

MOSSES FROM ROVNO AMBER (UKRAINE), 4.
SPHAGNUM HEINRICHSSII, A NEW MOSS SPECIES FROM EOCENE

МХИ ИЗ РОВЕНСКОГО ЯНТАРЯ (УКРАИНА), 4.
SPHAGNUM HEINRICHSSII, НОВЫЙ ВИД ИЗ ЭОЦЕНА

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Abstract

Sphagnum heinrichsii is the second specimen of this genus from Eocene amber of Europe, and is preserved with more detail than the first unnamed *Sphagnum* from Baltic amber, which was referred to the sect. *Acutifolia*. *Sphagnum heinrichsii* is represented by one stem fragment with about seven branches. The branch leaf pore arrangement points to a relationship with sect. *Cuspidata*. However stem leaf pores are rather more like those of sect. *Subsecunda*.

Резюме

Sphagnum heinrichsii – вторая находка сфагнома в эоценовом янтаре Европы. Его лучшая сохранность позволяет дать более детальное описание по сравнению с образцом сфагнома из балтийского янтара, который был отнесен предположительно к секции *Acutifolia*. *Sphagnum heinrichsii* представлен фрагментом стебля с 7 веточками. Расположение и строение пор веточных листьев сходно с таковым у современных видов секции *Cuspidata*. Строение пор стеблевого листа *S. heinrichsii*, однако, соответствует секции *Subsecunda*.

KEYWORDS: bryophytes, mosses, fossils, Sphagnaceae, Spahnales, sect. *Cuspidata*

INTRODUCTION

Mosses from the Baltic amber have been studied since the mid 19th century (Goepfert & Berendt, 1845; Goepfert, 1853; Caspary & Klebs, 1907), and from the Bitterfeld amber since the second half of the 20th century (Liemann, 2013). Frahm (2004, 2010) summarized mosses known from these collections, enumerating 33 genera. Most of them belong to epiphytic groups, which is natural as this habitat obviously favors embedding epiphytic bryophytes into resin from trunk cracks. The same predominantly epiphytic ecology of amber inclusions is even more apparent in the hepatic flora, where about half of all specimens from Baltic and Bitterfeld amber belong to the genus *Frullania* (Grolle & Meister, 2004).

Rovno amber bryophyte studies started less than ten years ago (Ignatov & Perkovsky, 2011, 2013; Ignatov et al., 2016), however the same pattern is apparent: epiphytes prevail among moss (*Hypnum*, *Sematophyllites*,

Hypnodontopsis, *Calymperites*, *Trachycystis*, *Neckerites*, *Palamocladium*, *Ctenidium*, *Tristichella*, and *Isopterygium* (Ignatov & Perkovsky, 2011, 2013; Ignatov et al., 2016) and hepatic genera (*Frullania* and *Acrolejeunea*) known in this amber (Konstantinova et al. 2011; Mamontov et al., 2013, 2015a,b, 2017, 2018).

One specimen from Baltic amber belongs to the genus *Sphagnum* (Frahm, 2009, 2010). It was referred to sect. *Acutifolia* based of areolation patterns in leaves from one branch fragment.

The new finding of *Sphagnum* in the Late Eocene Rovno amber is noteworthy, as it comprises more details suggestive enough for discussion of its sectional position within *Sphagnum*.

MATERIAL AND METHODS

The Late Eocene amber specimen SIZK-VT-88 originates from the Velyki Telkovichi (Vladimirets District)

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in the Rovno Region of the Ukraine. Over the last year this locality and localities situated near it in Vladimirets District yielded many species and genera of insects (Perkovsky & Olmi, 2018; Radchenko & Perkovsky, 2018) not known from Klesov deposit, which remains the main source of Rovno amber inclusions (Perkovsky *et al.*, 2007, 2010; Perkovsky, 2017), and where from nearly all above mentioned records of bryophytes were done. Having about the same age as Baltic amber (Perkovsky *et al.*, 2007, 2010), Rovno amber comprises a somewhat more southern fauna (Dlussky & Rasnitsyn, 2009; Naiden *et al.*, 2016; Perkovsky, 2011, 2016; Sokoloff *et al.*, 2018; Legalov *et al.*, 2018).

The specimen was studied under a compound light microscope (Olympus CX41) and a stereomicroscope (Olympus SZX16 equipped with an Infinity 4 digital camera). Incident and transmitted light were often used simultaneously. Most micrographs were obtained from a series of optical sections and composed using the software package HeliconFocus 4.50 (Kozub *et al.*, 2008) for a better illustration of the three-dimensional inclusion.

TAXONOMY

Genus **Sphagnum** L. gen. nov. [order Sphagnales, family Sphagnaceae]

Type species: *Sphagnum palustre* L., extant.

Diagnosis: Single layered laminal cells dimorphous: narrow chlorocysts form loops embracing hyalocysts forming a regular cell network of which the latter have conspicuous fibrils and often also pores.

Comment: *Sphagnum* (and related genera, recently segregated from *Sphagnum*, but similar, so previously placed in this genus), have many features unique for bryophytes in both sporophyte and gametophyte structure. Here we mention only a character which is easy to observe even in a small leaf fragment, and therefore alone is sufficient to refer a specimen to the order Sphagnopsida. Until recently this order was treated as containing the only genus *Sphagnum*, however phylogeny reconstruction (Shaw *et al.*, 2010b) revealed ancient groups, segregated in two families with three genera: Flatbergiaceae (*Flatbergium*), and Ambuchananiaceae (*Ambuchanania* and *Eosphagnum*). Two latter genera are characterised by strongly concave, not acuminate and usually blunt branch leaves, very different from our amber specimen. *Flatbergium* has completely e fibrillose hyalocysts thus not worthy further enumeration of numerous distinctions.

Sphagnum heinrichsii sp. nov. (Figs. 1–42).

