed, cf. Fig. 10b), with comparison of cell rows in *Funaria*, inset in Fig. 11D.

little later. Cell arrangement is especially "rosette-like", formed by concentric rings, with progressive increase the cell number in these rings from ca. 16 to ca. 24. Rosette-like cell arrangement starts from the apical part of the capsule, and the more or less conspicuous concentric peristomial layers appear since ca. 30 µm from the apex. Cells in the centre of sporophyte become large, and at since Fig. 6-32, the large cell, ca. 16 µm in diameter, appears in the middle. From the serial sections its shape can be assumed as tetrahedral. After ca. 15 µm (since Fig. 6-46), the peristomial layers acquire a regular structure.

Series in **Figs. 7 and 8** comprise almost the same pattern, with triradiate or rosette-like cell arrangement in the uppermost part of the operculum. Central cell surrounded by a triangular group with 12 cells in outer endothecial layer is very similar in them, despite it appears in Fig. 7 at 50 µm from the apex (i.e., the same as in Fig. 6-52), while in series in Fig. 8 only at about 100 µm. Roughly, these two situations (in Fig. 6 & 7 and Fig. 8) correspond to the longitudinal sections shown in Figs. 9 and 10 respectively. The knob-like operculum makes the "top of endothecium" deeper and deeper immersed in the course of sporophyte growth. The operculum cells are very large, to 70 µm. Although chloroplasts are scattered (Fig. 10), the capsule is bright-green (Fig. 1).

Longitudinal sections in **Figs. 9 and 10** roughly correspond to the stages of capsule development shown in Figs. 1C and 1D respecitively. IPL is definitely recognizable in Fig. 10 due to the transition to sporogeneous tissue which is conspicuously differentiated in the lower part of the capsule, as well as by strongly enlarged cells. PPL is interpretable mostly just as a layer next to IPL.

In Fig. 9 the IPL can be recognized not that easily, as at least four layers are more or less differentiated there. We recognize it by (1) the most conspicuous differentiation and longest extension compared to other layers; (2) by the position against conspicuous obovate (assumingly tetraherdal) cell in the subterminal endothecium.

This cell occupies the unusual position in this place, breaking the regular order known in almost all mosses (cf. Figs. 10-0a and 10B). In Fig. 9 and 10 its position is similar, and in four other studied series in longitudinal sections (not shown) it keeps subterminal position, being the second cell below the arc of cells which belongs to IPL. Such arrangement allows homologisation of conspicuously differentiated layer in the earliest series (Fig. 2, cf. Fig. 11). Additional comments on this subterminal cell will be given in Discussion section.

Cells around the upper end of conspicuously differentiated peristomial layers are shown in Fig. 11 in deep cyan color, indicating cells presumably retaining meristematic activity: those cells begin S-shaped cell rows (Fig. 10a, 11B) conspicuously descending along the capsule wall, terminating on the operculum surface much below their beginnings (cf. also Fig. 15a). Light cyan color denotes descendants of the deep-cyan cells.

Fig. 12 shows one more longitudinal section at stage slightly earlier than in Fig. 10, studied under TEM. Most cells are highly vacuolised, in both endothecium and amphithecium. Some vacuoles in amphithecium have whitish homogeneous content (presumably carbohydrates), whereas other have grey inclusion, putatively proteins, while all endothecium cells have only electron-whitish vacuoles. Vacuole size and shape (Fig. 12) allow their subdivision into four categories: especially large vacuoles (Vxl), over 25 μm, fill almost whole cell volume in the cell near the capsule apex; large vaculoes (Vl), 10–15 μm, occur along the endothecium middle, they are only slightly lobate; medium-sized vacuoles (Vm = 4–8 μm), are characteristics of transition to outermost endothecial layer, where vacuoles are smallest (Vs = 1.5–3 μm). TEM observations revealed abundant chloroplast in upper parts of capsules, much more visible than in e.g. in fluorescent images, e.g. in Fig. 10a, where they are concentrated around the upper part of endothecium, in a zone presumably retaining meristematic activity (at least this region has the least vacuolized cells).

In general, the outermost endothecial cells are the most conspicuous in TEM images: their cytoplasm is condensed and looks granulose, making, among others, chloroplasts not contrasting as in neighboring cells (cf. Figs. 12B and 12D). The content of these cells contrastingly differ from cell next outwards (IPL and its continuation): the latter often possess dark areas with agranular endoplasmic reticulum (Fig. 12C, E). Cell walls between IPL and outermost endothecium cells are thick and lack plasmodesmata, which occur in cell walls between neighboring cells belonging to outermost endothecium layer.

The border between outermost endothecium layer and layers inward is occasionally conspicuous, as the latter may also have agranular endoplasmic reticulum along cell wall. However, sometimes granulose content occurs in several cell layers, hampering layer delimitation.

Pleated cone: The development of an endosotme in *Buxbaumia* is in general described by Edwards (1984), but early stages of its formation remained little known. Our numerous preliminary attempts to make transverse sections at these stages failed, as shortly after some cells of IPL and PPL start to enlarge, these layers break, thus the picture looks like in Fig. 18-308 for *Buxbaumia viridis*. Series shown in **Fig. 13** demonstrates the process at different levels, from top to ca. 100 μm, while below the structure does not change much up to the peristome base (i.e. in the further ca. 700 μm).

All the cases we studied show the cell inflation starting from a single point and spread to embrace the endothecium. PPL cells are especially strongly enlarged and seem to acquire an ability for intrusive growth by cell projections (Fig. 13-194, arrowed [note that such projections are not unique and occur also in *Buxmaumia minakatae*, Figs. 20-130]). The tissue of the primary cone is very delicate, almost unseen in capsules, opened even on considerably later stages (Fig. 15B).

The number of folds within this series starts from 26 (Fig. 13-264 and 13-274), then 28 (Fig. 13-300), 32 (Fig. 13-320), 39 at 1016 μm (Fig. 13). The number of folds between 24 and 29 is seen in razor-blade sections in a relatively upper part of the peristome (Fig. 14), and in SEM picture (Fig. 16A) in the upper part of cone the number of folds is 24.

Later on, the cone material becomes firmer (**Fig. 14)** and covered by material which makes its surface papillose (Fig. 16). Note however, that the papillose substance is easily falling off the pellucide endostome membrane, which becomes bold at places (Fig. 16E, F).

Inner surface of endostome cone is less papillose (Fig. 16). The folds at base are somewhat fusing, what is well-seen from the inner surface (Fig. 16, arrowed), thus the number of folds decreases, as it was already noted above.

Columella. The longitudinal sections (Figs. 9, 10, 11) and scheme of explanation of peristomial layers (Fig. 12) in *Buxmaumia* may lead to the conclusion that peristomial layers are overarching an endothecium, thus the columella does not exceed the peristome. This is not so. Columella in *Buxbaumia* is strong, especially in *B. viride* (Fig. 17A), where it forms distally even a kind of epiphragm with a projection similar to those in some Polytrichaceae (albeit fairly irregular). Similarly, the columella in *B. minakatae* is difficult to remove from the spore sac side in the recently opened capsule (Fig. 20E). In the premature capsule of *B. aphylla,* after its operculum was cut into two unequal halves, the columella was stout and firmly attached to the operculum (**Fig. 15**). At the raptured end of columella, a firm-walled vessel-like structure was opened, with three unequal cells on cross section, one about twice bigger than others, thus being similar to the upper cells showin in Fig. 8-2.

Collections of ***B. viridis*** and ***B. minakatae*** available for our study were much fewer in number: five for the former and just one for the latter species for cutting and one for SEM and stereomicroscope observations. However, their study confirm the main structural details revealed in *B. aphylla*. In *Buxbaumia viridis*, prostome is multistratose, although the number of circles are difficult to say (Fig. 17A). The folds on endostome cone are approaching to 32 in number (Fig. 17B). The operculum is knobby in *B. viridis* (Fig. 18A), and endothecium is deeply immersed, being in the young capsule (stage similar to that shown in Fig. 1C) at about 200 μm below apex. The endothecium is relatively narrow in diameter. Amphithecial cells are more inflated and less regularly arranged (Fig. 18) as compared to *B. aphylla*. Radial, rather than quadrate cell arrangement is clearly visible (Fig. 18), and cells are not rarely arranged in imperfect spiral rows (Fig. 18).

Buxbaumia minakatae differs from *B. aphylla* and *B. viridis* by a much shorter prostome (Fig. 19A, B), also partly remaining on the inner surface of operculum (Fig. 19D), and the pleated cone has 24 folds throughout (Fig.

