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BRANCH DEVELOPMENT AND PSEUDOPARAPHYLLIA OF HYPNUM CUPRESSIFORME (HYPNALES, MUSCI)

РАЗВИТИЕ ВЕТОЧЕК И ПСЕВДОПАРАФИЛЛИИ HYPNUM CUPRESSIFORME (HYPNALES, MUSCI)

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Abstract

Foliose and subfilamentose structures around branch primordia are studied in *Hypnum cupressiforme* and *Amblystegium serpens*. In the former species the branch primordia are surrounded by subfilametnose structures of problematic homology, while in the latter they are surrounded by the proximal branch leaves arranged according to the pattern most common in pleurocapous mosses. Series of cross sections of 2 μm thick were used to study their early stages of development. Results demonstrate that the branch primordium in *Hypnum* has at the earliest stages the same developmental pattern as that in *Amblystegium*, but three to five proximal branch leaves soon become split into narrow lobes. Some lobes may appear at a certain distance from the branch primordium. The splitting of one proximal branch leaf occurs in *Amblystegium* only occasionally. The principal difference between the proximal and more distal branch leaves seems to be absent, thus the segregation of pseudoparaphyllia as a separate morphological structure seems unnecessary, despite the former may have contrastingly different shape.

Резюме

Изучены ранние стадии развития веточек у *Hypnum cupressiforme* и *Amblystegium serpens*. Зачатки веточек первого вида окружены узкими листоподобными образованиями не вполне понятной природы, в то время как второй вид имеет расположение первых листьев вокруг зачатка веточки типичное для большинства бокоплодных мхов. На сериях срезов толщиной 2 μm изучены ранние стадии развития веточек обоих видов. Выяснено, что узко линейные ‘псевдопарафиллии’ *Hypnum cupressiforme* формируются из изначально нормально развивающихся зачатков листьев, которые, однако, вскоре разделяются на узкие доли, б. ч. в одну клетку шириной. Аналогичные разрывы первых веточных листьев у *Amblystegium serpens* редки и находятся преимущественно в местах, где идет более активное растяжение. Существенных отличий в закладке и раннем развитии развитии первых веточных листьев по сравнению с появляющимися позже не отмечено, хотя форма их может значительно отличаться. Тем не менее, это отличие вряд ли является основанием для выделения псевдопарафиллий как самостоятельной морфологической структуры.

KEYWORDS: mosses, anatomy, *Hypnum, Amblystegium*, pseudoparaphyllia, branch development, ontogenesis

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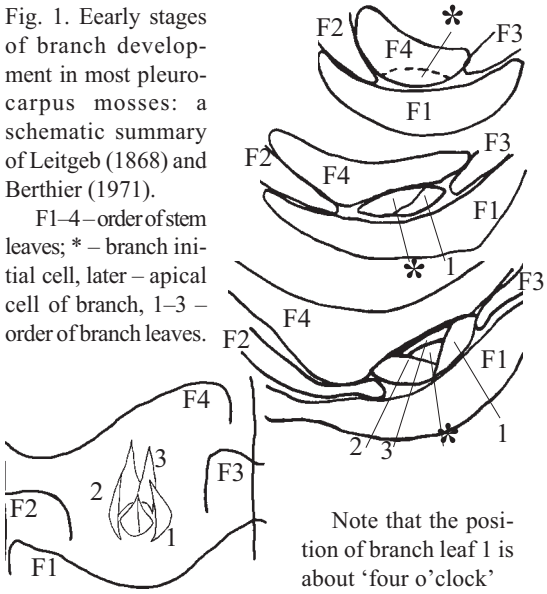

Fig. 1. Eearly stages of branch development in most pleurocarpus mosses: a schematic summary of Leitgeb (1868) and Berthier (1971).

F1–4 – order of stem leaves; * – branch initial cell, later – apical cell of branch, 1–3 – order of branch leaves.

INTRODUCTION

The branch primordia in most pleurocarpous mosses are covered by foliose or subfilamentose structures, usually called "pseudoparaphyllia", although an extensive discussion on their definition, homology and, consequently, also the proper terminology continues (Iwatsuki, 1963; Akiyama, 1990a,b; Akiyama & Nishimura, 1993; Ignatov, 1999; Ignatov & Hedenäs, 2007).

Spirina & Ignatov (2005) compared pseudoparaphyllia in two genera of pleurocarps, *Brachythecium* and *Calliergon*. They found that the sequence of the first cell divisions and the earlier stages of development is similar, but the first and second pseudoparaphyllia remain not developed in *Brachythecium*, thus, resulting in a contrastingly different pattern of their arrangement around the branch primordia (Ignatov, 1999). The similar development of first and subsequent branch leaves indicates that either pseudoparaphyllia shoud be considered as absent in these two genera, or they are nothing but somewhat modified proximal branch leaves, and in the latter case are maybe not worth recognition as a separate morphological structure.

In the present paper we continue to study cases of the arrangement of foliose and subfilamentose structures around branch primordia that deviate from the most common pattern, called the 'first pseudoparaphyllium in a "four o'clock" position', as it appears laterally and somewhat below the middle of branch primordium (Figs. 1, 2: 2, 2: 4, 2: 6).

Hypnum cupressiforme Hedw. is unusual among most of the north-temperate pleurocarpous mosses being described as having very narrow 'pseudoparaphyllia' around branch pimordia (Figs. 2: 1, 2: 3, 2: 5, 2: 7). This character is stable and has been included in identification keys of handbooks and floras, especially for separation of this species from the superficially similar *Stereodon vaucheri* (Lesq.) Lindb. ex Broth. (=*Hypnum vaucheri* Lesq.), the latter having ovate-triangular 'pseudoparaphyllia'.

Some authors noted also that in addition to filamentose 'pseudoparaphyllia', *Hypnum cupressiforme* also has forked 'pseudoparaphyllia' (e.g. Ando, 1989).

The immediate aims of this study is to find out the homology of narrow 'pseudoparaphyllia' of *Hypnum cupressifome*, and also the homology of an enigmatic filamentose structure often (although not always) observed in a position lateral to the main group of 'pseudoparaphyllia' (arrowed in Figs. 2: 3, 2: 5, 2: 7). For this, we compare the early stages of the branch primordia development in *Hypnum* with that in *Amblystegium serpens* (Hedw.) Bruch et al., where one outer 'pseudoparaphyllium' is often divides into two subequal (Fig. 2: 2) or unequal (Fig. 2: 6) lobes.

MATERIALS AND METHODS

Specimens of *Amblystegium serpens* (Moscow, Main Botanical Garden, coll. Spirina 4.X.2008, and 1.IV.2009) and *Hypnum cupressiforme* (1 – Stavropol Territory, V-2006, coll. Zolotov, MHA; 2 – Leningrad Province, VI-2008, coll. Zolotov, MHA); and 3) Krasnodar Territory, Malyj Utrish, 4.V.2005, coll. Ignatov & Ignatova, MHA) were studied. As the variation between specimens of one species was found not exceeding that within specimen, the following data are referred just to species.

Stem apical parts of ca. 5 mm length were isolated, and after removing the external leaves, were fixed in 4% paraformaldehyde in Na-phosphate buffer, pH 7.0, for 12 h. Some specimens of *Hypnum cupressiforme* were fixed in 4% glutaraldehyde for 5 days, post-fixed with 1% osmium tetroxide in Na-phosphate buffer, pH 6.8, for 10

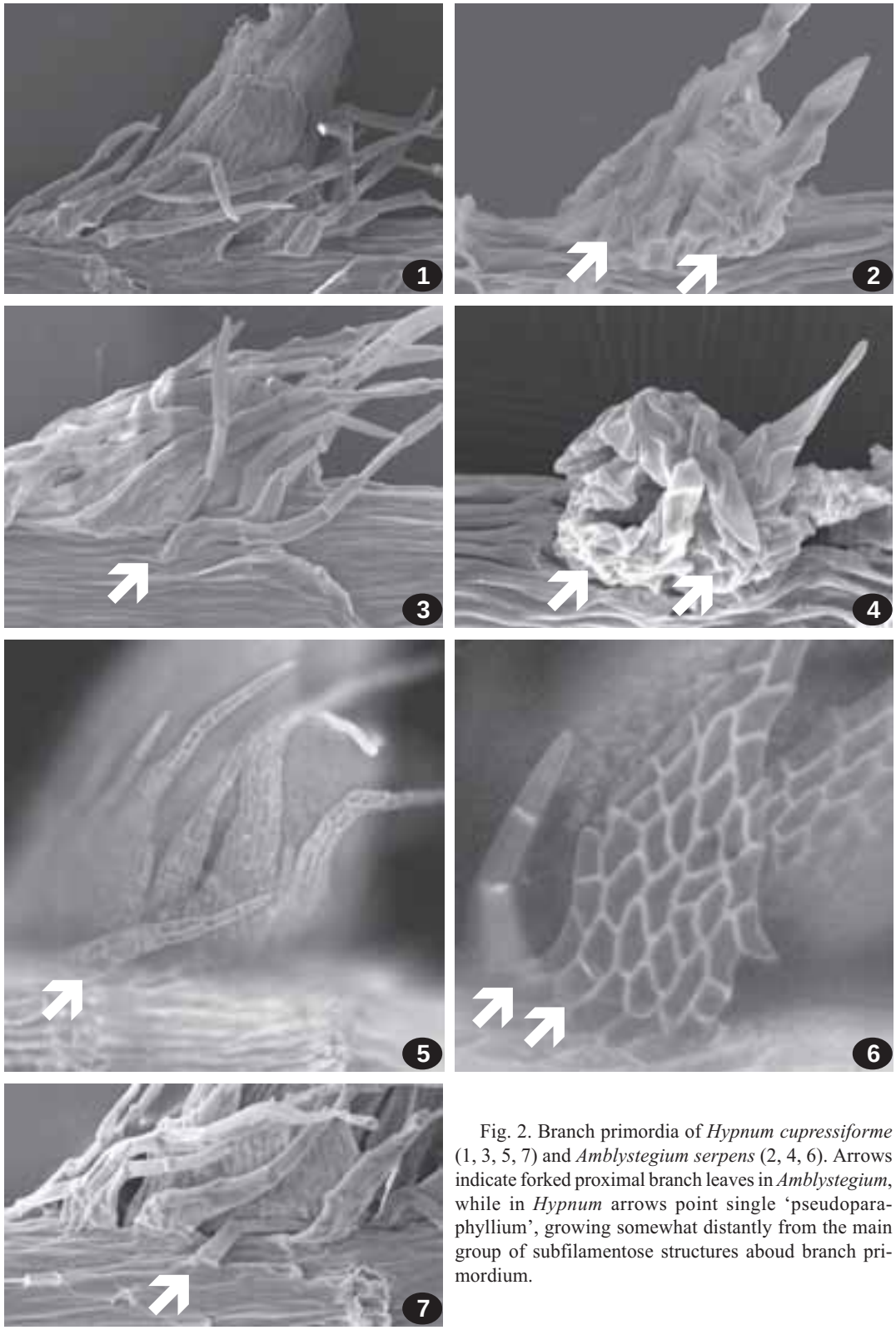

Fig. 2. Branch primordia of *Hypnum cupressiforme* (1, 3, 5, 7) and *Amblystegium serpens* (2, 4, 6). Arrows indicate forked proximal branch leaves in *Amblystegium*, while in *Hypnum* arrows point single 'pseudoparaphyllium', growing somewhat distantly from the main group of subfilamentose structures aboud branch primordium.