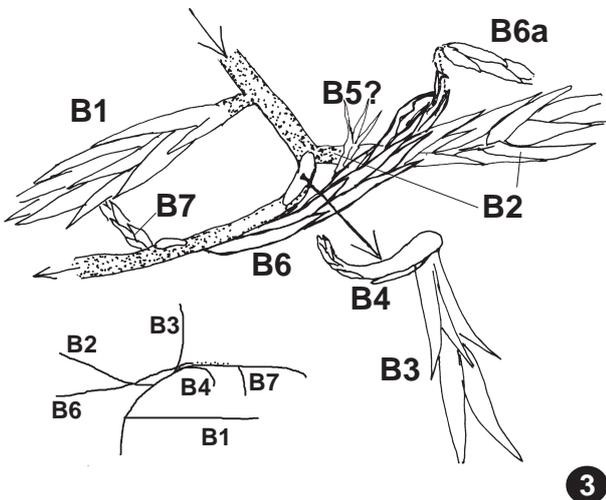
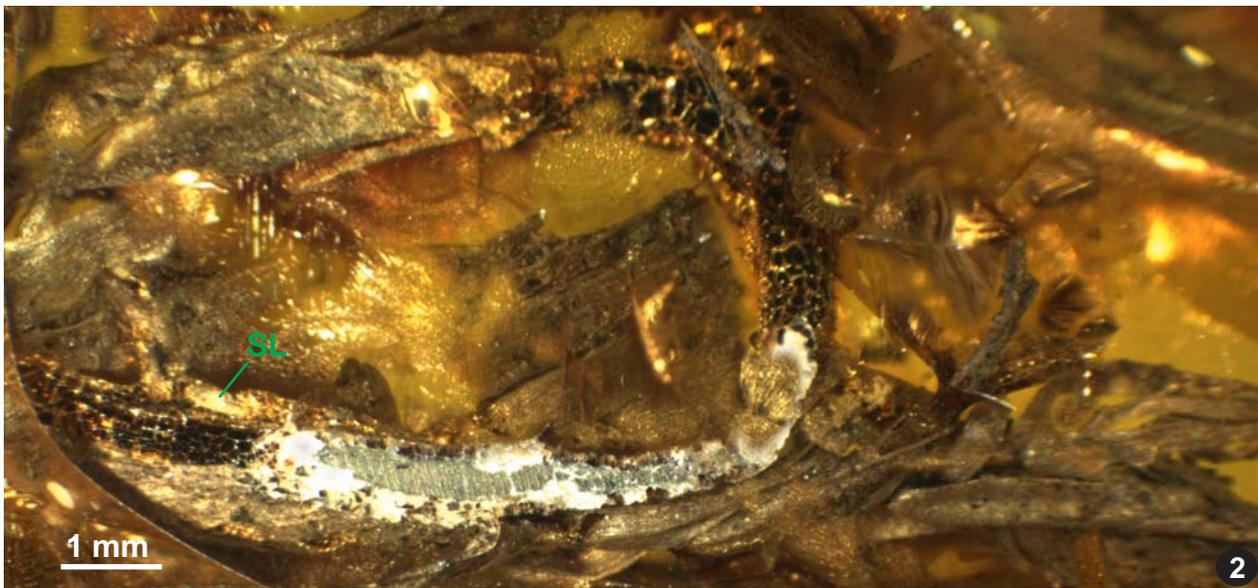
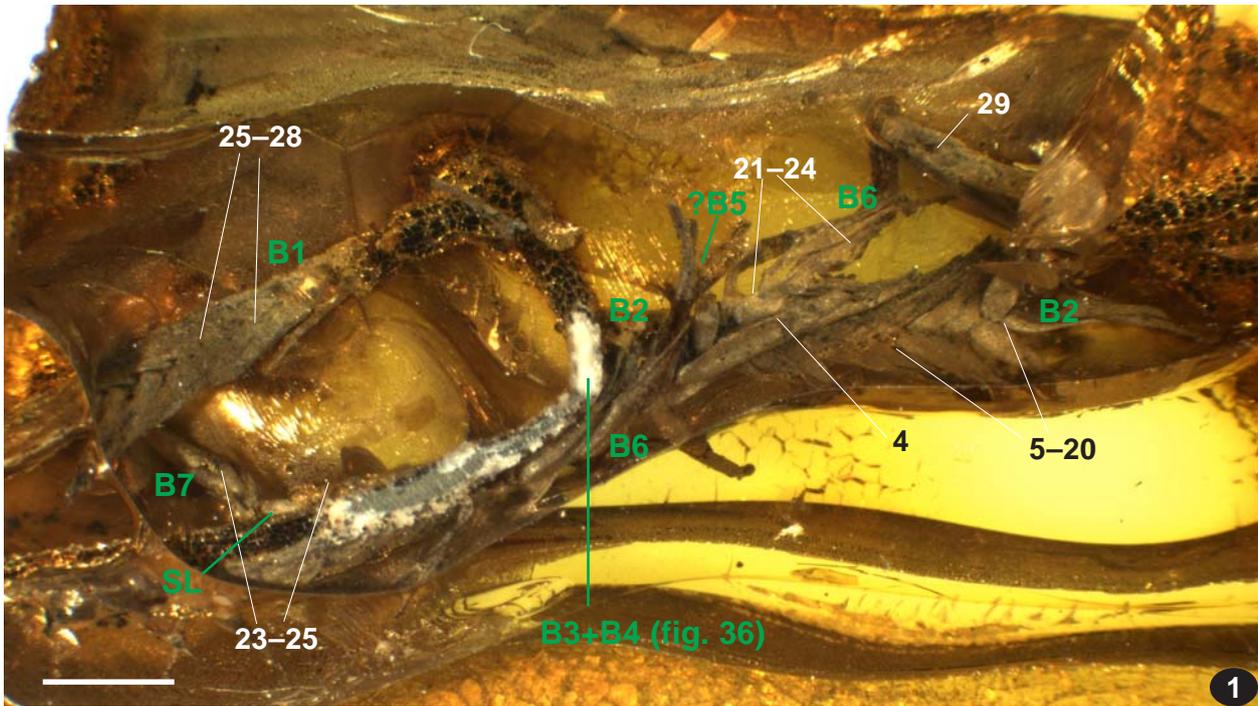
Holotype: Rovno amber. Late Eocene. SIZK-VT-88 (Fig. 1) [original piece of amber SIZK-VT-115 was cut into three parts, two containing parts of the *Sphagnum* plant(s): VT-88 (Figs. 1-35) and VT-88A (Figs. 36c42) [scheme of their connection is in Fig. 3].

Etymology: In honour of Jochen Heinrichs (1969–

2018), outstanding German bryologist and paleobotanist.