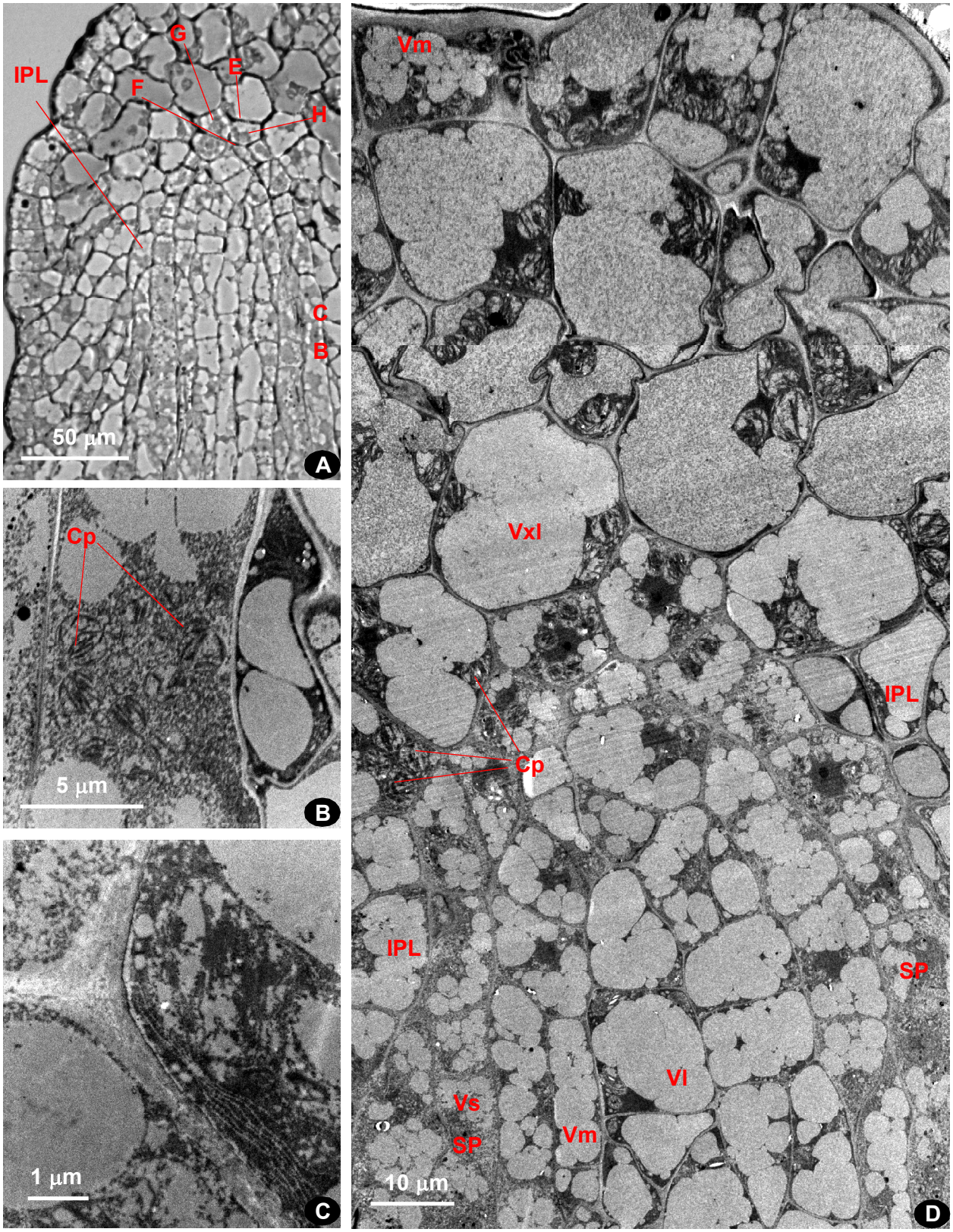


Fig. 12a. *Buxbaumia aphylla*, longitudinal section; A: under light microscope, letters show position of pictures in B, C, E–H (see also next page), showing details of their structure under TEM. Pictures D and I cover considerable parts of section, the former including peristomial part and above, while I illustrates upper portion of peristomial part of sporophyte. Cells are stratified by vacuole size, which are labelled as Vs, Vm, Vl, Vxl (small, medium, large, very large). Vg: vacuoles with grey inclusions; Other labels: Cp: chloroplasts, N: nucleus, ER: endoplasmatic repiculum; Pd: plasmodesmata. IPL: inner peristomial layer; SP: outermost endothecial layer, the continuation of sporogenic layer.

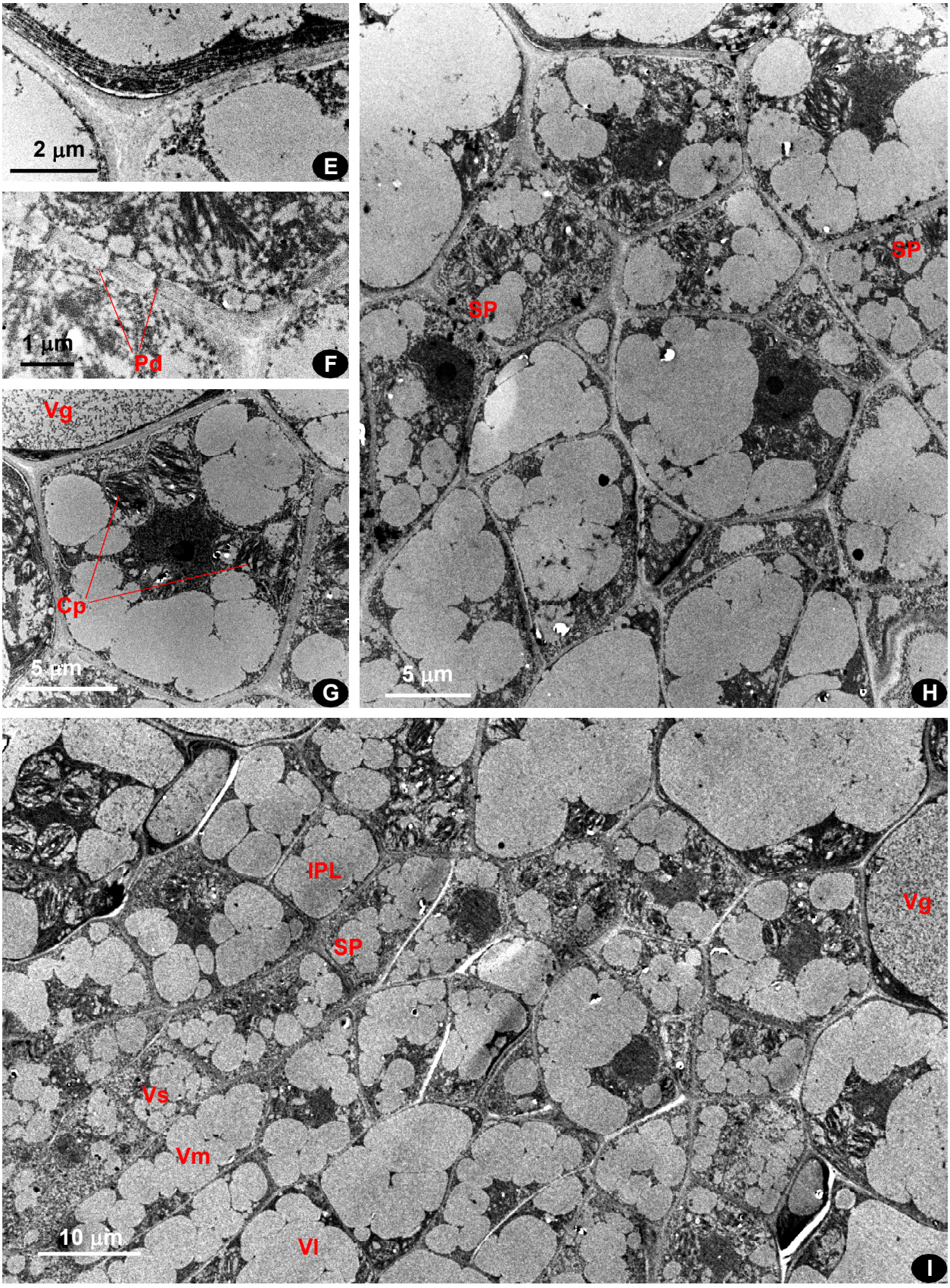


Fig. 12b (TEM). *Buxbaumia aphylla*, longitudinal sections (continued from the previous page). E: border of the upper endothecial cell and cell above with agranular endoplasmic reticulum, note thick cell wall; F: plasmodesmata in cell wall between upper endothecial cell and another cell of outermost endothecial layer; note condensed cytoplasm; G: cell of outermost endothecial layer next to upper endothecial cell; H & I: General views, showing distal portion of peristomial parts of capsule, with variously vacuolized endothecial cells, granulose content of outermost endothecial cells (SP) and cells especially rich in chloroplasts near the upper endothecial cell.