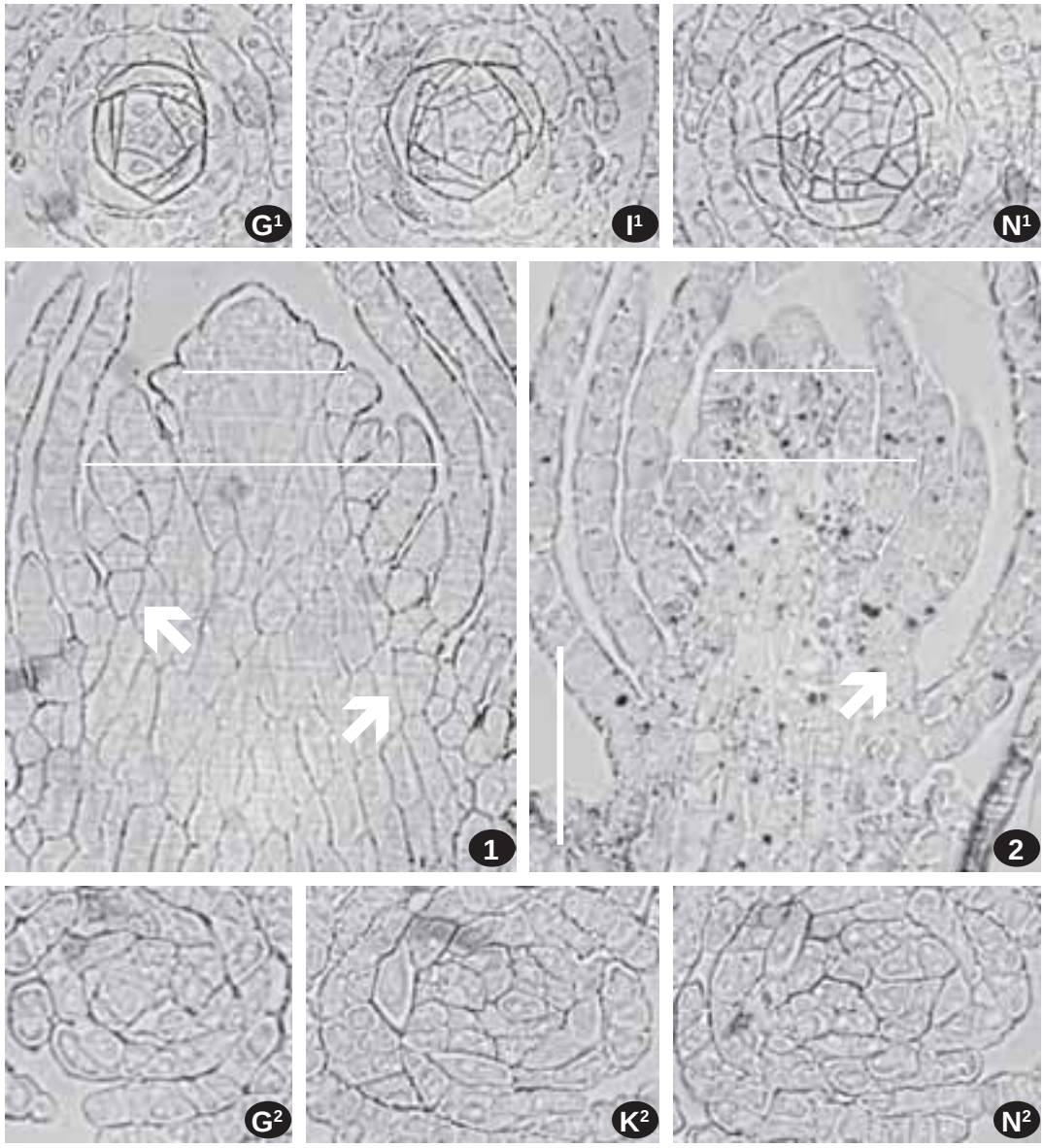

Fig 3. Longitudinal sections of stem apical part of *Hypnum cupressiforme* (1) and *Amblystegium serpens* (2). Upper row presents a series of transverse sections of stem at 14 (g), 18 (i) and 28 (n) μm from apex of *Hypnum cupressiforme*; and lower row is the same for *Amblystegium serpens*, at 14 (g), 22 (k) and 28 (n) μm from apex. Scale bar 50 μm. White horizontal lines in pictures of longitudinal sections indicate approximate level of upper and lower transverse sections shown above and below. Arrows indicate branch primordia; note the much wider room for them in *Amblystegium*.

h. The material was then dehydrated in 70% ethanol, stained in uranil-acetate (2% solution in 70% ethanol for 10 h, and then dehydrated through a graded ethanol/acetone series to 100% acetone. After that, samples were embedded in araldite 6005 medium, according to the protocol of manufacturer.

Sections were cut 2 μm thick with glass knives, put on glass slides without mounting medium and photographed under Leitz compound microscope.

Since the main target of the study was the arrangement of the foliose structures around the branch

primordia, we tried to obtain cross sections transverse to the axis of the branch primordia (and more or less tangential to stem). Sections transverse to stem (and longitudinal to branch primordium) and longitudinal to stem (also longitudinal to branch primordium) were studied as well. Supplementary photographs were made under SEM LEO-430 and fluorescent Olympus C41 microscopes.

Terminology

Presenting series, we label individual sections by letters or number, and the missing of sequential letter/number means that the corresponding section is omitted, as uninformative.

The individual leaves and their continuations within the stem tissues can be delimited on the cross sections as a groups of cells delineated from the neighboring ones by more thick cell wall. All of them will be called 'leaves' and numbered according to number of cell division that cut off the corresponding merophyte. Lobes of lacerate leaves are denoted in letters (cf. Figs. 8, 15). Asterisk (*) always indicate branch apical cell.

Results

Series of sections are shown in:

— Figs. 5-9: sections transverse to branch promordium and plus-minus tangential to stem;

— Fig. 3 (G-N) & Figs. 10-17: sections transverse to stem and longitudinal to branch primordia;

— Fig 3 (1-2), Fig. 4 and 18-19: sections longitudinal to both stem and branch primordia.

Stem apical cell

In *Hypnum,* the clearly visible cell wall delimits the stem apical cell together with young cells with non-contrasted cell walls, thus forming an 'apical group' (Fig. 3: 1). This 'apical group' is deeply 'inserted' in the stem tissue to about 80 μm. In *Amblystegium*, the apical cell was much more difficult to find in many sections, and it, apparently, easily falls off during the preparation. In few cases where it was seen, it is small and not forming a conspicuous 'apical group' with other young cells. Cells in apical part are much more differentiated in *Hypnum* (Fig. 3: 1, 3: G^1-N^1), than in *Amblystegium* (Fig. 3: 2, 3: G^2-N^2) where they are essentially parenchymatous.

The early divisions of branch apical cell

The branch primordia become apparent from the fairly early stage, located ca. 40 mm from apex, as the branch apical cell becomes enlarged and divided, cutting off the first merophyte cell by a characteristic oblique partition (cf. Figs. 5, 20). The early divisions of branch apical cell have similar direction in both *Hypnum* and *Amblystegium*, so the first cell that cut off from the branch apical cell appears in a position of '4 o'clock' (mirrored 8 o'clock is discussed as 4 o'clock). The subsequent cutting off branch leaf initials proceeds in *Hypnum* in a clockwise direction, and in *Amblystegium* in counterclockwise direction (seen from apex). Later, the second and further cells should be cut off 'theoretically' forming an angle of 135°–144° from the previous cell, but due to a displacement in the course of branch development, the first and second leaves appear in fact at a wider angle (120-150° in *Hypnum and* 160-190° in *Amblystegium*), while the angle between the second and the third leaves is narrower (90-120° and ca. 90° correspondingly). Later the angle approach to the normal, 144° for 2/5 spiral and 135° for 3/8 spiral of leaf arangement (Figs. 8-9).

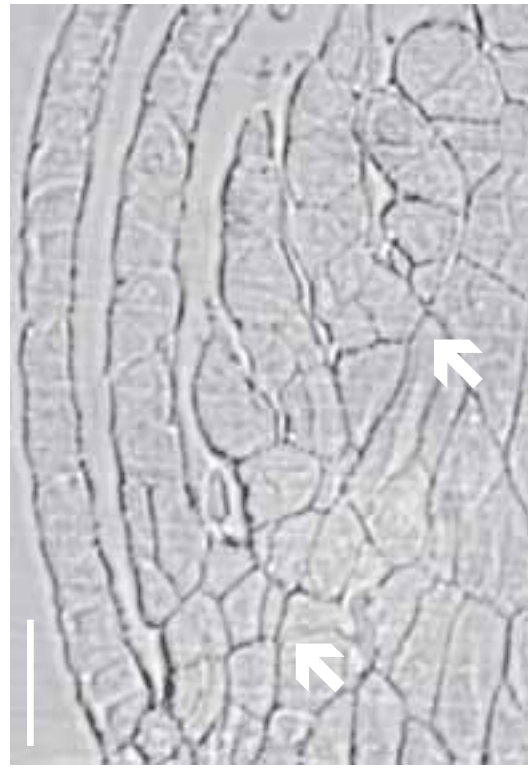

Fig. 4. Longitudinal section of stem of *Hypnum cupressiforme*, showing rather definite limit (arrows) between outer cells (derived from the same cell as leaves and branch primordia) and cells of central part of stem (I and II, in Frey's (1970) terminology). Scale bar 20 μm.

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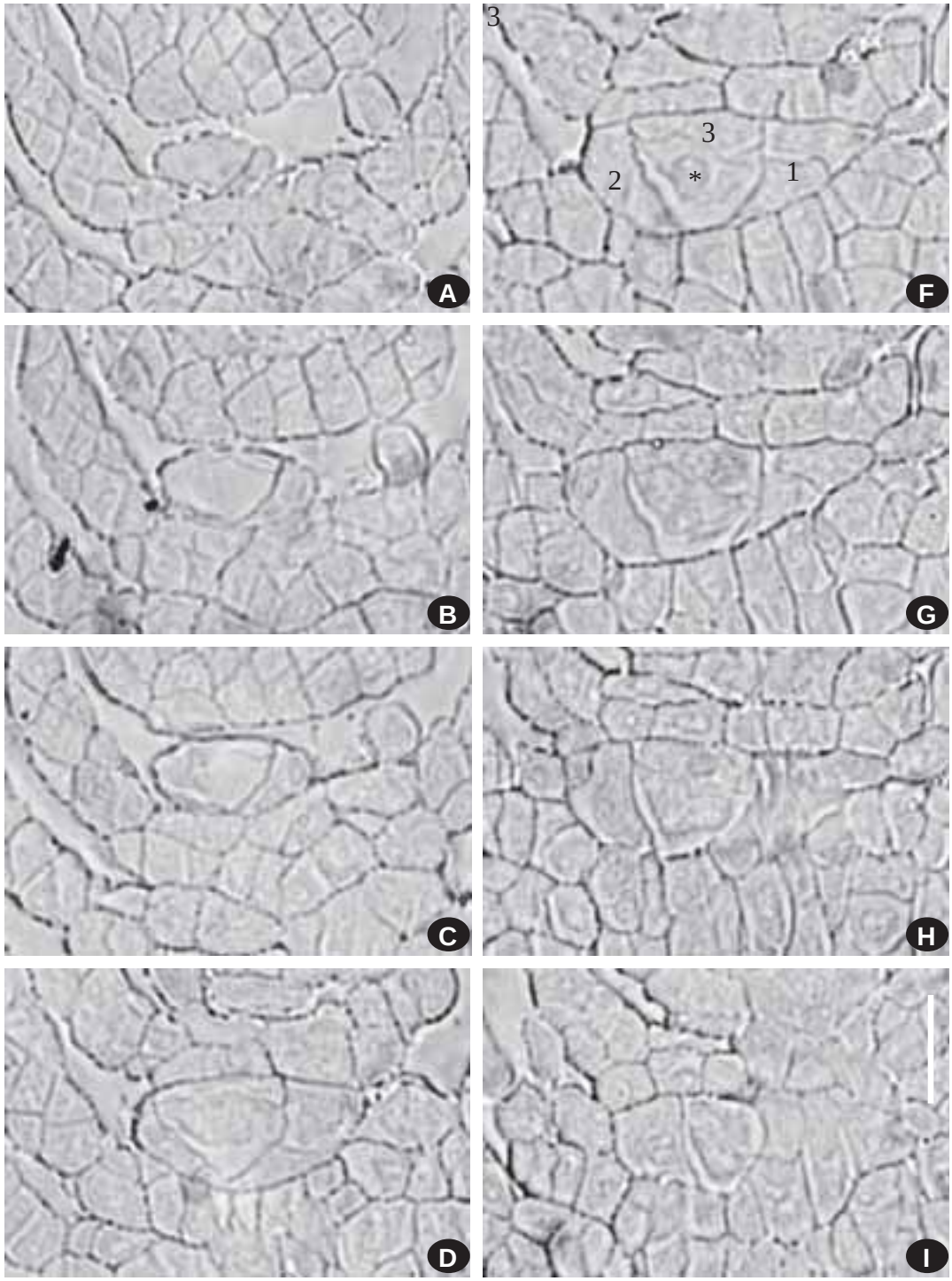


Fig. 5. Series of 2 μm cross sections transverse to branch primordium of *Hypnum cupressiforme* at 60-70 μm from stem apex. Cells that will develop into three proximal branch leaves are cut off from the branch initial cells (# F). At this stage primordium is very slightly raised above stem surface. Scale bar 20 μm.