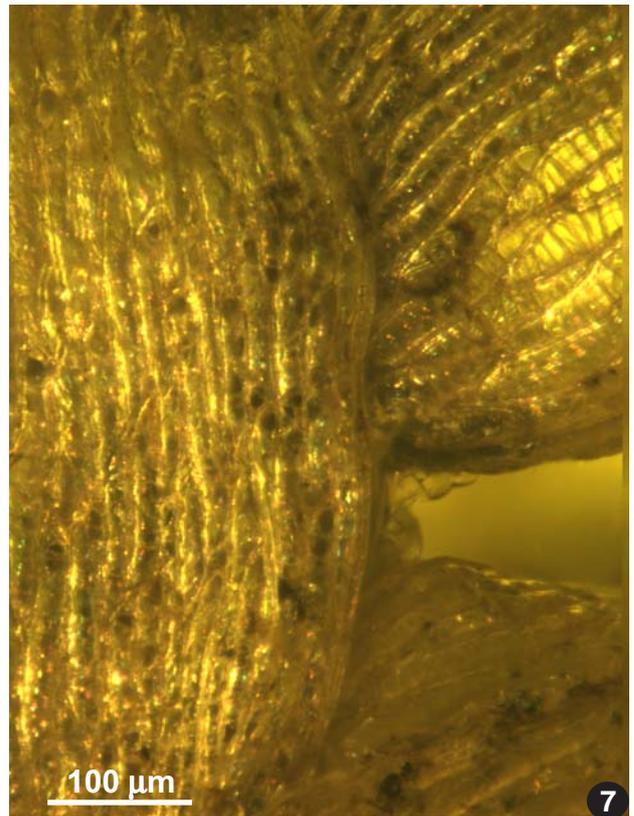
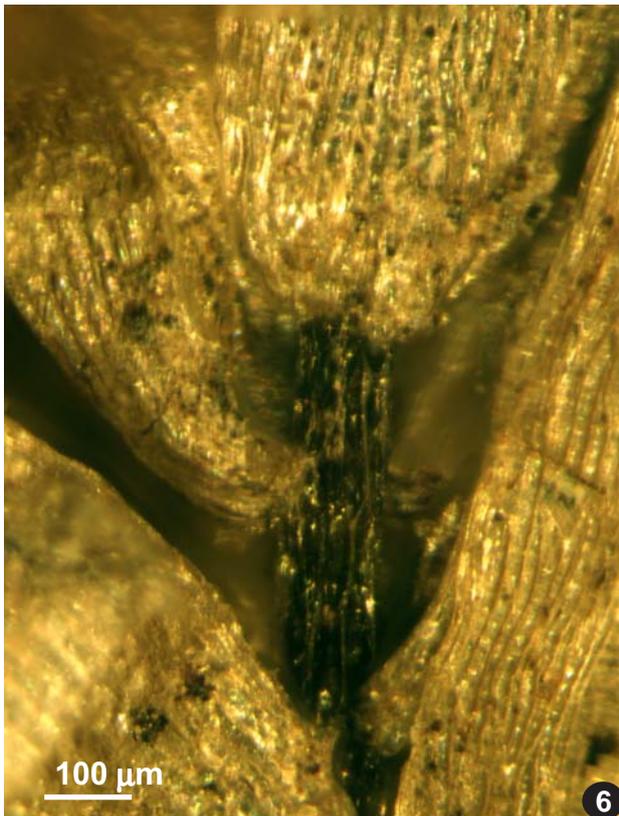
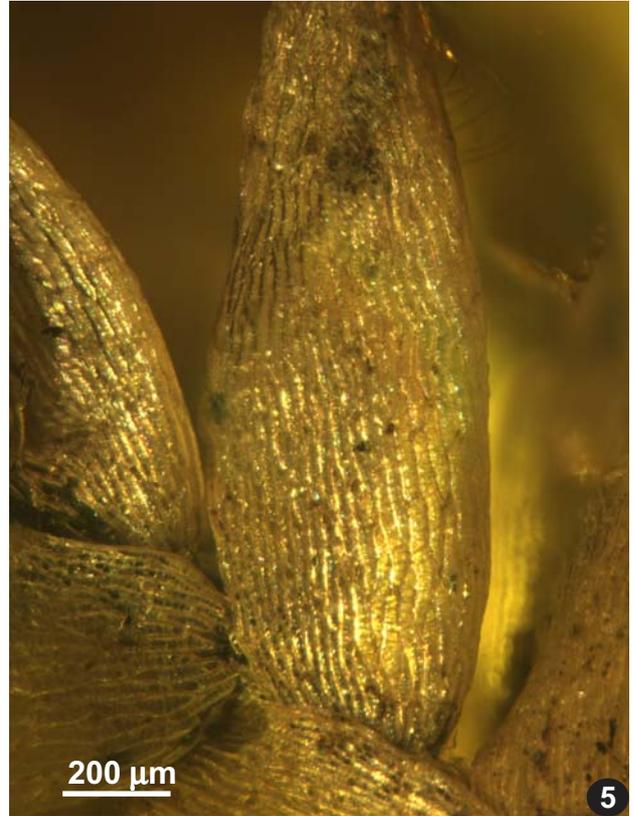
Description: Stem longer than 1 cm, sparsely branched, with branches separated at ca. 2 mm one from another, branches single or in fascicles of two, one being much smaller than another. The bigger branches spreading from stem at right angles, as well as one branch (B7 in Fig. 1) with considerably smaller leaves. Stem leaf (only one observed) small, lingulate, appressed, 0.7×0.3 mm; distal margin likely irregularly broken; hyalocysts of proximal to middle part broad, ca. 140×70 μm, towards margin and above elongated, to ca. 150–200×50–70 μm, on dorsal side with numerous imperfect pores (with clear outline but without true perforation) along commissures 17–23 μm in diameter, separated one from another by 5–10 μm, arranged in regular rows, occasionally with few similar pores along convex hyalocyst median part; perfect (with perforation) pores few, more numerous towards apex; chlorocysts exposed to dorsal surface as narrow strips ca. 5 μm close to leaf base among especially broad cells. Branch leaves on long branches apparently arranged in rows, up to 3.0×0.7 mm, narrow lanceolate, gradually tapered to apex, flat to concave near base; hyalocysts 200–280×25–30 μm, fibrils numerous at 15–20 μm from each other (in both large leaves and in leaf only 1 mm long); pores only in few cells, mostly in distal hyalocyst corners, more rarely also in proximal corners, occasionally in other parts of leaves (some cells near base of concave leaf part with large pores along whole cell); in middle leaf part mostly imperfect pores occur and in distal parts of leaves from pendent branches cells are almost undifferentiated into chlorocysts and hyalocysts; border of longer cells not apparent, although cells close to margin in proximal part of leaf somewhat narrower; leaves from small branches are only 200 μm long; leaves in proximal part of branch 0.5 mm long, its hyalocysts distally with some pores of quite small size, <5 μm.