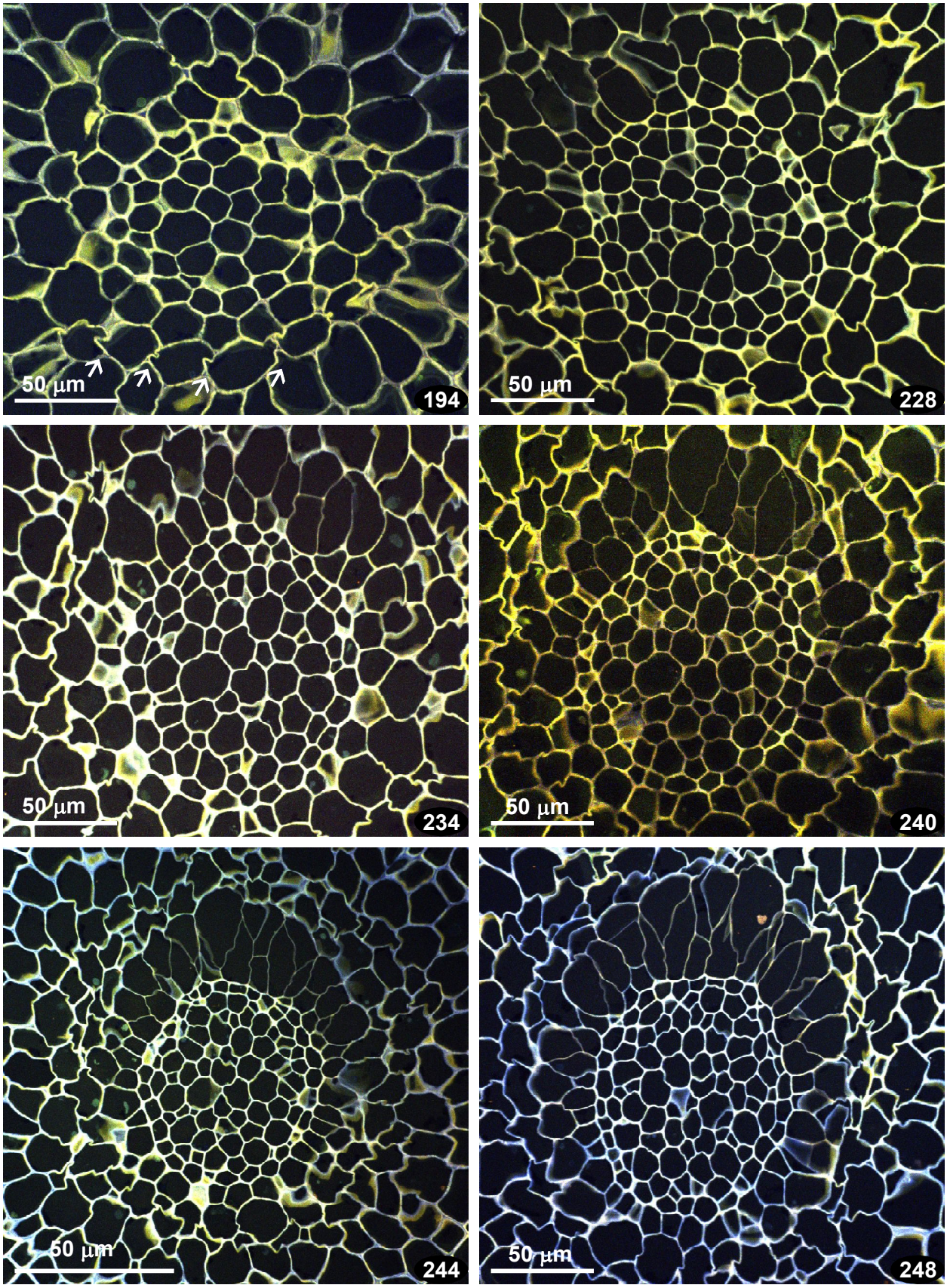


Fig. 13a (LCSM) (beginning of the series continued on the next page). *Buxbaumia aphylla*: transverse sections of young capsule, showing endostome cone formation. Numbers indicate the distance from the uppermost section, in µm. Arrows in Fig. 13-194 indicate a putative proliferation of PPL cells. Note a conspicuously differentiated outer endothecial layer in Fig. 12-240.

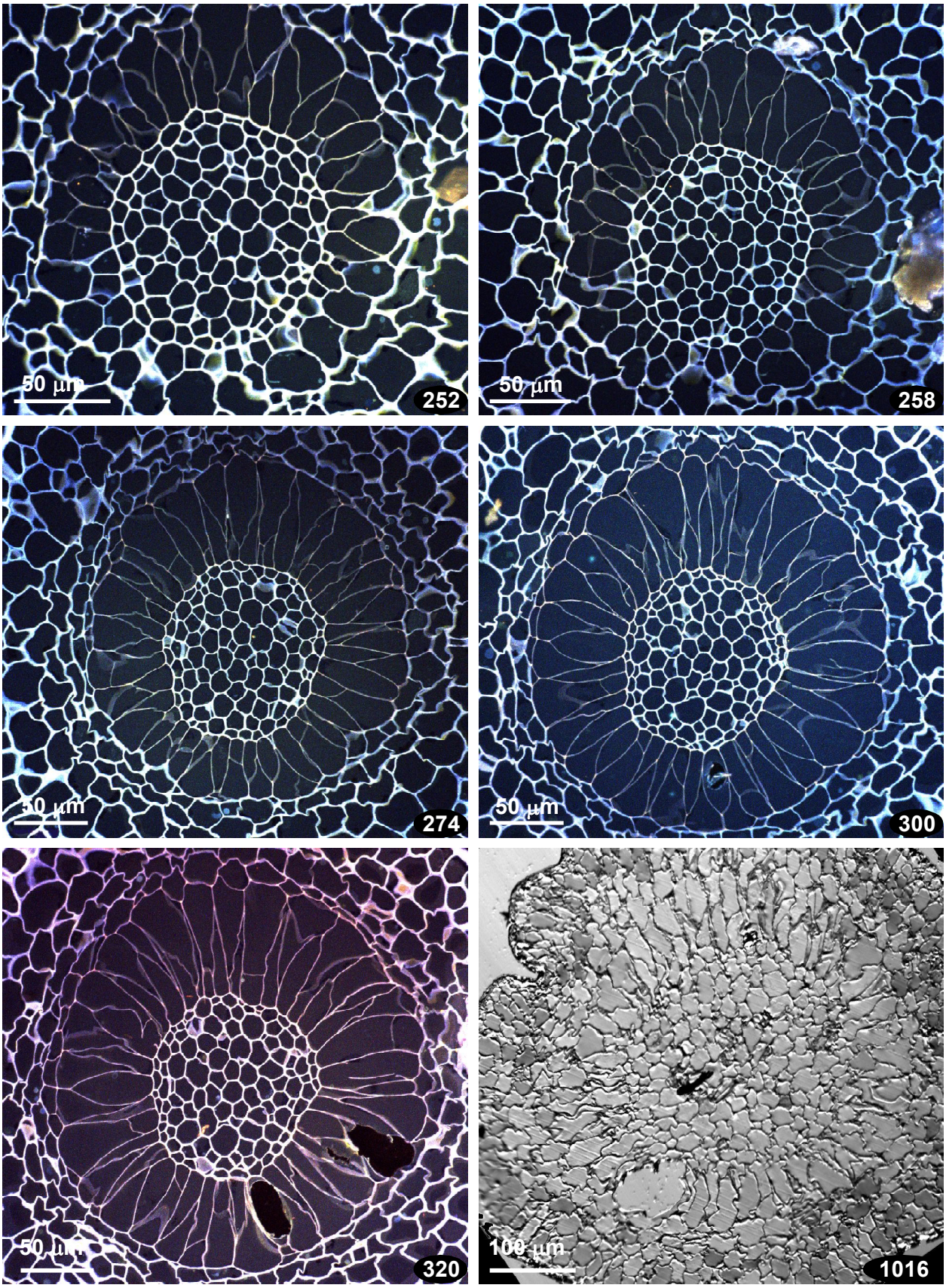


Fig. 13b (LCSM, 13-1015 – DIC) (end of the series started in previous page). *Buxbaumia aphylla*: transverse sections of young capsule, showing endostome cone formation. Numbers indicate the distance from the uppermost section, in µm. The last section is made at about the base of peristome (approximate position shown in Fig. 1E). At about 300 µm for sporophyte apex plicae are 24-27 in number, at base they are 39.