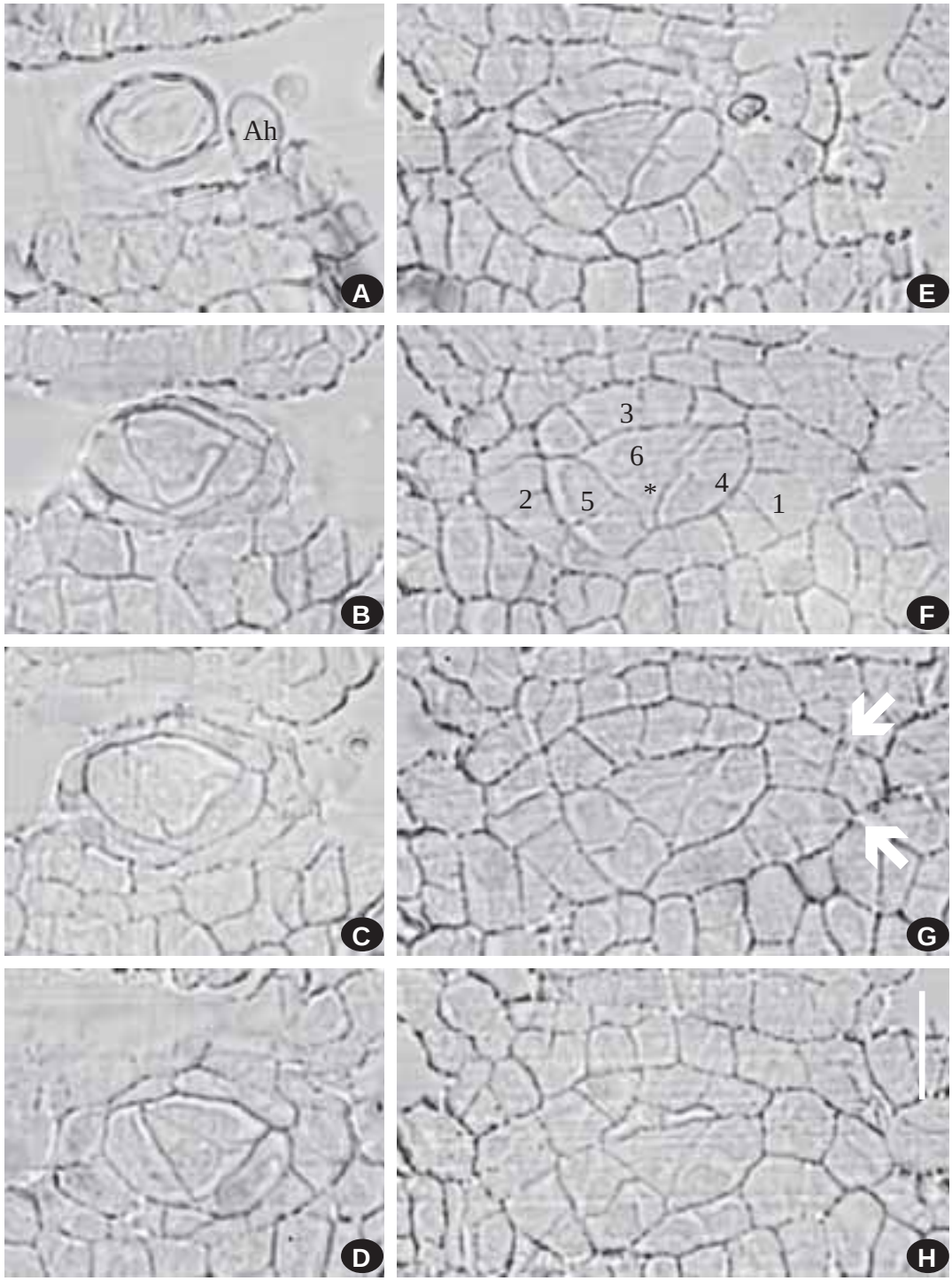


Fig. 6. Series of 2 μm cross sections transverse to branch primordium of *Hypnum cupressiforme* at 65-80 μm from stem apex. Cells that will develop into 5–6 proximal branch leaves are cut off from the branch initial cells (# F). At this stage primordium is raised above stem surface to ca.10 μm. Note a certain 'compartmentalization' in the basal past of the first branch leaf (G-H), compare with the Fig. 8F. Note also a regular subquadrate cells at the distal side of branch primordium (in F–H). Scale bar 20 μm.

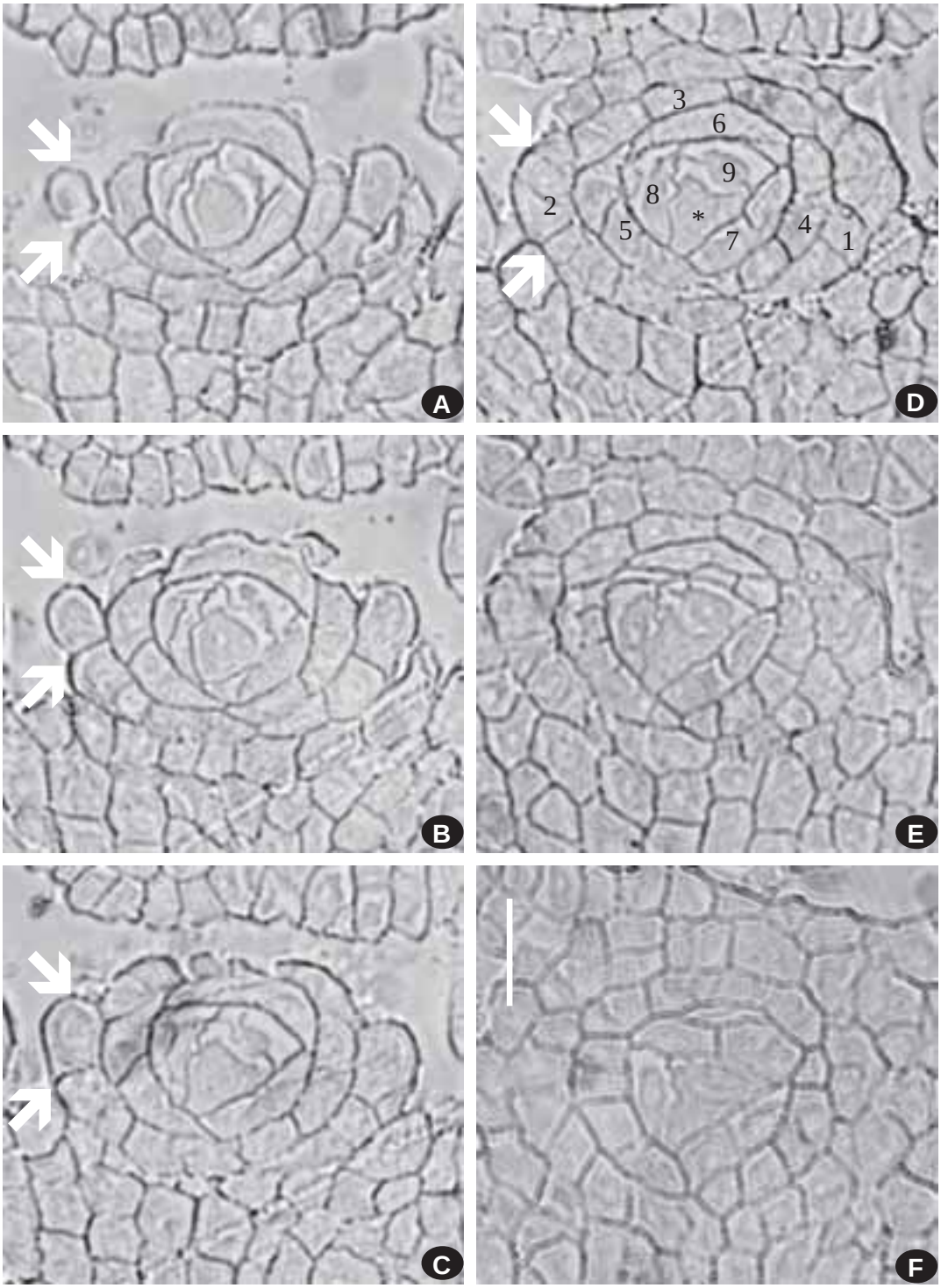


Fig. 7. Series of 2 μm cross sections transverse to branch primordium of *Hypnum cupressiforme* at 75-90 μm from stem apex. At this stage branch leaves appear above stem surface, and the certain tendency to their splitting can be seen in the second leaf (arrowed). Scale bar 20 μm.