Material: The piece of amber was cut into two unequal parts (before initial study). The *Sphagnum* specimen appeared mostly in a thinner slice, where its stem comes in from rough face, and then curved, lying parallel to the cutting. The stem is surrounded by amber metamorphosis along most length of the stem: it covers the stem surface so only one stem leaf (SL in Figs. 1, 3, 30–35) is available for study (ca. 0.5 mm below there is probably another one, but it is only slightly visible by its end and not allowing to understand any details). Several branches appear to be closer to the cut and polished face, allowing clear view of branches and a single stem leaf. The polarity of stem is not evident *per se*. We interpret it as shown in Fig. 3 mostly considering two types of evidence: (1) concave stem leaf orientation; although we are aware of a not rare stem leaf downwards orientation in *Sphagnum*, it is unlikely that adaxial surface of small-sized stem leaf can be strongly con-

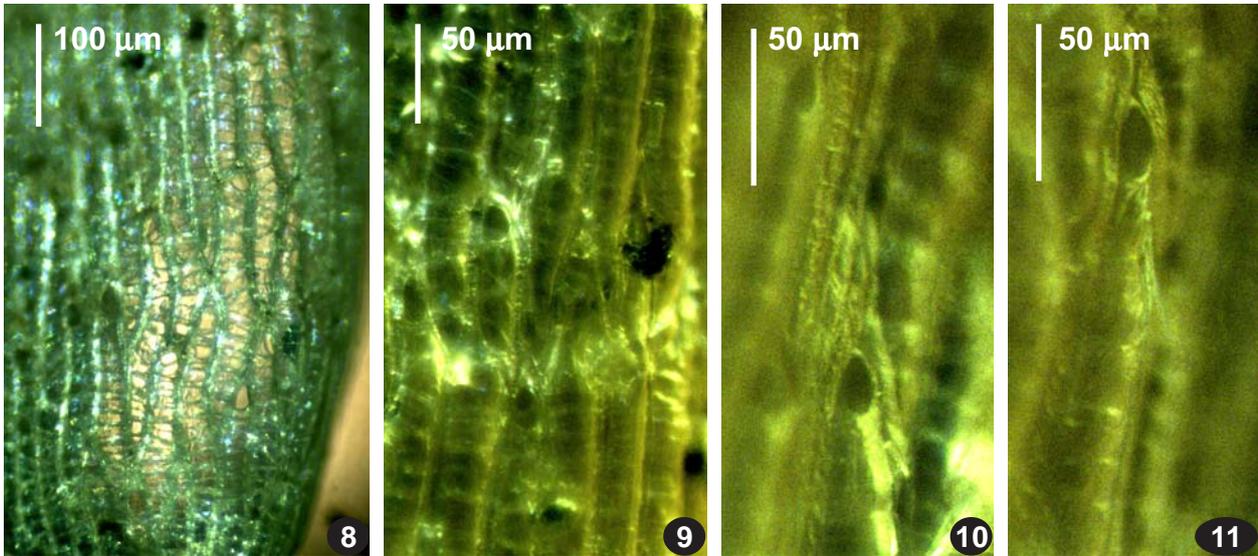


Figs. 1 & 2: *Sphagnum heinrichsii* (holotype): (1) general view with number indicating parts of plants shown by close-ups in subsequent pictures; (2) slightly enlarged view of holotype at a slightly different angle. SL: stem leaf, B1–B7: branches numbered for ease of discussion. The putative remains of one of pendent branches are denoted as ?B5 (its interpretation as a branch is not certain). Branch B3 (shown in Fig. 35) is situated at angle of ca. 70° to the polished surface of amber piece with the main part of specimen. SL (cf. Fig. 3). Branch B6a may represent apical part of B6 or otherwise the separate branch (similar to B7), fallen off and lying near the end of B6.

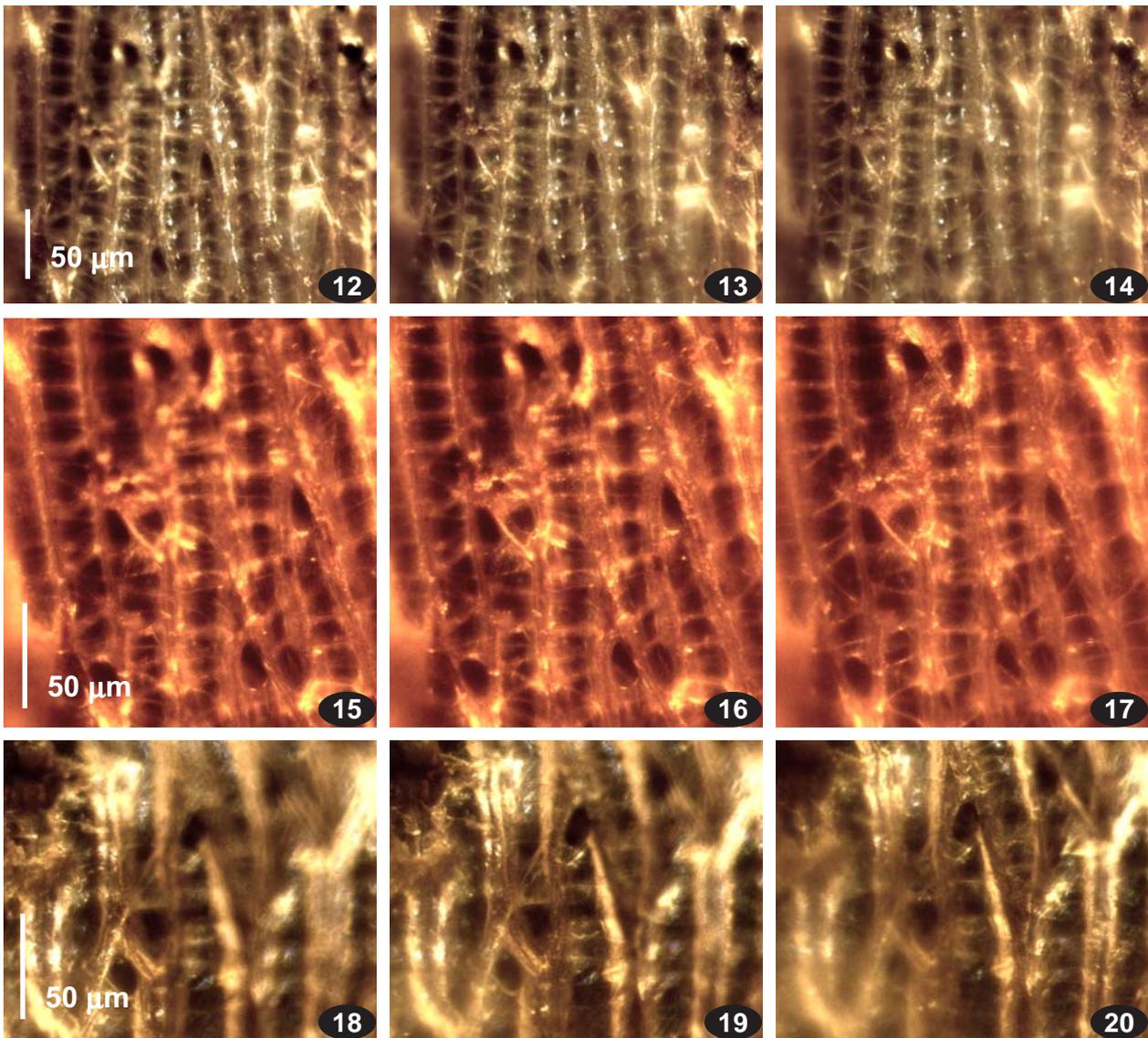
Fig. 3: Scheme of *Sphagnum heinrichsii* position in two amber pieces, with numbering of branches (B1, B2, etc.) for ease of discussion, and showing position of stem leaf (SL).