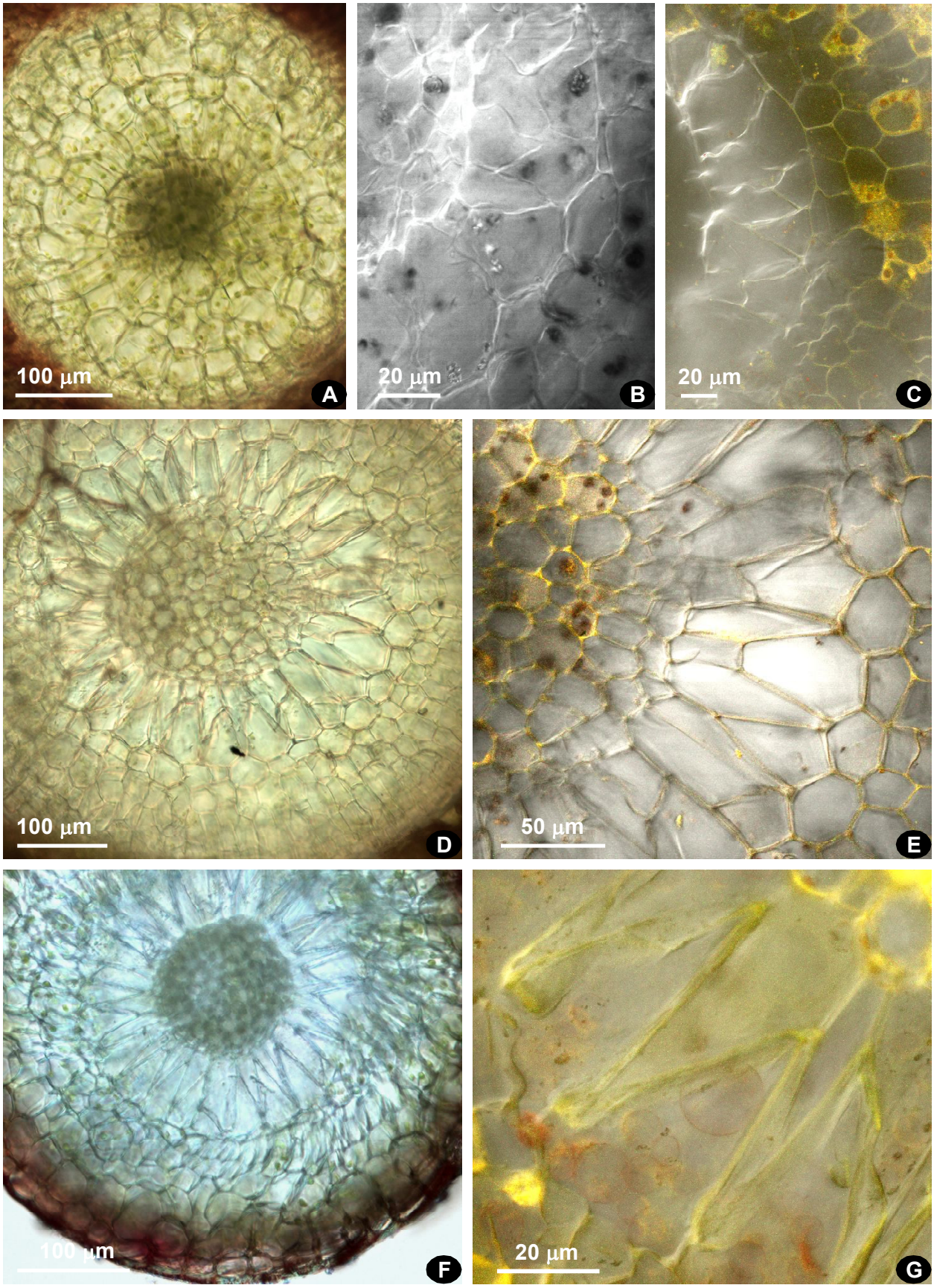


Fig. 14 (LCSM). *Buxbaumia aphylla* transverse razor sections of premature capsule, showing endostome cone distally (A–C), where the cone still did not start enlarging; F: note a severe spiral twisting in OPL and further layers.

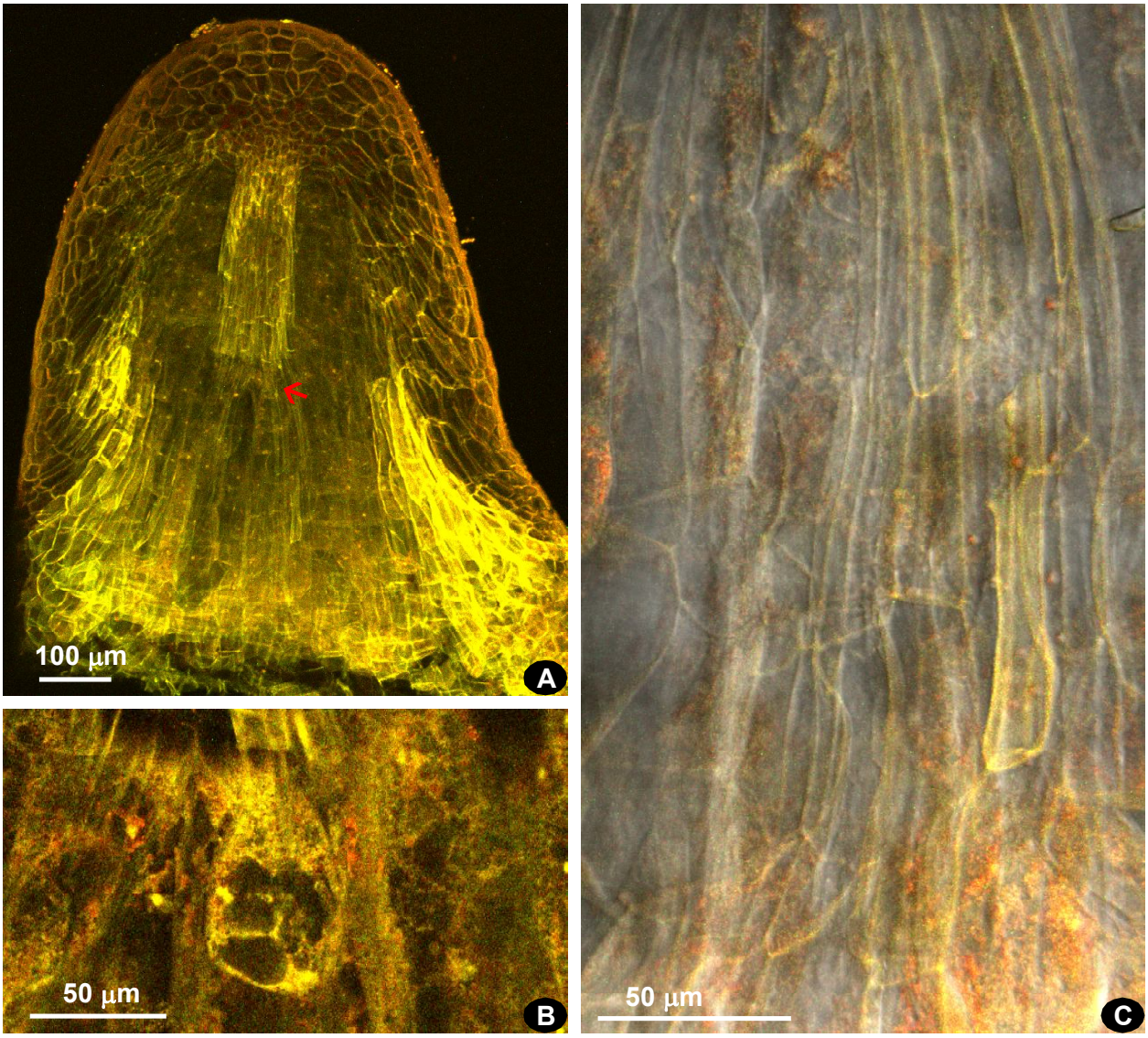


Fig. 15 (LCSM). *Buxbaumia aphylla* operculum from inside of premature capsule, showing columella joining operculum (A); a vessel-like structure hanging out of ruptured columella (B); cone membrane at stage shown in Fig. 13, which lost its shape after detachment from columella: cell outlines are visible.

E, F); note, however, that only one capsule was studied, although of perfect preservation, deoperculated just before the study. Cone surface is papillose (Fig. 19C), being very similar to *B. aphylla*.

Development of cone is also similar at moderately late stages (Fig. 19, G, H).