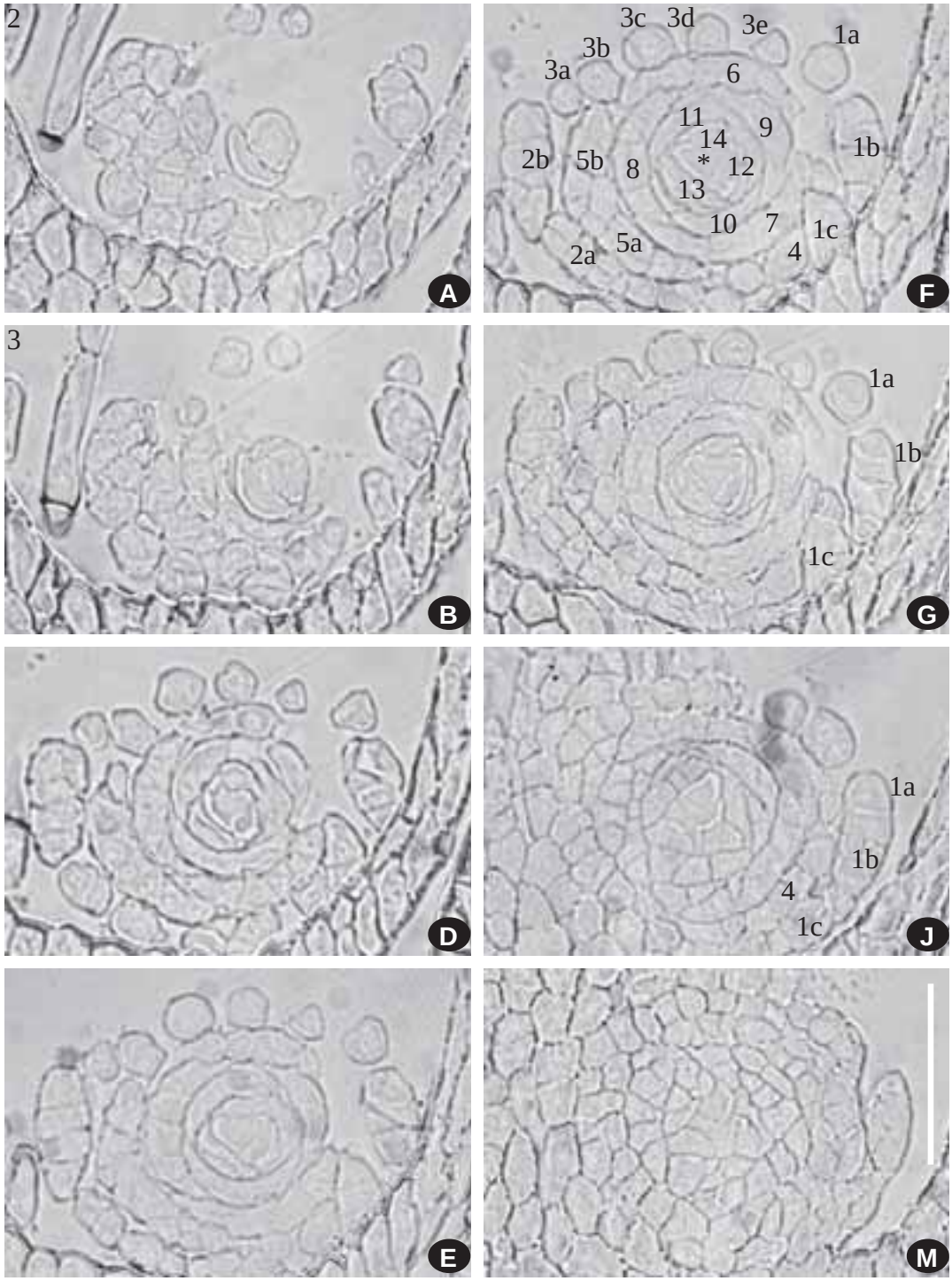


Fig. 8. Series of 2 μm cross sections transverse to branch primordium of *Hypnum cupressiforme* at 170-200 μm from stem apex. At this stage proximal branch leaves already appeared above stem surface and first, second, third and probably the fourth are split into lobes one or few cells wide. Number of branch leaves are shown in F (note that leaf 4 is only partly seen, being covered by 1b, but its real position is obvious from J). Scale bar 50 μm.

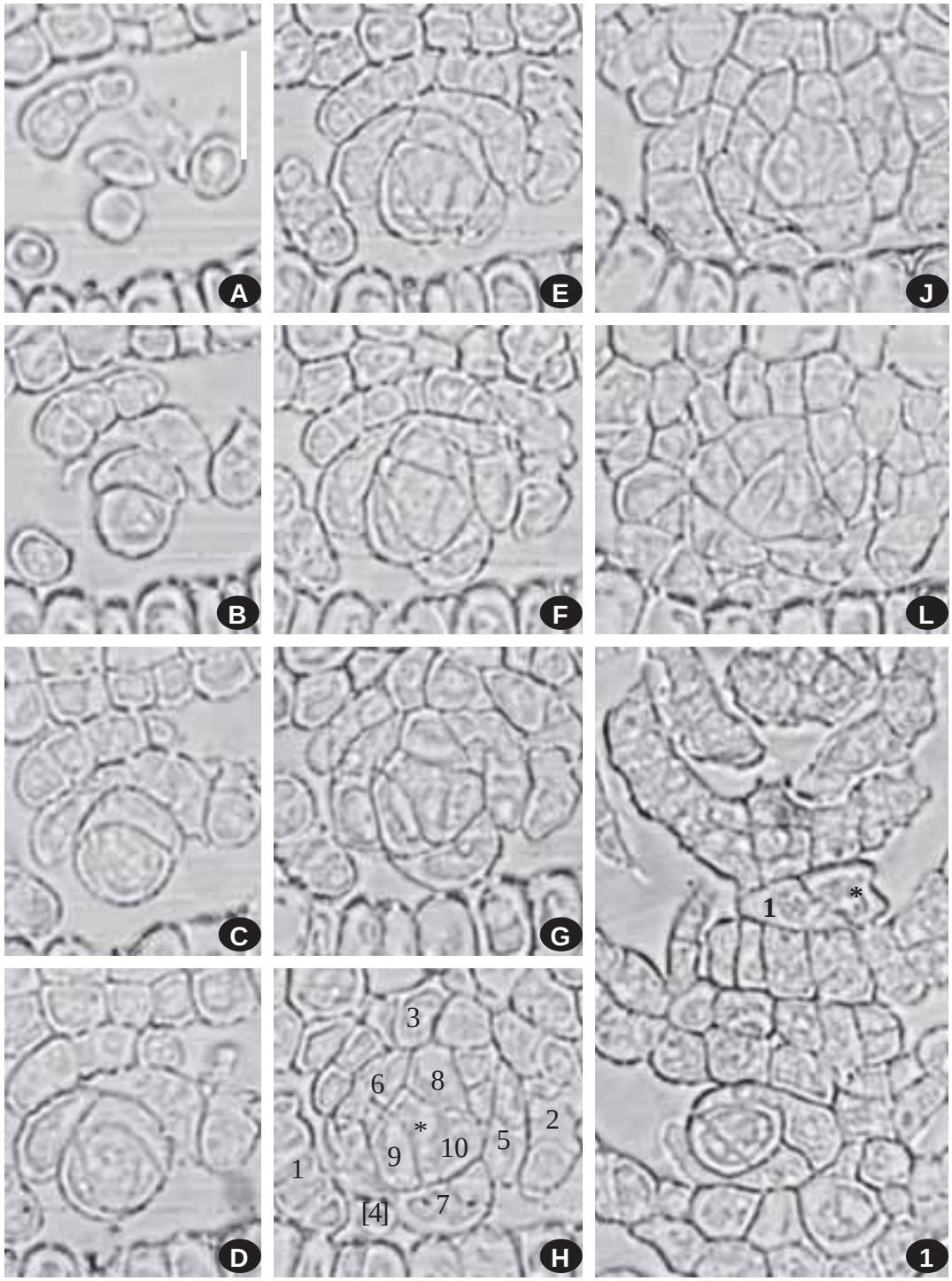


Fig. 9. A-L: Series of 2 μm cross sections transverse to branch primordium of *Amblystegium serpens* at ca. 105-130 μm from stem apex. At this stage three proximal branch leaves are well differentiated. 1 – section almost through the stem surface of *Amblystegium serpens*, showing two branch primordia at 35 and 65 μm from stem apex, the former is at the stage when the first branch leaf initial cut off from branch apical cells. The Scale bar 20 μm.

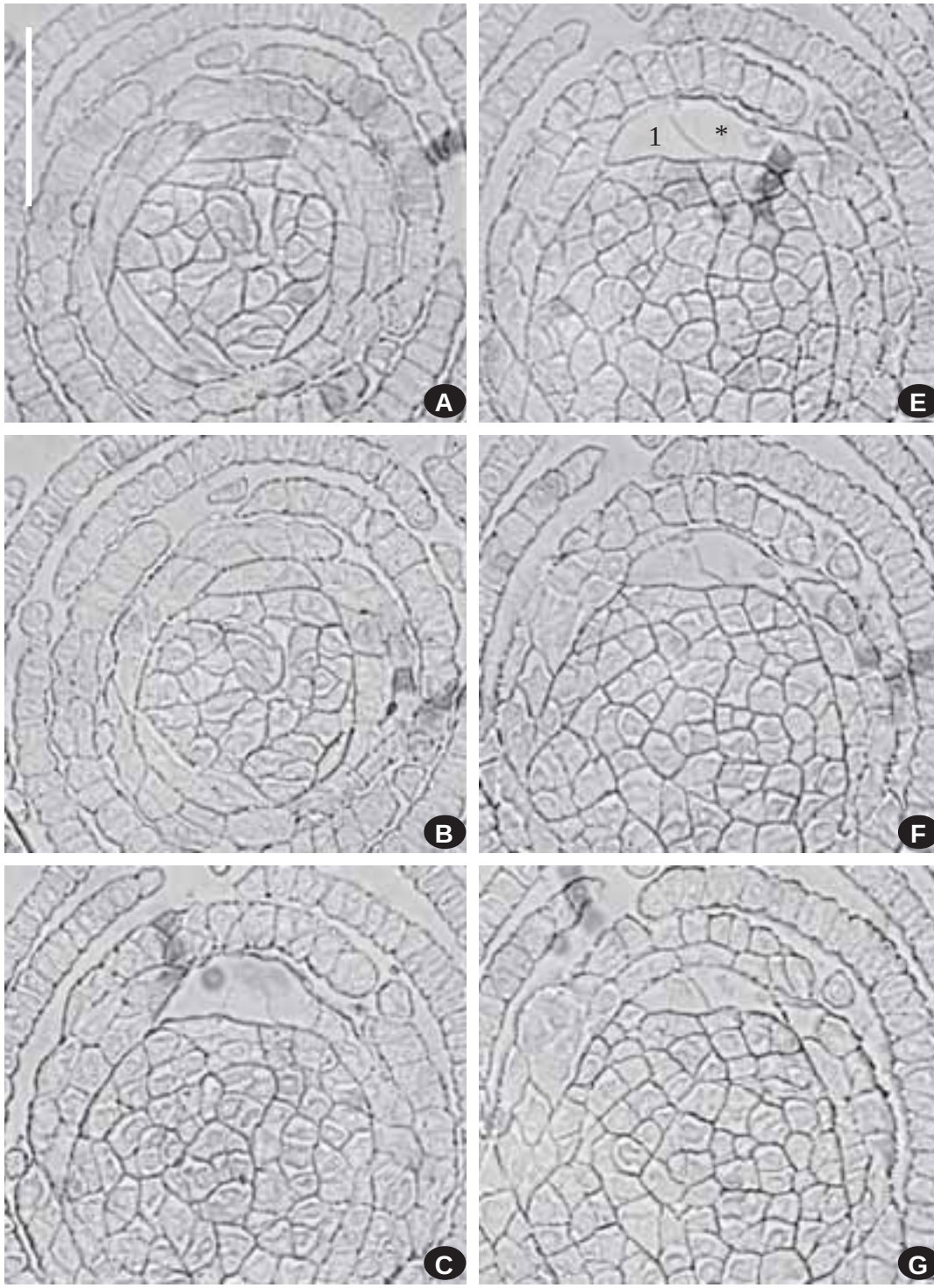


Fig. 10. Series of 2 μm section transverse to stem of *Hypnum cupressiforme* at 60-72 μm from stem apex. Branch promordia are at the stage when first merophyte cell is differentiated from branch initial cell; branch primordium is not raised above stem surface. Scale bar 50 μm.