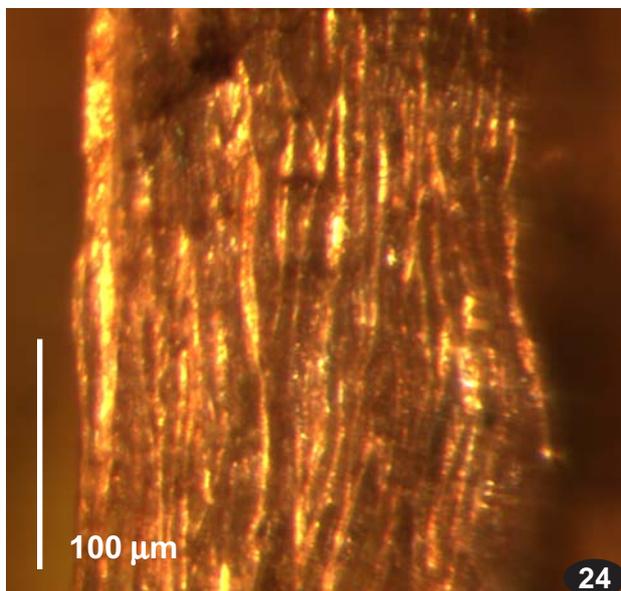
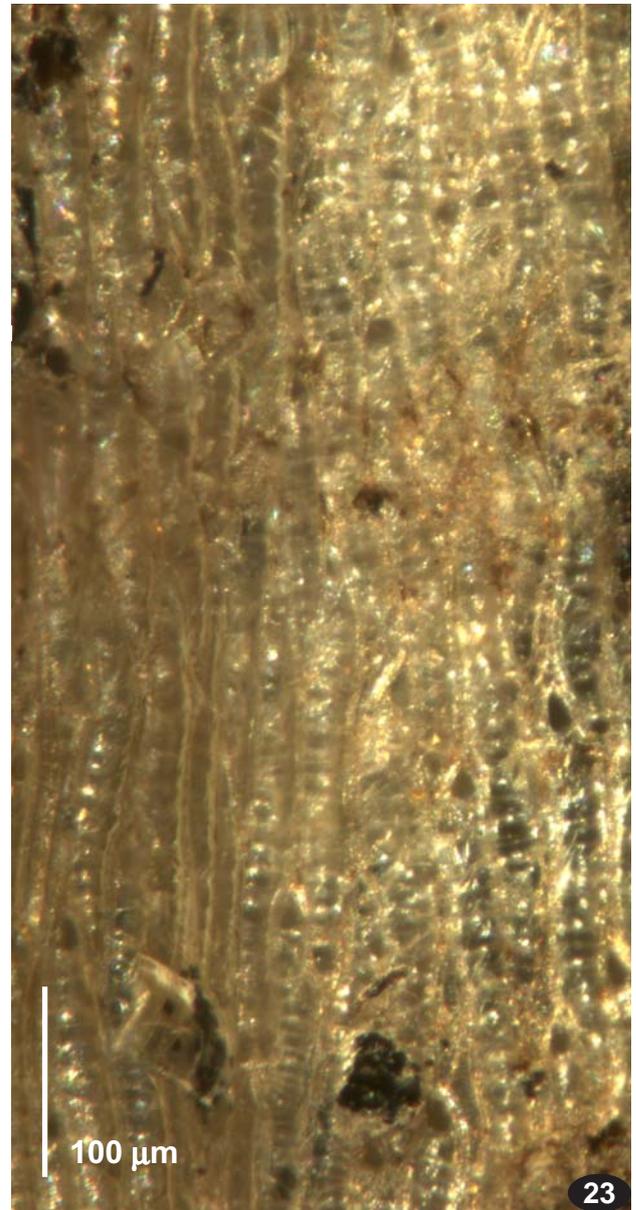
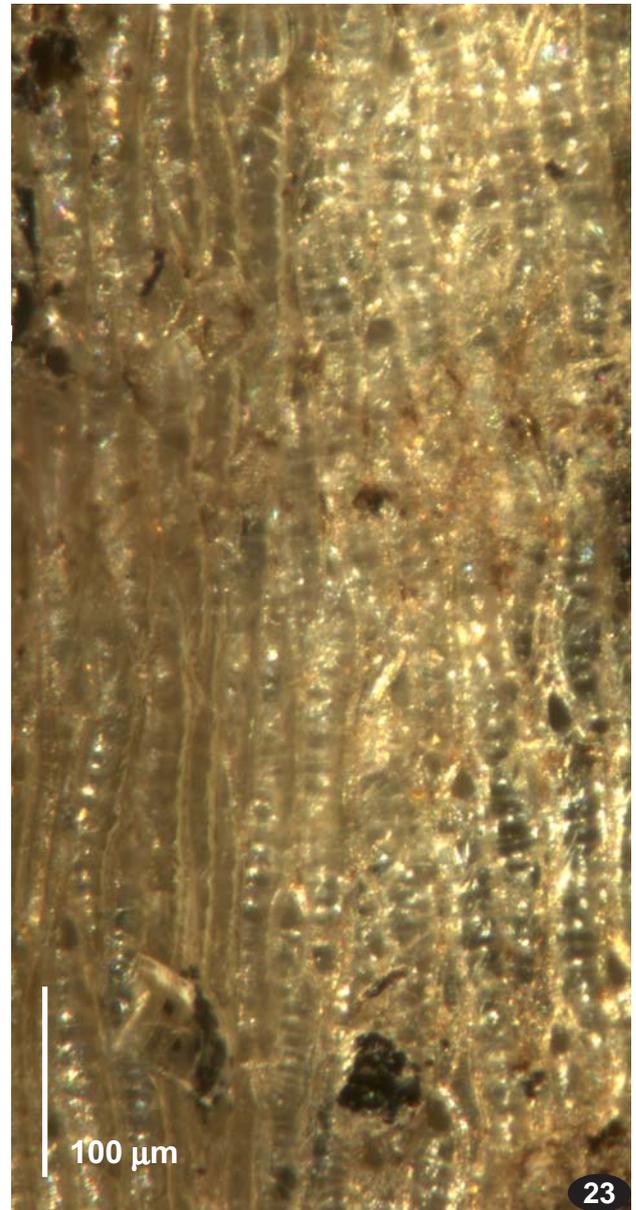
Figs. 4–7: *Sphagnum heinrichsii* (holotype): branch (3) and lower parts of branch leaves (4–6), showing pores mostly in distal ends of hyalocysts, however at places (especially in the middle of convex surface near leaf bases, cf. 6 and 7) scattered along whole cells. Marginal and submarginal cells (6, below, right) narrower and eporose.