Transverse sections of the young capsule of *B. minakatae* revealed an extremely soft cell walls and extensive intracellular spaces in the knobby operculum area (Fig. 20A). The knob-like operculum is more or less similar to *B. viridis*, endothecial part is less immersed, up to 100 µm (i.e., similar to the series in Fig. 8). Amphithecial cells around endothecium are less inflated and more regular in shape as compared to *B. viridis*. Cells are radially arranged around the larger cell in the centre.

***Diphyscium* peristome** is shown here to outline its similarity with *Buxbaumia*, especially in prostome structure, which is usually neglected as it is extremely fragile. At the same time, *Diphyscium* prostome is only a little shorter than in, e.g, *B. minakatae*. Endostome cone in *Diphyscium* is invariably 16-folded, although fold fusions sometimes occur. The OPL material is more abundant, and regularly represented on keels.

DISCUSSION

Different series of three species of *Buxbaumia* show a somewhat different pictures, but their common patterns represented in all series are as follow.

1) No fundamental square is seen, except the series in Fig. 3, where quadrate structure is distinct in cells of one outermost cell layer. Note that already in the second cell layer below the surface, no such cell arrangement can be traced.

2) Instead of four sectors developing in an extremely well coordinated way in all other mosses, cell assemblages in the central part of the sporophyte of *Buxbaumia*

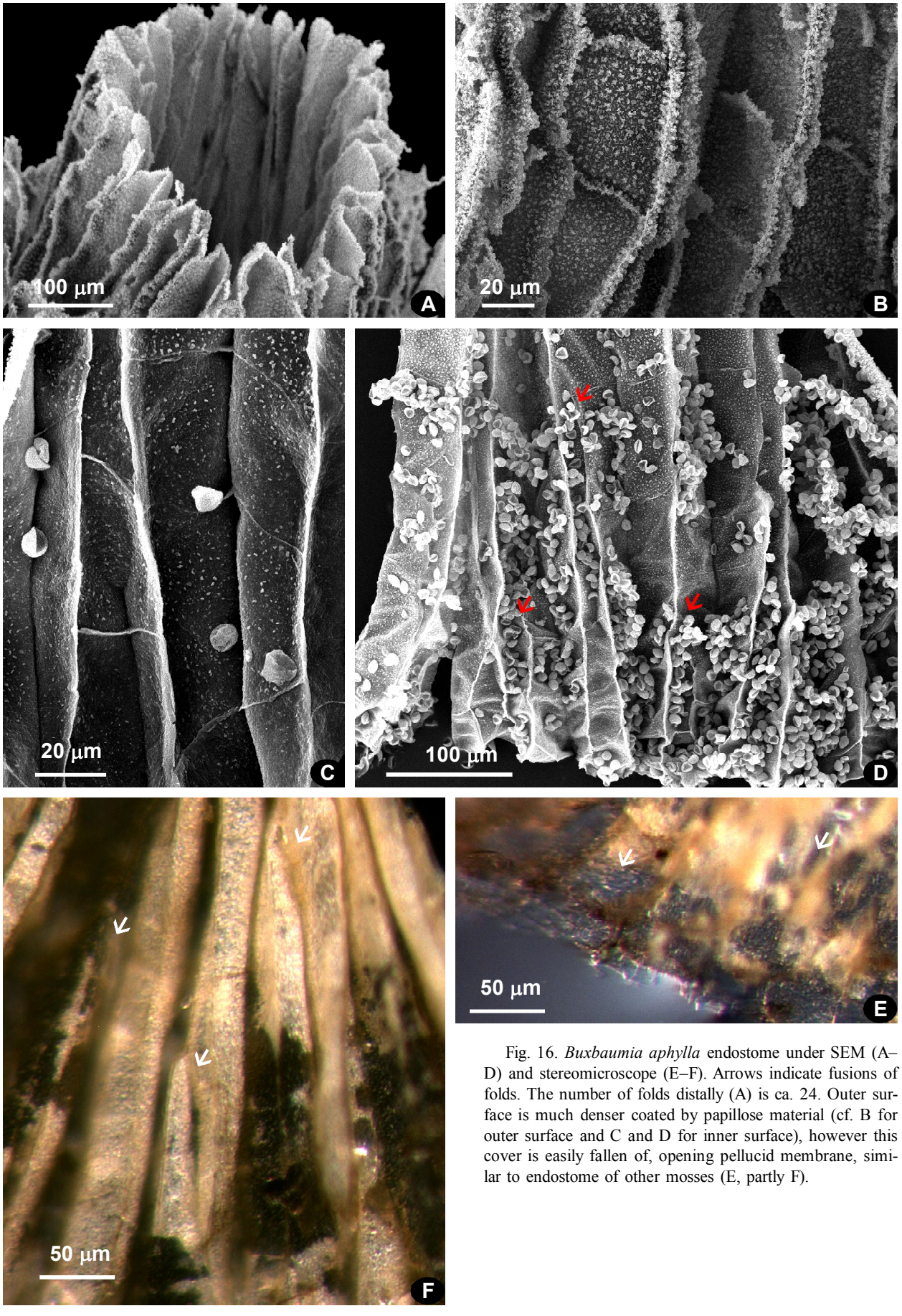


Fig. 16. *Buxbaumia aphylla* endostome under SEM (A–D) and stereomicroscope (E–F). Arrows indicate fusions of folds. The number of folds distally (A) is ca. 24. Outer surface is much denser coated by papillose material (cf. B for outer surface and C and D for inner surface), however this cover is easily fallen of, opening pellucid membrane, similar to endostome of other mosses (E, partly F).