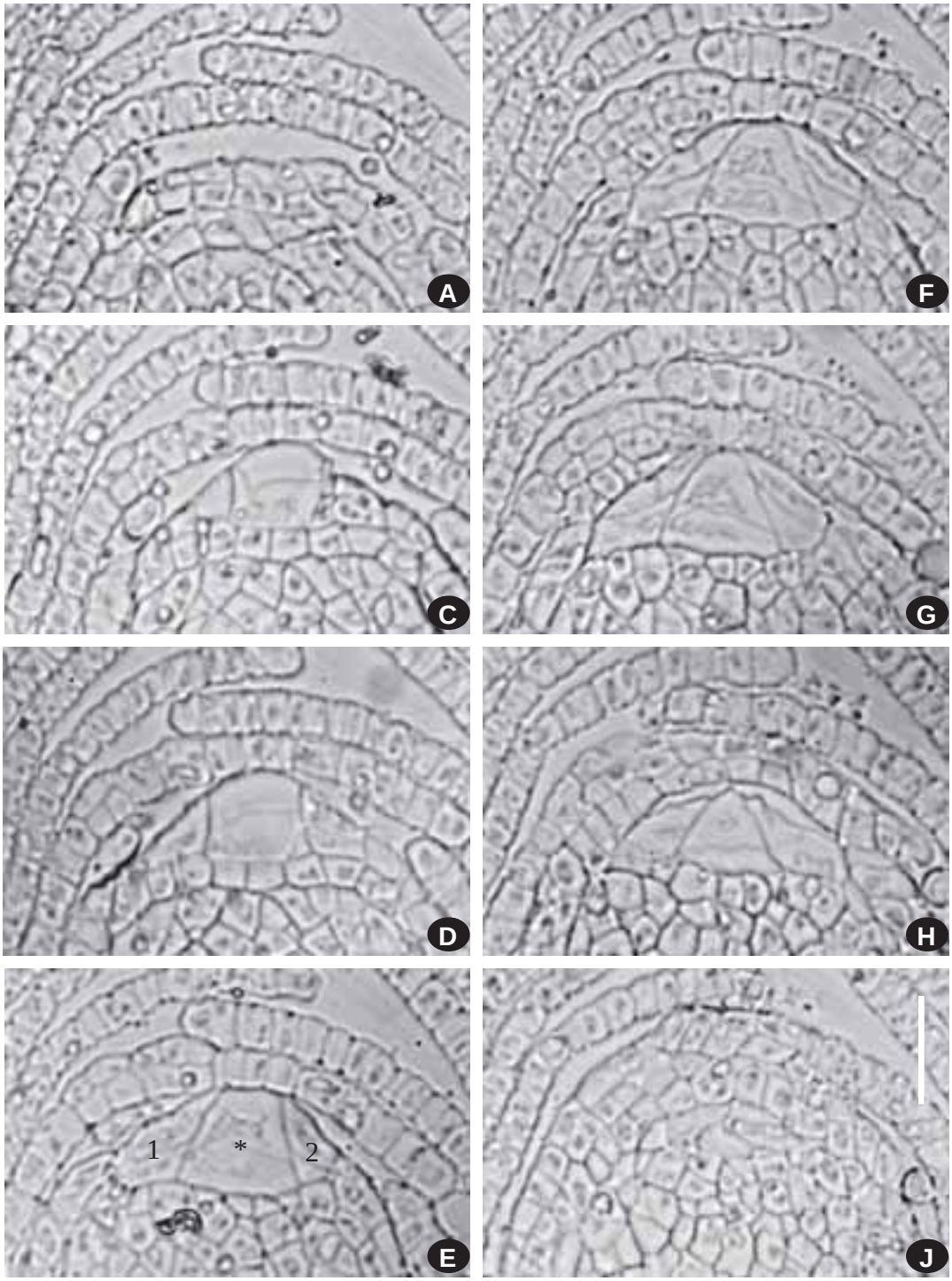


Fig. 11. Series of 2 μm section transverse to stem of *Hypnum cupressiforme* at 110-130 μm from stem apex. Cells that will develop into first proximal branch leaves are cut off from the branch initial cells. Branch primordium is very slightly raised above stem surface. Note a regular subquadrate cells underlying apical cell of branch (in D). Scale bar 20 μm.

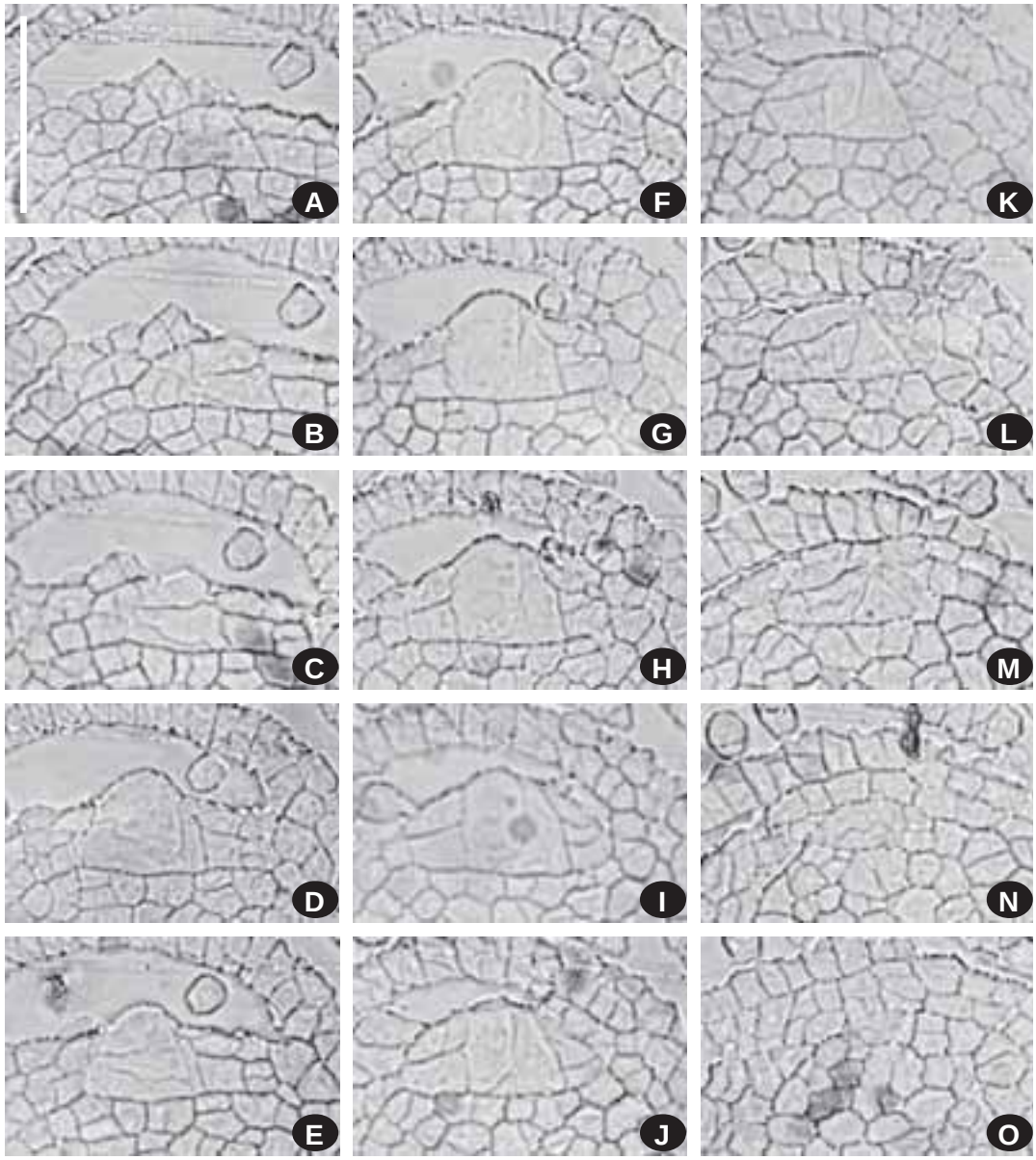


Fig. 12. Series of 2 μm section transverse to stem of *Hypnum cupressiforme* at 100-130 μm from stem apex. Proximal branch leaves are undifferentiated, primordium slightly raised above stem surface. Scale bar 50 μm.

Sections transverse to branch and plus-minus tangential to stem (Figs. 5-9).

In *Hypnum cupressiforme,* the branch primodia at the distance of 60-100 μm from apex and at the level of stem surface are 2.0–2.5 times wider than long (Figs. 5, 6). The cells of the first proximal branch leaf at about the level of stem surface are somewhat 'compartmentalized', i.e. subdivided into blocks by more thick walls between cells (Fig. 6, G, H; also compare Fig. 5 G, H). This 'breakage' of leaf is better seen in its distal corner that obviously undergone stronger elongation. Later on, as the branch primordium enlarge, the first, second, third, and occasionally also the fourth and fifth branch leaves become split into lobes of one or several cells wide (Fig. 8). The splitting into maximal number of lobes is observed in the third or second branch leaf (Figs. 8 and 15).

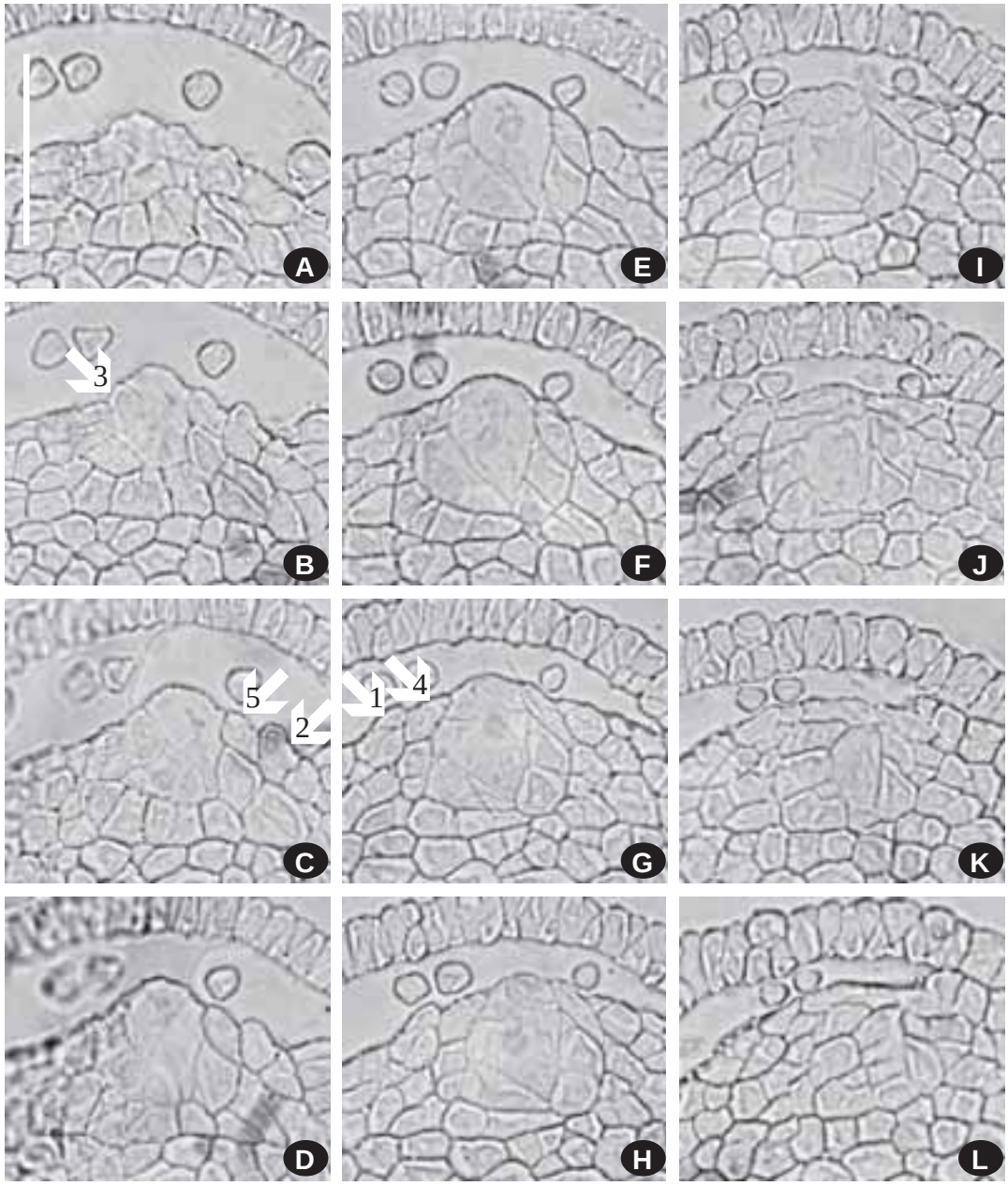


Fig. 13. Series of 2 μm section transverse to stem of *Hypnum cupressiforme* at 130-155 μm from stem apex. Branch leaves are at the earliest stage of emerging above stem surface (arrows in B, C, G). Scale bar 50 μm.

The earliest stage of the branch leaf splitting can be observed sometimes as early as ca. 80 μm from stem apex (Fig. 7).

In *Amblystegium serpens*, the branch primordium at the level of stem surface is ovate to round usually 1.0–1.5 times wider than long, and wider only at the most early stage, when the branch primordium is 2-3-celled (Fig. 9: 1). The apical cell is small and not sunken in the stem, so the whole primordium looks rather like lying on the surface and only weakly attached to the stem.

Sections transverse to stem and longitudinal to branch primordium (Figs. 10-17).