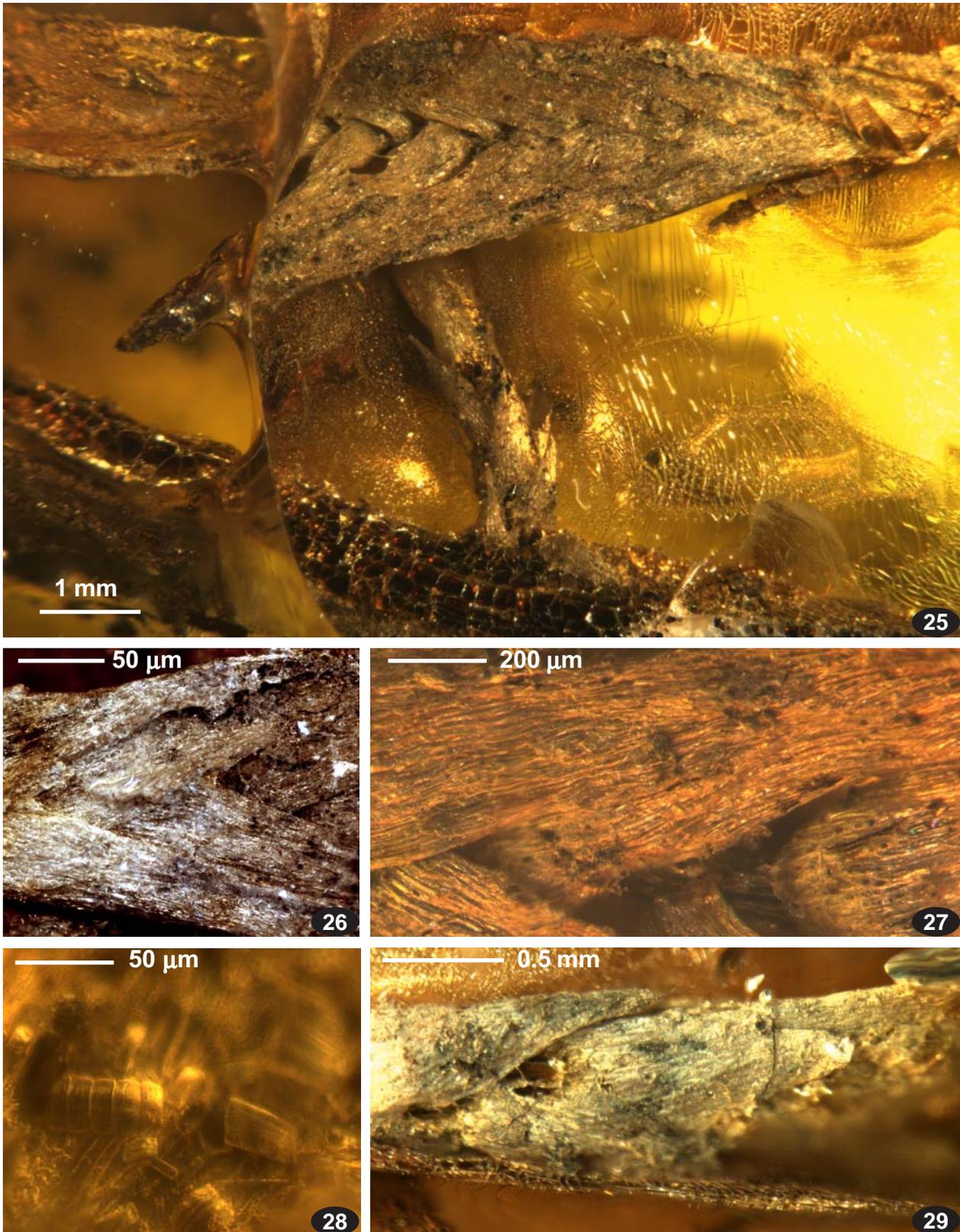
Figs. 8–11: *Sphagnum heinrichsii* (holotype): dorsal surface of branch leaves showing pores mostly in distal ends of hyalocysts.



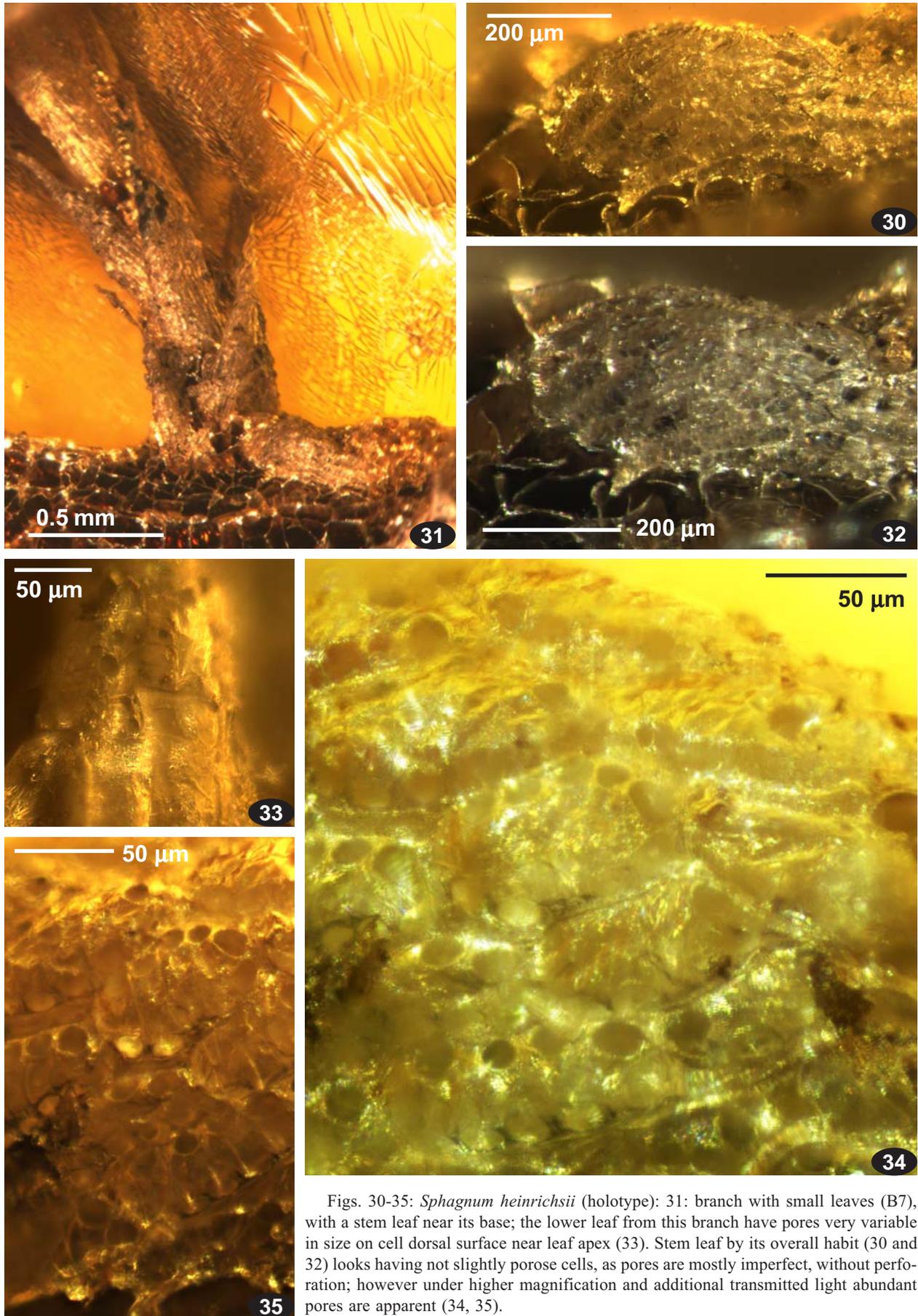
Figs. 12–20: *Sphagnum heinrichsii* (holotype): dorsal surface of branch leaves showing pores in ends of hyalocysts. Three series (11–13, 14–16, 17–19) show tree photos each with different focus to better understanding of pore position.