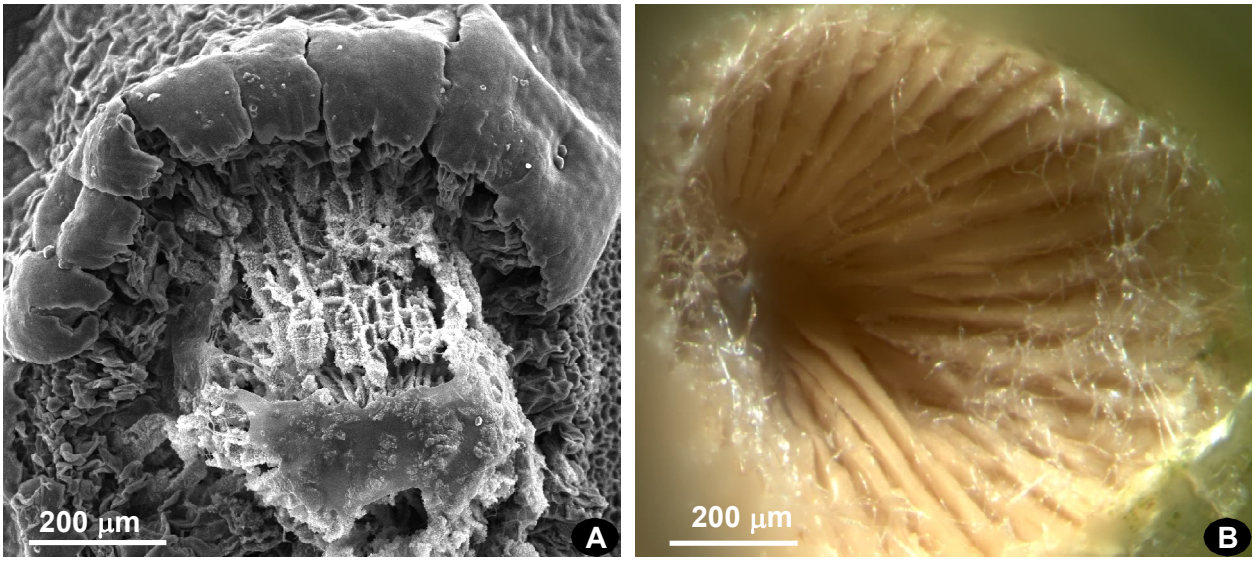
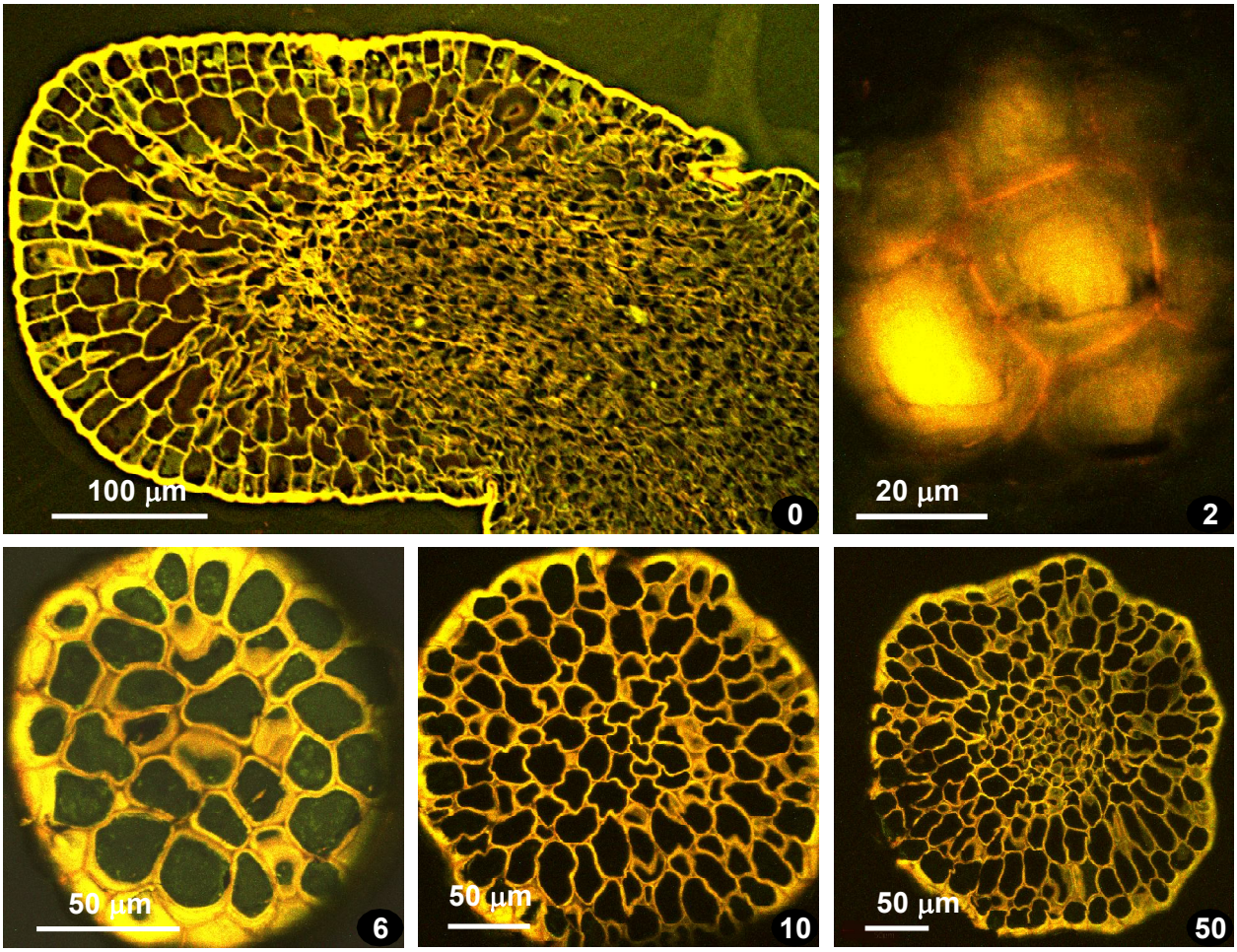
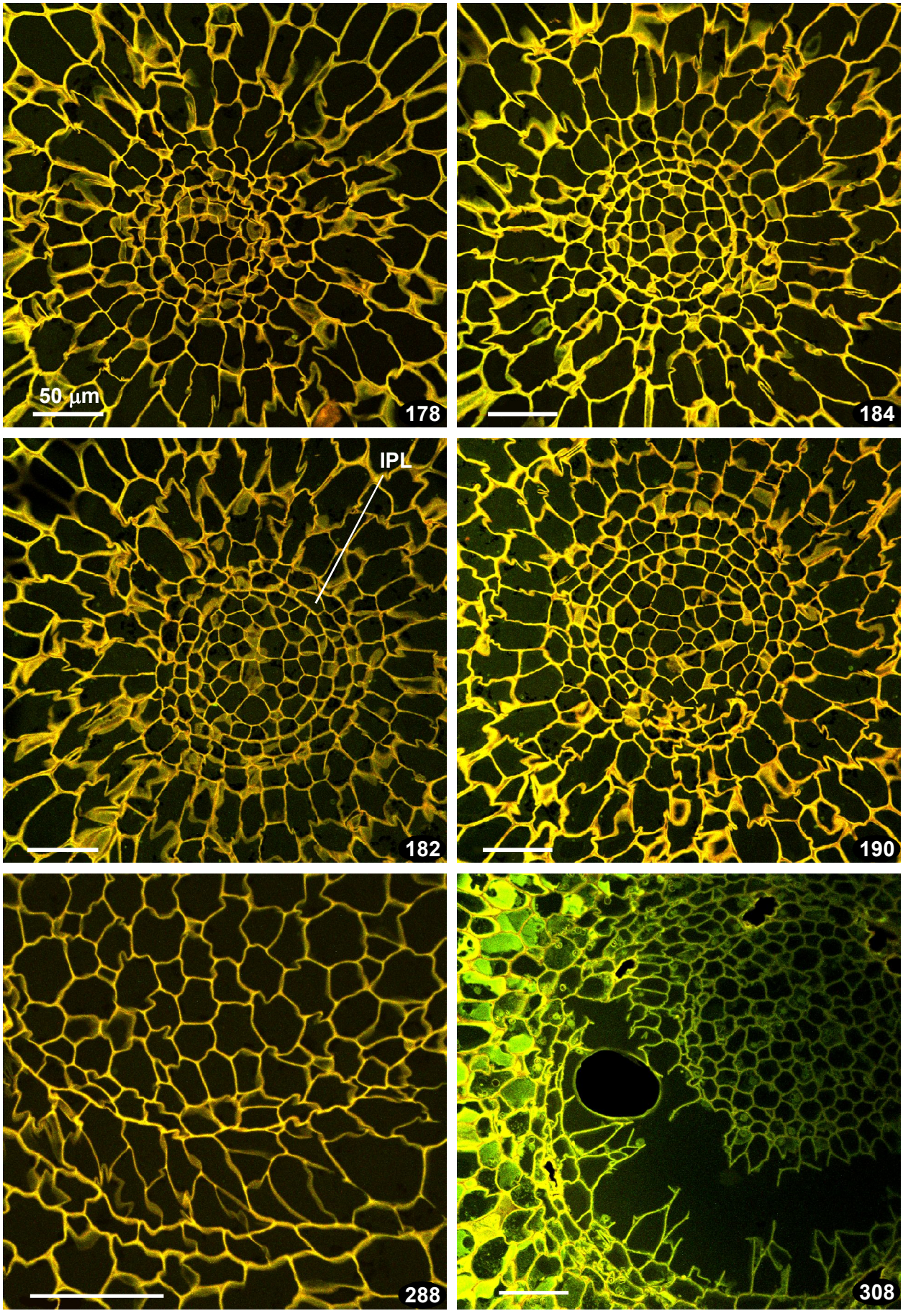


Fig. 17. *Buxbaumia viridis*: endostome under SEM (A) and stereomicroscope (B). View from spore sac side, showing ca. 24 folds in ca. 2/3 of circumference, where its structure is visible.

Fig. 18 (LCSM). *Buxbaumia viridis* (this and next page). Longitudinal sections, showing endothecium deeply immersed and surrounded by palisade-like tissue (Fig. 18-0), and transverse sections of young capsule, showing peristome formation (continued on next page). Numbers indicate the distance from the uppermost section, in μm. Note a difficulty in interpretation of layers on the border between endothecium and amphithecium (e.g. in Fig. 18-190).