The views of transverse stem sections at the early stages of branch development in *Amblystegium* and *Hypnum* are very distinctive. At the dis-

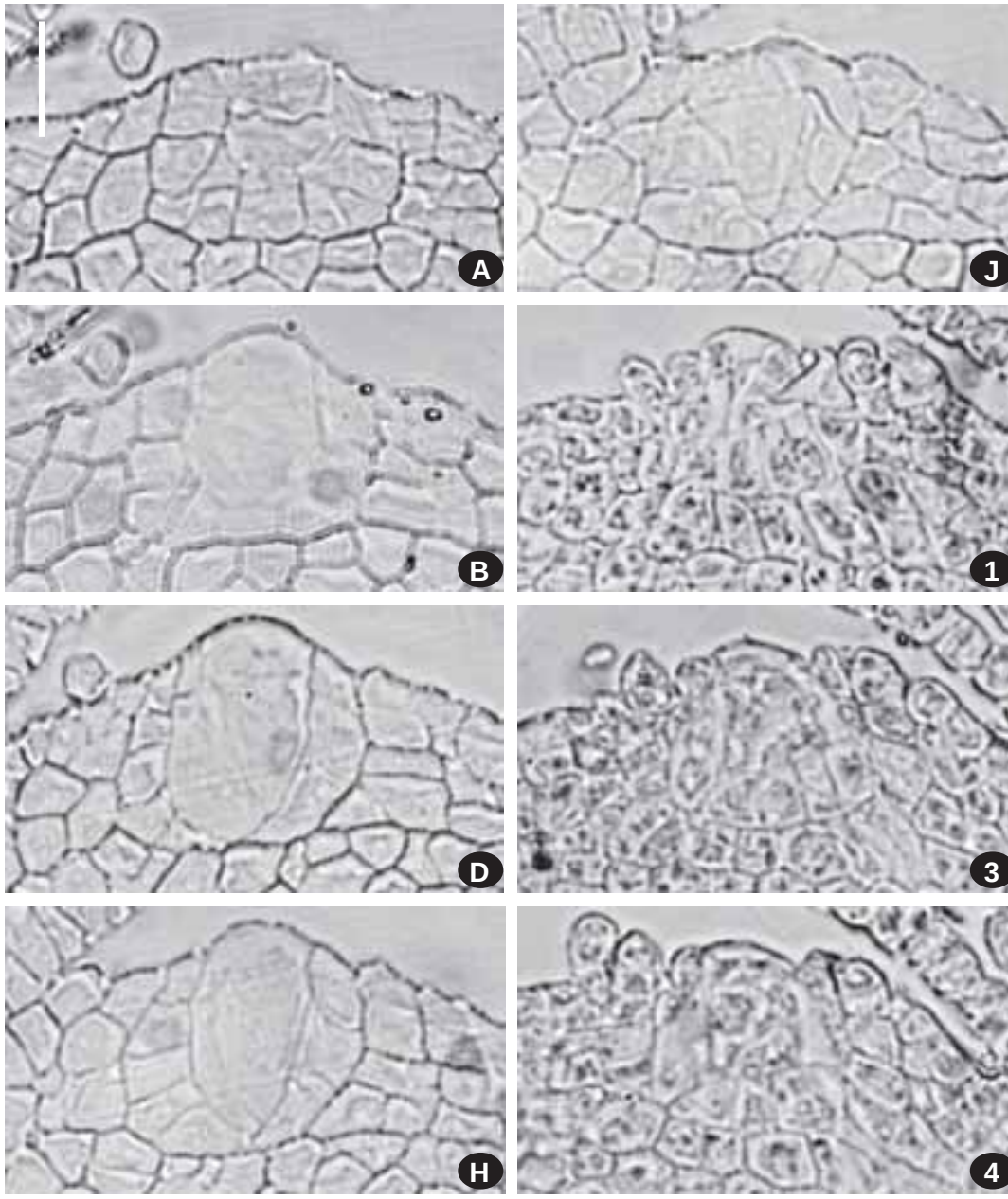
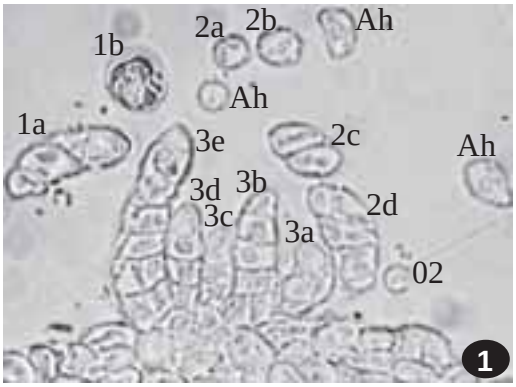


Fig. 14. Two series of *Hypnum cupressiforme:* A-J – series of 2 μm section transverse to stem at 140-165 μm from stem apex, and 1-4 – series of 2 μm section obligue (30% transverse, 60% longitudinal) to stem at 140 μm from stem apex,. Branch leaves are at an early stage of emerging above stem surface. Scale bar 20 μm.

tance of ca. 30-40 μm from stem apex, outer cells of *Hypnum* (that will develop into leaves and branches, I in Frey's terminology) are sharply differentiated from the cells of central part of stem, having much wider cells that are flattened tangentially. Contrary to this, stem of *Amblystegium* is composed by rather uniform parenchymatous cells (Figs. 3 G^1-N^1 and 3 G^2-N^2; 10).

Further on, in the series of cross sections of *Hypnum*, the large apical cell appears very suddenly (Figs. 10-13), and at its first stage, 60-130 μm from the stem apex, has trapezoid shape, being wider inside than outside (Figs. 11-12). At somewhat later stage, 140-180 μm from the stem apex, the shape of apical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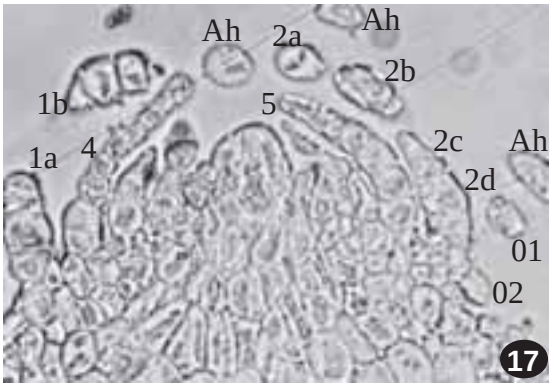
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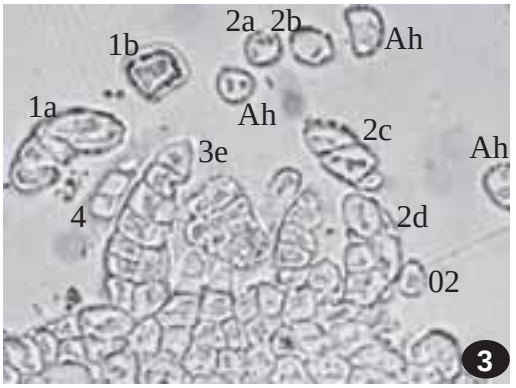
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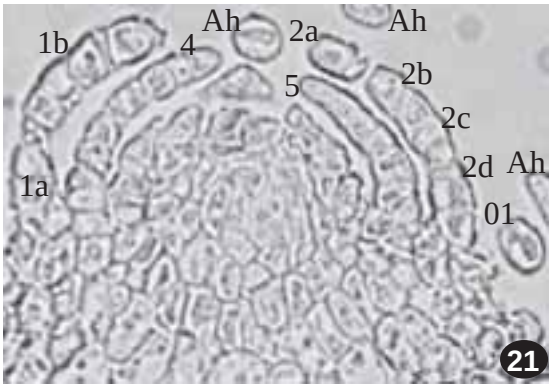
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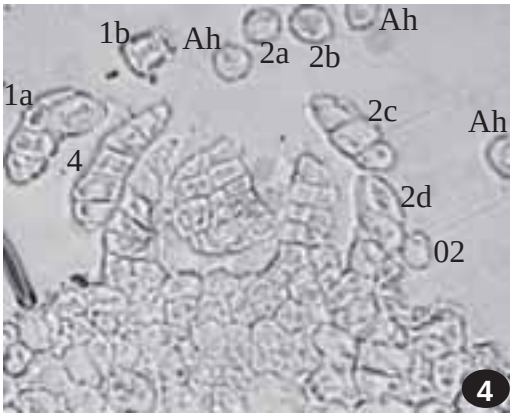
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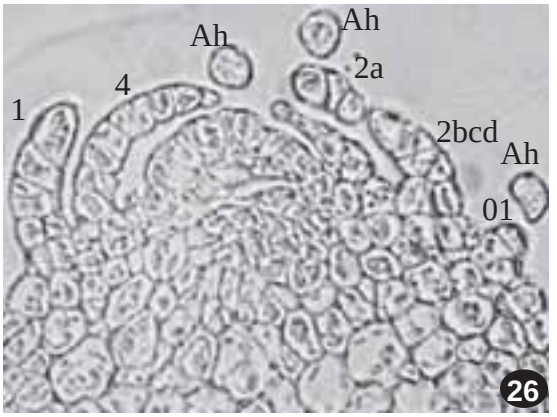
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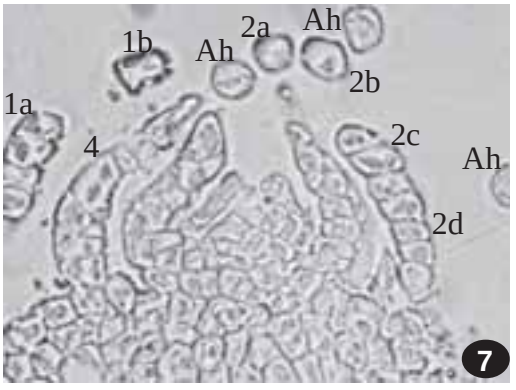
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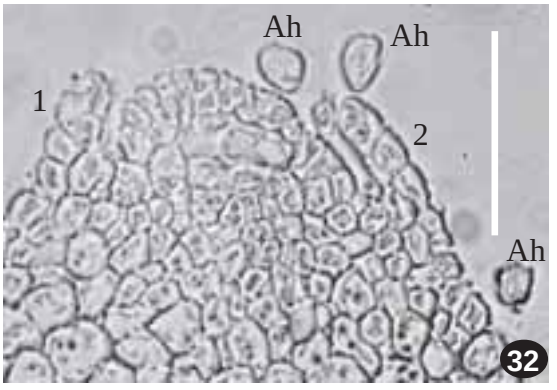
2a
Ah
2b
1a
2c
4
Ah
2d
7