Figs. 21-24: Pendent branch leaves of *Sphagnum heinrichsii* (holotype) and their areolation. (21–22): upper part of branch leaves with longly attenuate and narrowed acuminae, which are flexuose and irregularly crumpled. 21 taken from back, “raw” face of specimen; 22 from polished side, as all other photos; 23: median cells of long leaf closer to distal part of pendent branch; they are only slightly porose, with many imperfect pores (seen as rings covered by cell walls); (24) cells closer to leaf apex: pores are totally or almost totally absent.



Figs. 25-29: *Sphagnum heinrichsii* (holotype): 25: spreading branch B1, with leaves quite strongly covered by mud and detritus (26, 27), and diatoms (28). 29 is a small leaved branch B6a (unclear if it is a continuation of B6 or a separated branch), where leaves also covered by mud and quite damaged. Note a very few pores, mostly confined to upper hyalocyst corners in B6a.



Figs. 30-35: *Sphagnum heinrichsii* (holotype): 31: branch with small leaves (B7), with a stem leaf near its base; the lower leaf from this branch have pores very variable in size on cell dorsal surface near leaf apex (33). Stem leaf by its overall habit (30 and 32) looks having not slightly porose cells, as pores are mostly imperfect, without perforation; however under higher magnification and additional transmitted light abundant pores are apparent (34, 35).

vex as in Figs. 30–32; (2) branch assumed as pendent, B6 (Fig. 3), due to especially long, narrow and flexuose branch leaves, is likely directed downwards (as all pendent branches), despite during the fossilization its direction might be changed to unnatural direction. However, the coincidence of both of these facts justify our interpretation as the most probable.

The whole appearance of the plant, its coverage by debris and numerous diatoms indicates it grew submerged in water. Such environments sometimes result in a reduction in branching, so their single arrangement is unusual, but not totally exceptional. The bases of branches B1 and B7 are clearly visible, thus their solitary position is evident. Branch B2 is likely also solitary, although the position of branches B3, B4 and B5 (B5 is questionable whether this is branch however) are not clear enough to state anything definite about branch arrangement. The B3 and B4 (Figs. 3, 36) is the only case where a pair of two branches, apparently adjoining each other, is seen. We can not exclude that B3 and B4 can not be considered as one fascicle with B2, and maybe B5. Also B6 base is not seen and one can not exclude its close position to B7; however, these cases are much more hypothetical.

Three branches, B1, B2, and B3, are characterized by the largest and densely arranged leaves, and their position at about a right angle from the stem indicate that they are spreading. Uppermost branch leaves of them are not available for study, but all three leaves in lower few millimeters are appressed and rather flat, and only on B2 at ca. 5 mm from branch base the leaves are more loose, with concave bases (Figs. 4–7).

Branch B6 is seen partly, without its basal part, but its orientation is pendent, and uppermost leaves are narrow and flexuose; i.e., similar to pendent branches. Shoot B6a is difficult to interpret: it could be either a terminal continuation of B6, or a separate branch similar to B7, but fallen off and retained close to the mother plant. Leaves of B6a are very similar in shape and size to B7.

Stem leaf (Figs. 30–35) is partly emerging above alveolar medium surrounding stem. However, what is possible to see through this rather transparent amber, is its basal part and an indefinite part is its distal edge, which likely consists of partly decomposed cells. Micrographs with more intensive transmitted light show numerous pores (e.g. Fig. 35); however, in reflected light it is seen that they are mostly imperfect pores (Figs. 30, 32).

In branch leaves (e.g. Fig. 23) imperfect pores are also much more common than true window pores, which are more numerous only in concave leaf bases (Figs. 5–7).