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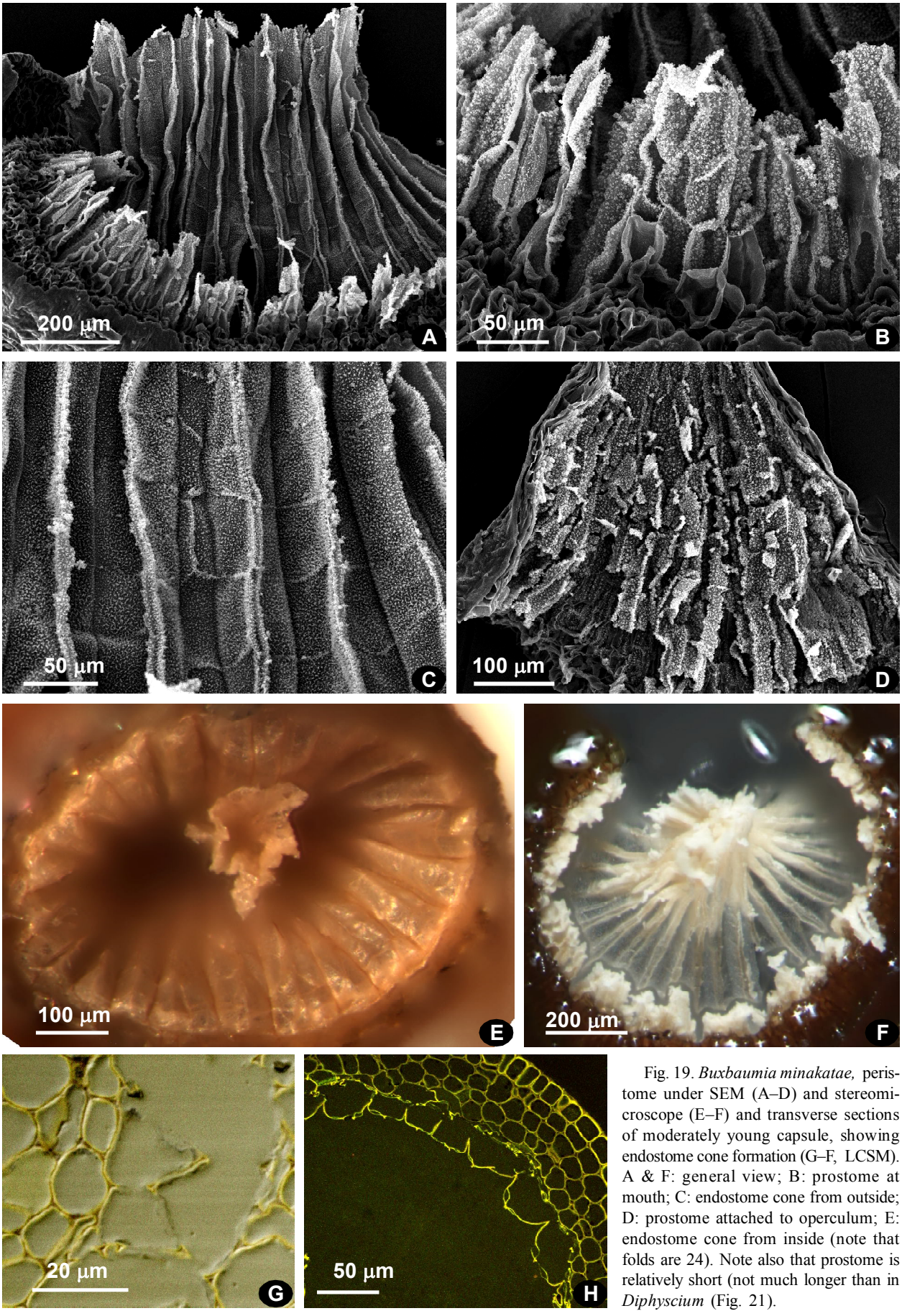

Fig. 19. *Buxbaumia minakatae,* peristome under SEM (A–D) and stereomicroscope (E–F) and transverse sections of moderately young capsule, showing endostome cone formation (G–F, LCSM). A & F: general view; B: prostome at mouth; C: endostome cone from outside; D: prostome attached to operculum; E: endostome cone from inside (note that folds are 24). Note also that prostome is relatively short (not much longer than in *Diphyscium* (Fig. 21).

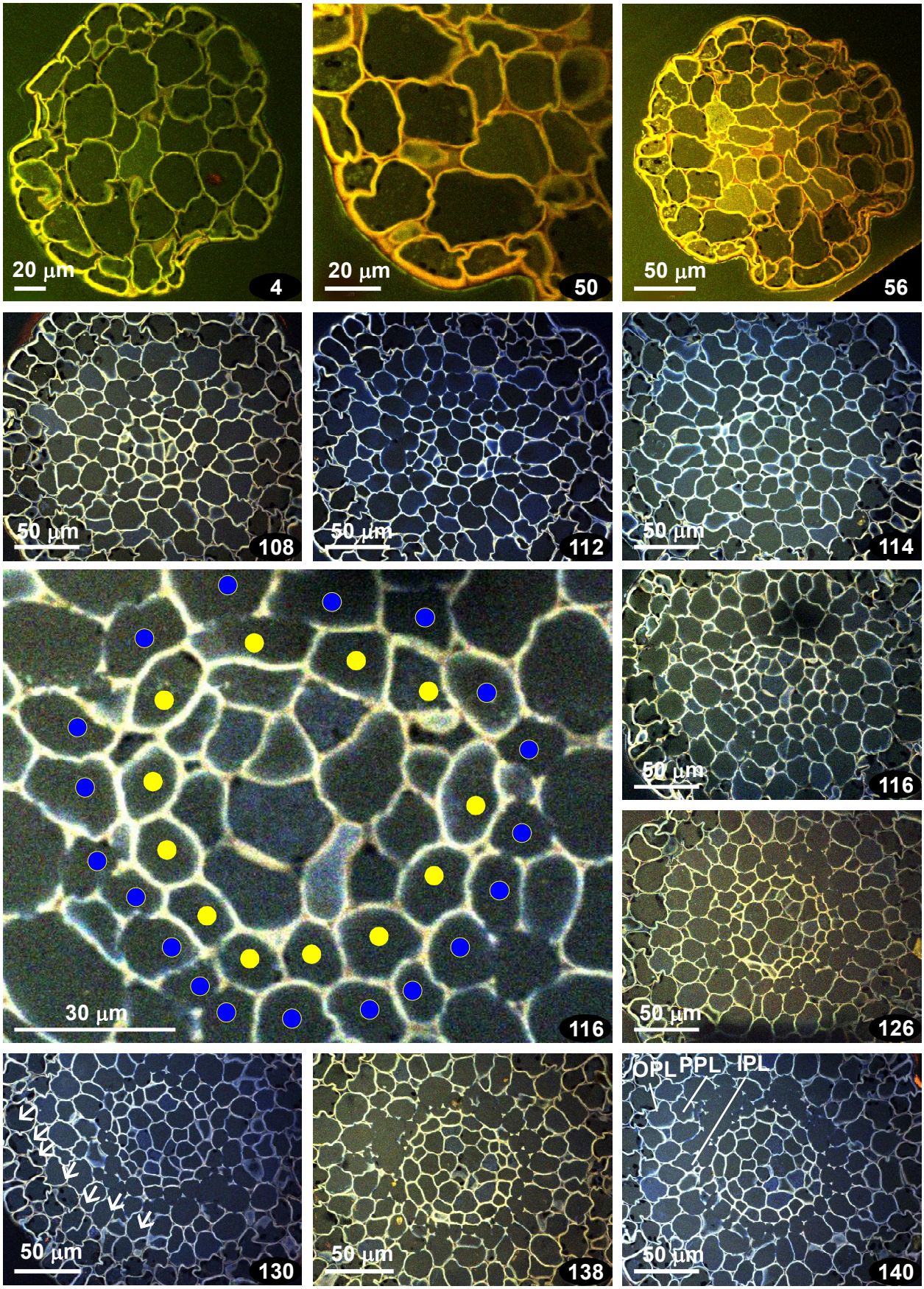

Fig. 20 (LCSM). *Buxbaumia minakatae,* transverse sections of young capsule. Numbers indicate the distance from the uppermost section in µm. Note a conspicuous pentagonal cells in the centre of endothecium.