Ah
Ah
1
2
Ah
32

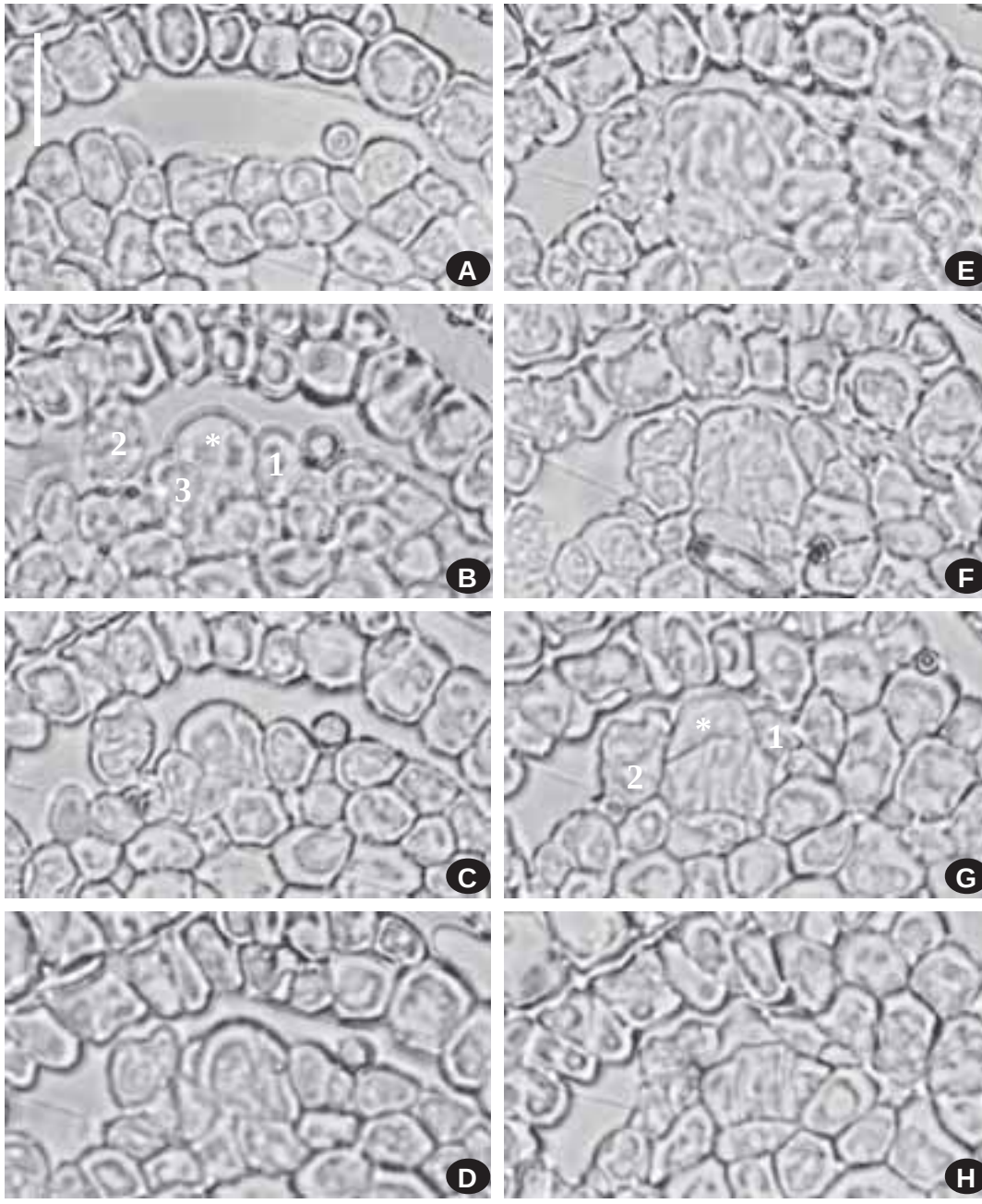


Fig. 16. Series of 2 μm sections transverse to stem of *Amblystegium serpens* at 80-100 μm from stem apex. Proximal branch leaves are at an early stage of differentiation. Note a rather small size of apical cell. Scale bar 20 μm.

Fig. 15 (page 154). Series of 2 μm section transverse to stem of *Hypnum cupressiforme* at 270-320 μm from stem apex. Branch primordium is relatively well developed, and the sections allow tracing the lobes of the first lacerate leaves. Sections demonstrate especially strong splitting of the second and the third branch leaves (cf. Fig. 8). Note a small structures to the rigth of primordium (01 and 02). They is interpreted as a subfilamentose structure sometimes seen beside the branch primordia (cf. Figs. 2: 3, 2: 5, 2: 7). Its origin can be linked to the 'breakage' of base of first branch leaves (cf. Figs. 6G, 20). Section shown in #7 was somewhat damaged, so this subfilamentose structures (02) is not seen. Scale bar 50 μm. Ah – axillary hairs.

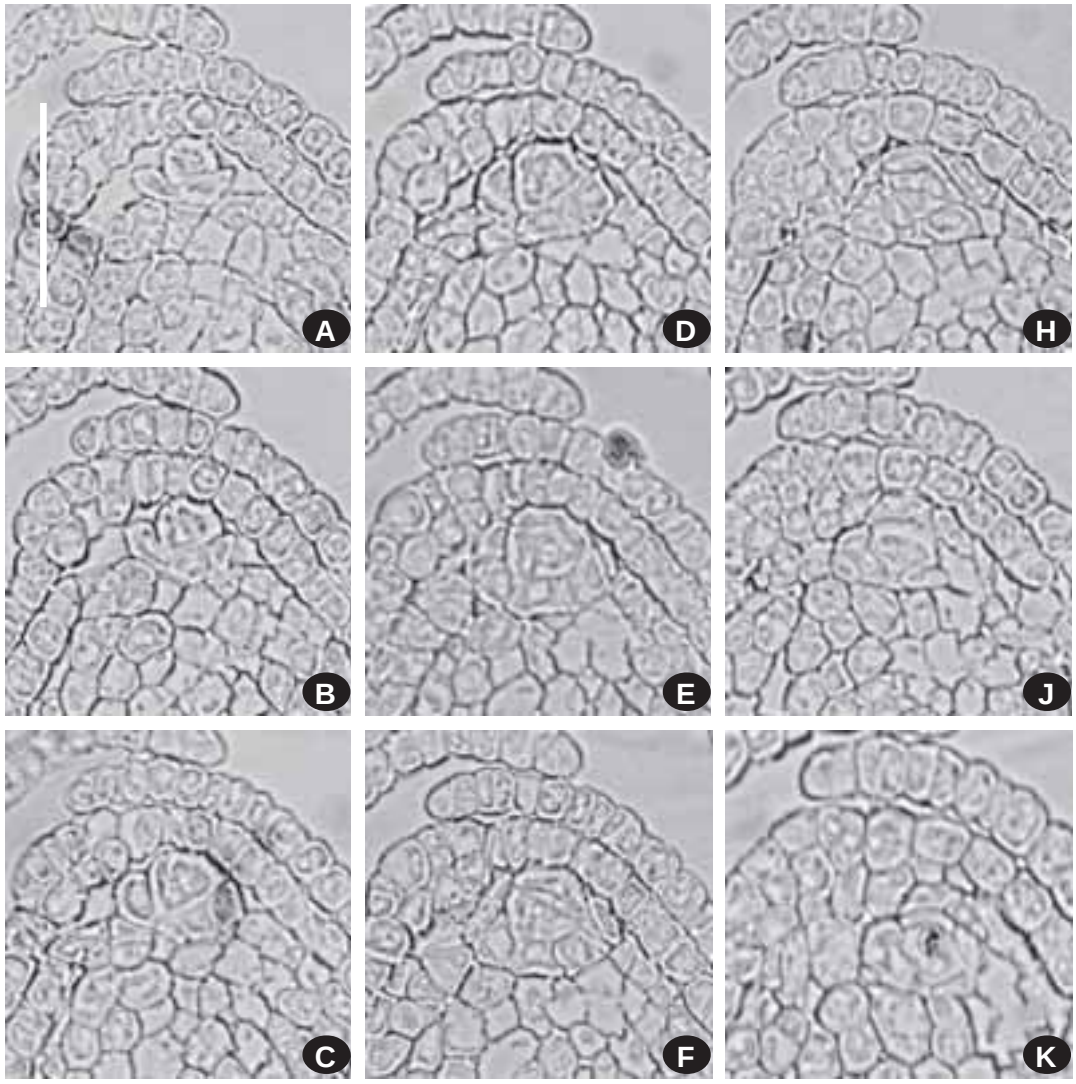


Fig. 17. Series of 2 μm sections transverse to stem of *Amblystegium serpens* at 100-120 μm from stem apex. Proximal branch leaves are at the early stage of their differentiation. Scale bar 50 μm.

cell approaches elongate-obconic, i.e., the common shape of apical cell after its surrounding cells (initials of first branch leaves) start to grow (Figs. 13-14).

Row of regular subquadrate cells underlie sometimes the apical cell (Fig. 11D), but they are observed not in all sections.

Branch leaves start to emerge above stem surface at 90-150 μm from stem apex. Interestingly, their growth begins rather similtaneously for leaves of several circles around the branch apical cell. The most distal outgrowths looks derived from the the 'broken off' portion of leaves (cf. distal parts in Fig. 6G).

At the distance of 200-300 μm from the stem apex, a rather well-developed branch leaves around branch primordia are observed (Fig. 15). Despite of strong splitting, their parts can be understood by comparison of neighboring sections. In addition to regular leaves (e.g. #1, 2, 3, etc.) and axillary hairs, the series in Fig. 15 includes a subfilamentose forked structures (01 and 02), that can be interpreted as the same as shown in Figs. 2: 3, 2: 5 and 2: 7. Its position is at the periphery of the area derived from the same branch initial cell.

In *Amblystegium,* the branch apical cell is not so much differentiated. It is small, round, not changing

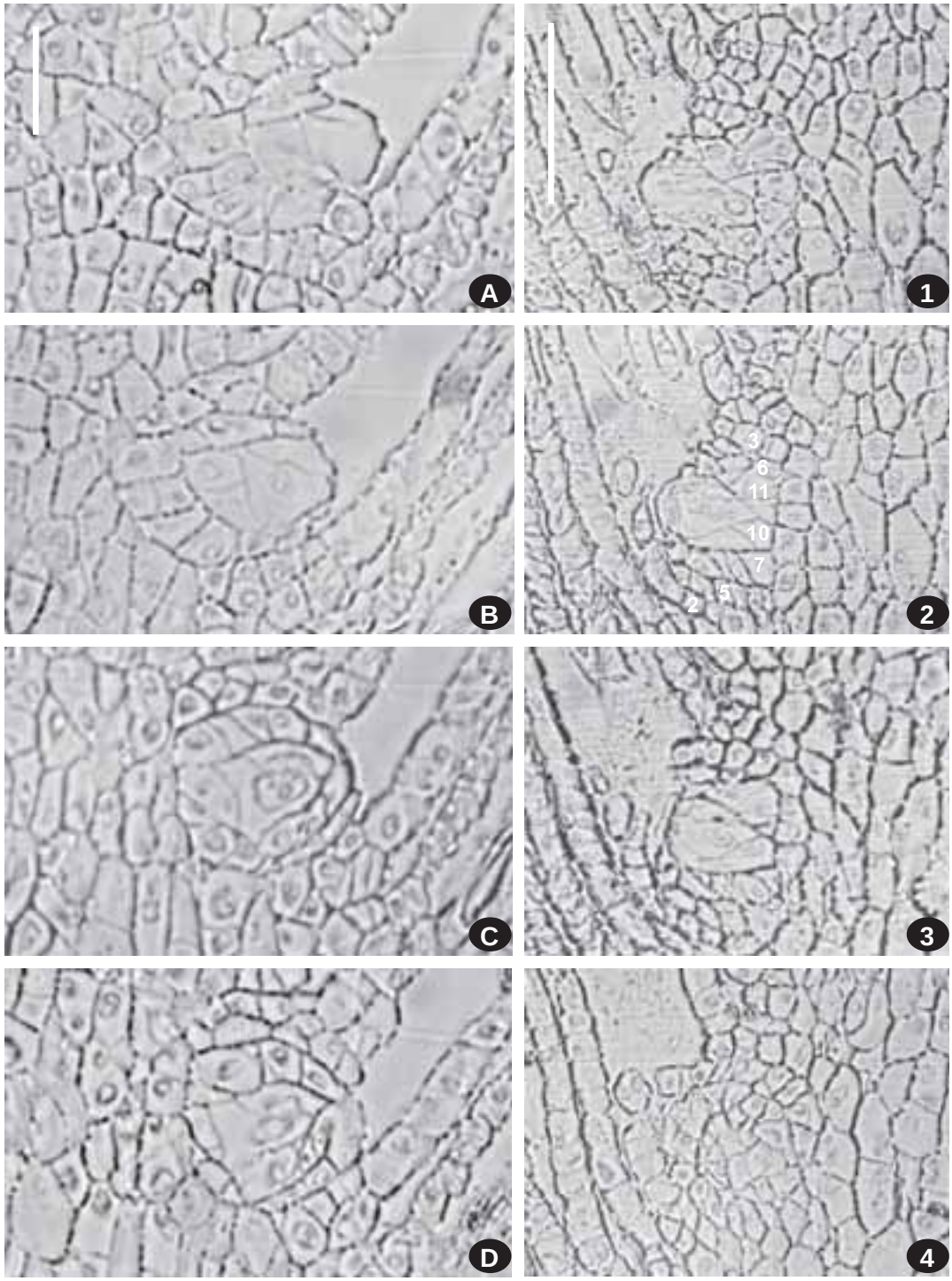


Fig. 18. Two series of 2 μm sections longitudinal to stem of *Hypnum cupressiforme*: A-D at ca. 65 μm from apex, when branch leaves still not emerged above stem surface, and 1-4 at 150 μm from stem apex, when first leaves are somewhat differentiated: their probable sequence is shown in #2 (assumed from the neighboring sections and from comparison with Fig. 8). Scale bar 20 μm for A-D, 50 μm for 1-4.