DISCUSSION

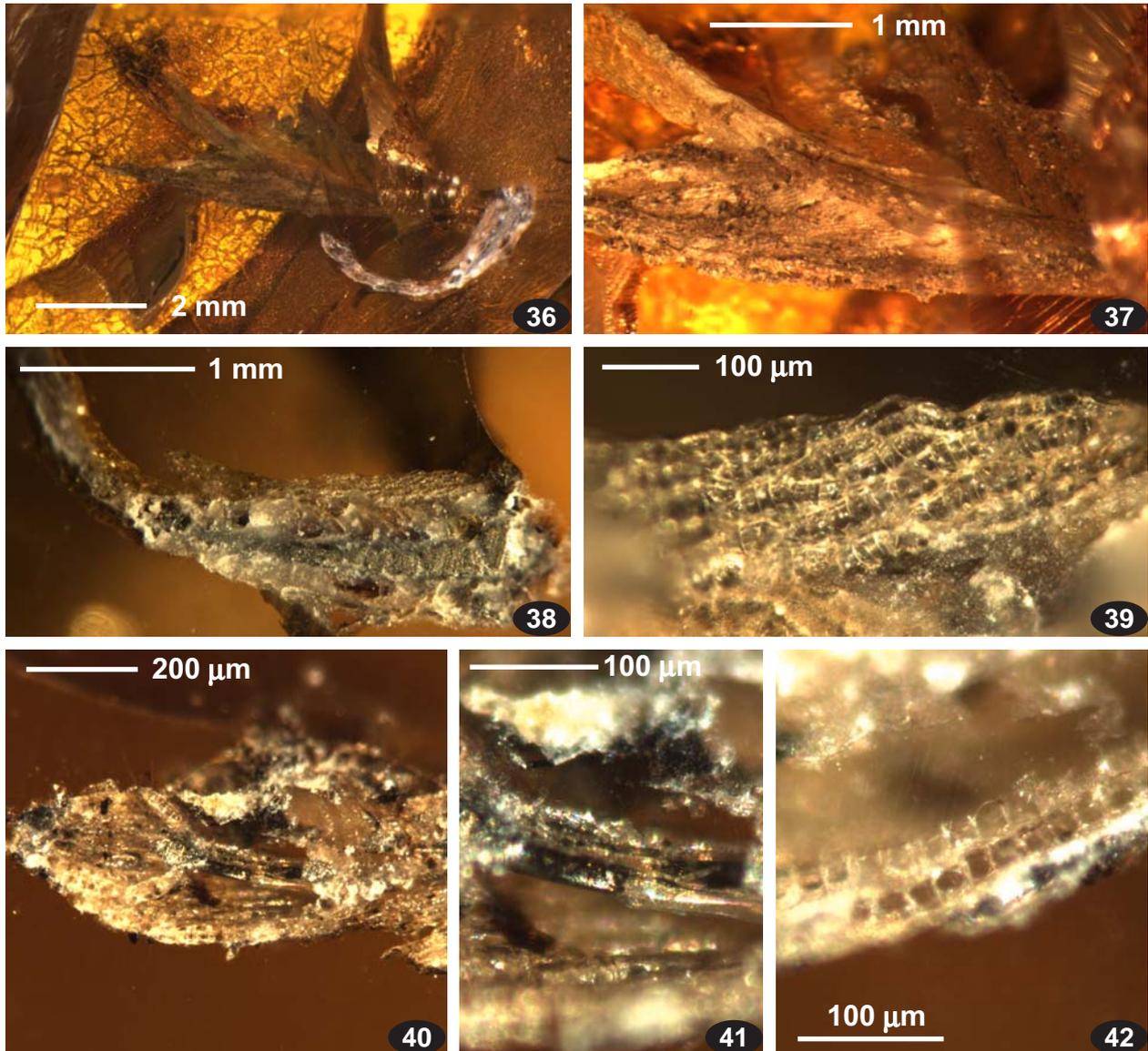
Sphagnopsida is one of oldest lineages in moss phylogeny (Liu et al., 2019; Chang & Graham, 2011; Shaw et al., 2010b), obviously separated from the stock of moss evolution no late than Devonian (Newton et al., 2007).

Recently *Sphagnum* was found in as ancient deposits as of Ordovician (Cardona Correa et al., 2016); however, this outstanding age affects the overall scenario of earliest stages of land plant evolutions so much that conservative refrain of accepting these age of *Sphagnum* prevails in recent literature (e.g., Tomescu et al., 2018).

The next *Sphagnum* records are dated to the Lower Jurassic of Germany (Reissinger, 1950), Upper Cretaceous coals of Greenland (Arnold, 1932), Upper Cretaceous of Wyoming (Wilson and Webster, 1946), Paleocene of North Sea (Boulter, 1994), early Eocene of Canadian Arctic (Kuc, 1973), and early Eocene of Germany (Riegel & Wilde, 2016). As most of mentioned publications appeared before the splitting *Sphagnum* into four genera, these records have to be considered as *Sphagnum* sensu lato, e.g. members of the order Sphagnales. Only one specimen from Baltic amber (branch with leaves, with apparent areolation) was compared with extant species *S. fuscum*, *S. capillifolium*, *S. subfulvum*, and placed in sect. *Acutifolia* (Frahm, 2009, 2010). The evidence for this placement is rather vague, as *Sphagna* are difficult to identify even by extant plants. The difficulties with interpretation of *Sphagnum heinrichsii* are even worse, as aquatic forms of the genus are especially troublesome. A few features however allows tentative determination of its section position in this case. *Sphagnum heinrichsii* in its structure of branch leaves, namely chlorocysts exposed to dorsal surface, pores mostly confined to upper cell corner, and longly gradually tapered lanceolate branch leaves in pendent branches are similar to aquatic forms of *Sphagnum* sect. *Cuspidata*. The branch leaf shape, reduced number of branches per fascicle and few pores of dorsal side of branch leaves are known in submerged forms in several species of sect. *Cuspidata* and infrasectional hybrids between species of sect. *Cuspidata* and sect. *Subsecunda* (Karlin et al., 2013; Karlin & Robinson, 2017).

However the stem leaf with large serial pores along commissures are not a characteristic for any group within sect. *Cuspidata*, but instead are characteristic for stem leaves of species of sect. *Subsecunda* (e.g. Laine et al., 2018).

The limited material precludes further interpretations, to avoid guessings from imperfectly seen specimen. However two comments have to be considered regarding interpretation of systematic position of *S. heinrichsii*. First, the diversifications of bryophytes as a whole (Laenen et al., 2014) and *Sphagnum* in particular (Shaw et al., 2010a) happened probably sufficiently later, in Miocene, thus the Eocene species maybe difficult to assign to extant taxonomic subdivisions. The close relationship of sect. *Cuspidata* and sect. *Subsecunda* (Shaw et al., 2018), as well as numerous intrasectional hybrids between them (Karlin et al., 2013; Karlin & Robinson, 2017) allow assuming that *S. heinrichsii* belongs to the lineage lead-



Figs. 36–42: *Spaghnum heinrichsii* (holotype, cut off second part). 30: General view: upper part of branch with large leaves (close up in Fig. 31) and attached (seemingly close to its base) small-leaves branch, partly cut longitudinally. Details of the latter branch are shown in Figs. 32–36: it bears one leaf ca. 1 mm long close to its base (Figs. 32–33), while leaves closer to its tip are only 200 µm long (Fig. 34). Fig. 35 shows part of this tiny branch, only 50 µm thick. Fig. 36 comprises longitudinal section of small leaf close to branch tip showing fibrils.

ing to sect. *Cuspidata* and sect. *Subsecunda* before its divergence, which even today can not be qualified as an absolutely complete.

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