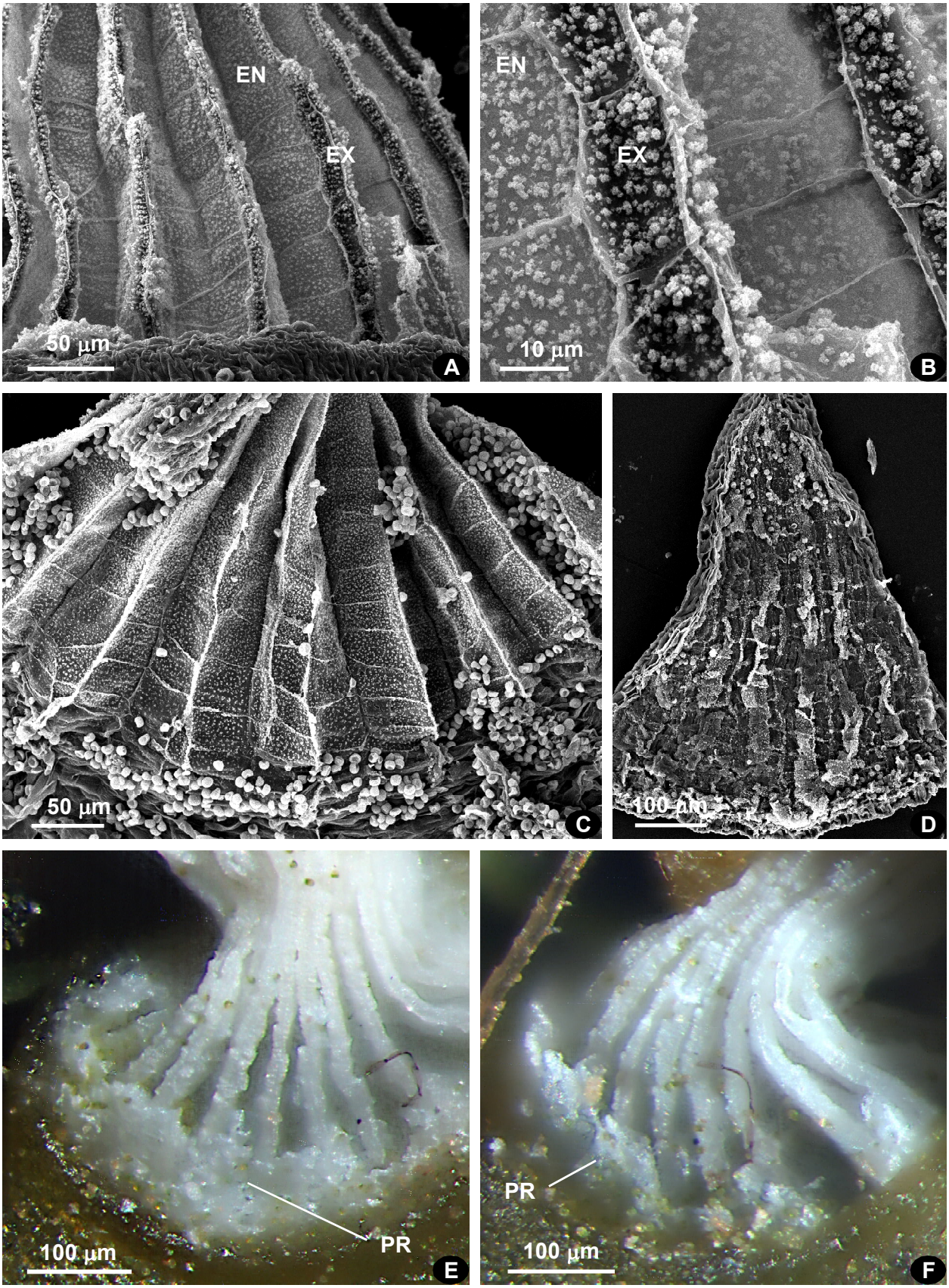

Fig. 21. *Diphyscium foliosum* peristome under SEM (A–D) and stereomicroscope (E–F). Note OPL material along keels of the pleated cone (A–B); a somewhat irregularity at cone base (C); prostome parts attached to operculum (D), in a way similar to that in *Buxbaumia* (cf. Fig. 19D); prostome after operculum removal (F), compare with prostome in *Buxbaumia minakatae* (Fig. 19).

are organized rosette-like with six cells surrounding a single enlarged cell, pentagonal in shape (Figs. 7-90; 20-118) (Fig. 20), being especially similar to apical cell of stem (Bertier, 1972, Spirina & Ignatov, 2005).

In some cases, especially closer to the urn base, three peristomial layers are clearly recognizable (Fig. 5): PPL cells are most regular, IPL cells are most transversally elongate and experience additional anticlinal divisions, while OPL cells are often twice more numerous than PPL cells (Fig. 5-76). However, in other cases, e.g. in series in Fig. 6, closer to its end, the concentric circles are very regular and sometimes they are four or even five in number. Such cases make difficult to understand their homologies. Additional complication comes from the equal or subequal number of cells in neighboring layers. And finally, cell circles look at places somewhat spiraling (Figs 7, 14. 18), raising the question if the peristomial layers in *Buxbaumia* are really homologues to those in all other mosses.

However, obvious continuation of IPL to the outer spore sac in Fig. 10 leaves no doubts that the peristomial layers in *Buxbaumia* are the same as in all other mosses (Edwards, 1979, 1984; Kreulen, 1972). Therefore the subdivision of the sporophytic tissue into amphithecium and endothecium should not be doubted by any means, despite not in all images it is easy to say to which layer a given cell belongs.

Despite of all uncertainties, the line between IPL and outermost layer of the endothecium can be revealed in most cases as the maximally conspicuous demarcating line between layers. Sometimes it can be explained by the difference in cell shape (Figs. 2-16; 8-106): the IPL cells are usually more angular compared to more rounded endothecial cells in transverse section. In other places a considerable enlarged IPL cells alone are enough to tell the layers. At the early stage of differentiation of peristomial layers, the cells of outermost endothecium layer became quite specialised (Fig. 12).

We failed to obtain material at the stages earlier than shown in Figs. 2 and 3, which makes the series incomplete and missing stages probably important for understanding the whole set of deviations from the most common type of development. The explanation on this unusual structure of *Buxbaumia* is however required and, with a hesitation, we suggest the following scenario, basing on the fact that the structure of the sporophyte with IPL completely overarching semi-globose endothecium allows not that much possible developmental pathways.

The cell with cuneate base is one which is ultimately responsible for the fundamental square formation by means of division pre-peristomial cells into two equal halves. Being shown already by Kienitz-Gerloff (1878), its fine structure and mode of division were described in details by Wenderoth (1931). In *Buxbaumia* we see equal cell divisions only in epidermal cells near the top of sporophyte and only in one series where the whole capsule is shorter than 100 μm. Thus we may conclude that cells immediately or shortly below the apical cell block cell divisions into two equal halves even if they have started. It is still unclear if this happens in the second, or third, or fifth division, but we definitely see that cells in IPL start to divide morphologically transversally / spatially almost radially due to only slightly convex surface of the capsule top since a very early stage preceding those observed in Figs. 2 and 3.

Later the uppermost cells of the IPL (or, being precise, a continuation of this layer) produce clorophyllose parenchyma immersing young peristome in it.

The pleated cone develops from IPL and PPL by means of strong inflation of their cells, which elongate to more than 100 μm long (Figs. 10, 16C) and up to 80 μm wide in radial direction (Fig. 13). To keep such giant construction, the continuation of sporogeneous layer, at the level of peristome, acquires apparently a mechanical function (cf. Figs. 12–14), and OPL forms another rigid ring so to stretch properly extremely delicate membrane (Figs. 13-14).

Before the pleated cone formation, the cells of IPL and PPL elongate in the course of capsule growth in length. It seems important that the growth proceeds by means of subterminal endothecial cells, conspicuous on both longitudianl (Fig. 11 cf. Figs. 9-10) and transverse (Fig. 6–8) sections. Such growth also explains how capsule with endothecium of about ten cells wide on the early stage of development (Fig. 2) narrowing, so endothecium distally becomes five or even less cells wide (Figs. 9–12).

As the uppermost part of IPL (or its continuation) became specialised for chlorenchyma production, the number of IPL cell originally involved in peristome building are limited to few, but due to series of transverse divisions a cell groups of four or eight cells are forming and constituting peristomial layers shortly before inflation stage (Fig. 9).

The explanation of the morphological change which is resulted in a buxbaumioid type of peristome can be referred to the oligomerization, a very common mode in invertebrate evolution. While in most mosses the number of "primary peristome initial cells", if count by number of divisions resulted in separation endothecium and amphithecium, is ca. 10 to 20 (Fig. 11D, E), in *Buxbaumia* this number reduces to very few, which shortly after appearing have to change the mode of division so to grow radially, being subtended by broad urn base or seta. Interestingly, *Diphyscium* also has seta wider than urn at the similarly early stage of development (Shaw *et al.*, 1987).

In addition to subterminal endothecial cell, the uppermost cells of IPL also retain meristematic activity, thus forming descending layers of cells (Fig. 9-12) and numerous cells forming capsule knob, apparently important in feeding young sporophytes. Such change of IPL functioning, i.e. production by its part the chlorenchyma instead of peristome is understandable, since *Buxbaumia* is a moss with extreme reduction of gametophyte, which is represented mainly by protonema.

The sporophyte structure in *Buxbaumia* seems does not represent an archaic type, but extremely specialised.

Since the early beginning, amphithecial cells start to work for sporophyte self-feeding, and cells are dividing without any special order. The number of peristomial elements is determined largely by cell size, or how many of them may surround the endothecium. Naturally, the number of cells in circumference increases downwards, as peristome base becomes broader along with the urn maturation. In such situation, the peristomial formula, which was introduced to compare structures of cell columns (cf. Fig. 11D, E), even if calculated by counting all cells in moderately regular cell rings around endothecium and dividing these by eight, will have quite a different meaning. Concerning progressive increase in the cell number in peristomial layers, we consider *Buxbaumia* to have peristome of a special type, which should not be compared with other peristomes using peristomial formula.

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