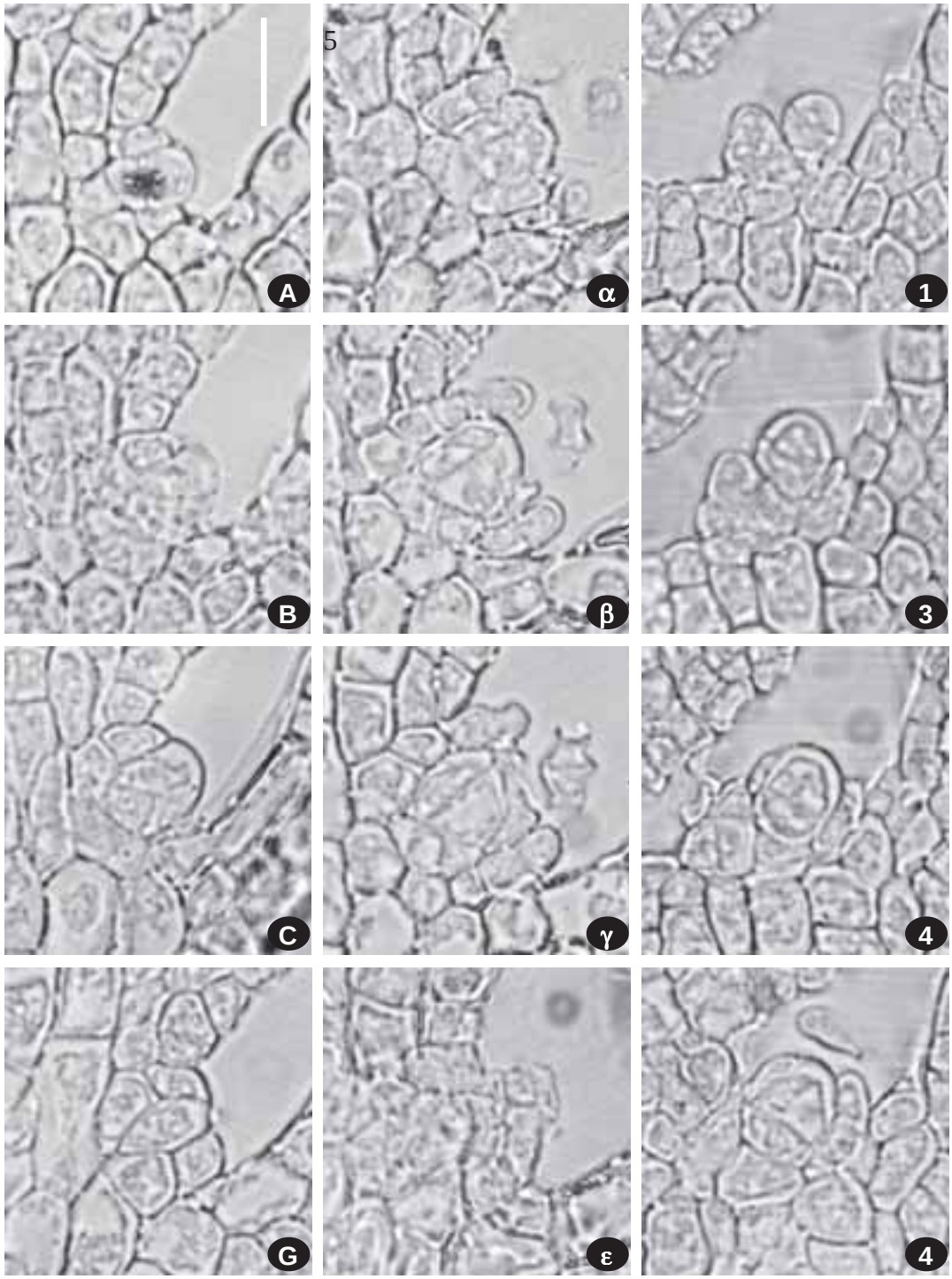


Fig. 19. Three series of 2 μm longitudinal sections of stem of *Amblystegium serpens*: A-G at 200 μm from stem apex, α–ε. – at 120 μm, 1-4 – at 100 μm. Proximal branch leaves are at early stages of their differentiation. Note that the distance from stem apex not always correlate with the development of branch primordium and proximal branch leaves. Scale bar 20 μm.

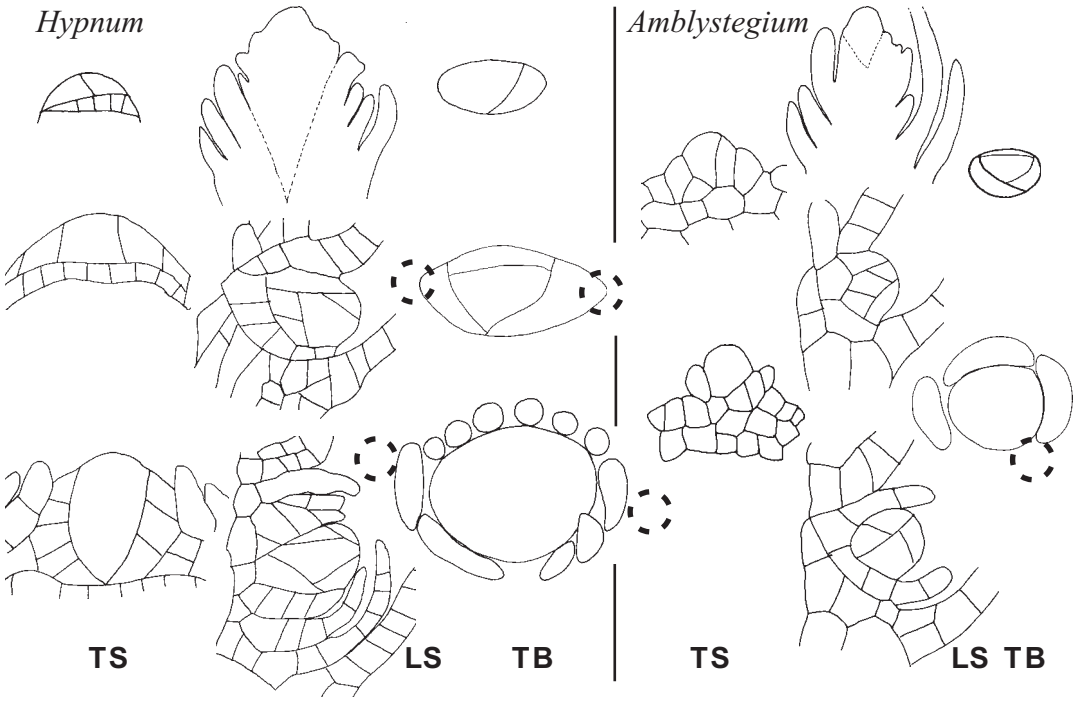


Fig. 20. Schemes of branch development of *Hypnum cupressiforme* and *Amblystegium serpens*, at the interval of 50 to 200 μm from stem apex. Sections transverse to branch primordium (TB), transverse to stem (TS), and longitudinal to stem (LS) are shown. Brocken-lined circles indicate positions where splitting from the regular proximal branch leaves is more common (cf. Fig. 2).

shape during the branch development (Figs. 16-17). It has about the same width and depth (i.e., dimension along the radial axis), and not much differentiated in size from surrounding cells (Figs. 16-17).

Sections longitudinal to stem and branch primordium (Figs. 18-19).

The longitudinal sections show almost similar differences between *Hypnum* and *Amblystegium* that were already discussed. They provide also an additional view of the "underlying layer", i.e., a row of fairy regular, subquadrate cells situated immediately inside from the branch apical cells or apical cell group (Figs. 18-A, 18-2, cf. Fig. 11D). Similar cells are not seen in *Amblystegium,* and they also are absent in cross sections of *Hypnum* in places not immediately proximal to branch primordia. As can be assumed from comparing the sections, this layer of cells is derived from cells forming the central part of stem (i.e., cells derived from cell II in terminology of Frey (1970)), not from apical cell of the branch. Longitudinal sections (e.g., Fig. 18 C) show these cells developed along the border with the "mother-leaf". Their small size may indicate a meristematic activity, which is likely, as the branch primordia later are shifted from the "mother-leaf" to a considerable distance, to approximately the axil of next lower leaf (Fig.1).

More developed branch primordial lack small cells below them, having, however, elongated cells similar to that seen below the apical group of stem (cf. Figs. 15R and 3: 1).

Discussion

The branch primordia in *Amblystegium* are small and they grow in a relatively wider space, not being strongly pressed by surrounding cells and leaves and therefore they are not or only slightly deviate from the basic pattern (Fig. 1). In *Amblystegium,* usually the second (more rarely the first) branch leaf is split into two lobes (Figs. 2: 2, 2:4, 2: 6), but subsequent leaves are entire. The splitting of the second (or first) proximal branch leaves may be corresponded to the maximally wide angle between these two leaves (obviously correlating with higher elongation rate at this side of branch primordium (Figs. 9, 20).

Branch apical cell in *Hypnum* is much enlarged and flattened upon stem surface, but not penetrating into the stem. Initials of first 3-4 branch leaves appear to be strongly laterally expanded and elongated at this early stages, so the foliose structure formed from them seems often have 'broken base'. This corresponds to splitting of several first branch leaves into narrow lobes, and probably also an occasional formation of subfilamentose structures at a certain distance from the branch primordium (Figs. 2: 3, 2: 5, 2: 7). One of such subfilamentose structures is shown in Fig. 15, labeled 01 and 02, as it seems to be forked. The occurrence of such structures is rather irregular, and they may be considered as a something different from the regular branch leaves. Seems that Akiyama & Nishimura (1993) considered this kind of structures to be different from the proximal branch leaves and thus representing the true pseudoparaphyllia.

However their origin, at least incase of *Hypnum,* is not principally different from that of lobes of proximal branch leaves: in this case certain lobes just appear more distantly. In practice, these subfilamentose structures, in *H. cupressiforme* are sometimes so close to the main group of lacerate proximal branch leaves that it would be an impossible task to say in many (if not most) cases if they belong to group of proximal branch leaves or not. Ignatov & Hedenäs (2007) suggested not to oppose such structures from leaves and describe them under different names, but rather consider them to be the same, but provide more detailed description of their shape, size and arrangement. We believe that this approach will bring more information on their structure and development.

* * *

The important role of a mechanical tension for the splitting of proximal branch leaves in *Hypnum* may be implied based on two observations: first, the splitting of proximal branch leaves into lobes is very irregular (Figs. 53-59 in Ando, 1989; Fig. 2); and second, the places of maximal elongation at early stages of development seems to be correlated with the maximal splitting of proximal branch leaves (Fig. 20). The testing of this hypothesis might be interesting in further studies.

* * *

Summing up, the development of branches and branch leaves in *Hypnum* follows, in general, the 'classical scheme' (Fig. 1), thus, demonstrating no need to recognize the proximal branch leaves as a separate morphological structure usually called pseudoparaphyllia. A number of first leaves, however, may have a shape contrastingly different from the fully developed distal leaves. Some foliose and subfilamentose structures may appear at a certain distance from branch primordium due to the aberrations in cell division at the early stage of branch development.

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