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Fossil mosses: What do they tell us about moss evolution?

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Abstract

The moss fossil records from the Paleozoic age to the Eocene epoch are reviewed and their putative relationships to extant moss groups discussed. The incomplete preservation and lack of key characters that could define the position of an ancient moss in modern classification remain the problem. Carboniferous records are still impossible to refer to any of the modern moss taxa. Numerous Permian protosphagnalean mosses possess traits that are absent in any extant group and they are therefore treated here as an extinct lineage, whose descendants, if any remain, cannot be recognized among contemporary taxa. Non-protosphagnalean Permian mosses were also fairly diverse, representing morphotypes comparable with Dicranidae and acrocarpous Bryidae, although unequivocal representatives of these subclasses are known only since Cretaceous and Jurassic. Even though Sphagnales is one of two oldest lineages separated from the main trunk of moss phylogenetic tree, it appears in fossil state regularly only since Late Cretaceous, ca. 70 million years ago (Ma), while earlier they were found twice as small leaf fragments from Lower Jurassic (ca. 200 Ma) and Late Ordovician (ca. 455 Ma). Pleurocarpous mosses appear in fossil state near the border between Jurassic and Cretaceous, although most Cretaceous mosses belong to acrocarps. Only in Eocene amber pleurocarps become more numerous than acrocarps. Some Eocene mosses can be assigned to extant families and sometimes genera, although the majority of Eocene pleurocarps are difficult to identify up to the family, as their morphology often allows placement of a particular specimen into several different families.

Keywords: Bryophyta, evolution, paleobotany, protosphagnalean

Introduction

Since late 1990s, bryologists were provided with a bulk of new methods based on DNA sequence studies. The following ‘high wave’ of novel results strongly influenced bryophyte taxonomy and biogeography. Almost simultaneously, the molecular phylogenetic approach commenced to be used for the reconstruction of the evolutionary history of mosses, with dated phylogenies based on time calibration by means of some fossils (Newton *et al.* 2007). In this first attempt to time calibrate moss phylogenies, the oldest node in moss phylogeny was estimated as 380 (362–399) million years ago (hereafter, Ma). Later, Laenen *et al.* (2014) used a somewhat different methodology and estimated the age of mosses by three methods as 602, 507, and 488 Ma. This dating is in agreement with the origin of ancient Embryophytes in the Ordovician-Silurian (Kenrick & Crane, 1997), or earlier judging from the cryptospore records (Taylor & Strother, 2008; Rubinstein *et al.* 2010).

However, such dating for mosses does not coincide in general with the bulk of the paleontological data, as more or less numerous fossil moss records began to appear only during the Permian (ca. 299–252 Ma), while more ancient records are quite few. This discrepancy obviously relates, among others, to the extreme paucity of fossil moss records. Tomescu *et al.* (2018) provided a list of fossil bryophytes, showing that amber inclusions (known from Eocene and Cretaceous) remain the main mode of moss preservation in the period from Carboniferous to Eocene (101 out of 226 records). However, fossil mosses in amber are scarce compared with insects. For example, from Taimyr amber a single moss inclusion is known, while there are 7000 identified specimens of insects, and in Rovno amber the rate is 20 mosses vs. 36000 insects, excluding unidentified remains (data of E. Perkovsky, Mamontov & Ignatov 2019). Krassilov & Schuster (1984) suggested, as a putative explanation of moss rarity in fossil state compared to hepatics, that the earliest mosses perhaps evolved rapidly into drought-tolerant forms that occupied sites where fossilization was

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unlikely. However, not only xerophytic mosses may have failed to fossilize, but also species that may have grown on permanently wet rock faces, like extant *Andreaeobryum* Steere & B.M. Murray (1976: 407), or on rock overhangs, often inhabited by, e.g., extant *Takakia* S. Hattori & Inoue (1958: 133), avoiding competition and growing in habitats not suitable for burial.

In addition to the paucity of the fossil record, another problem with fossil moss specimens is that their morphology in most cases is not rich enough to assign them to any family and/or order with a reasonable level of confidence. The position in mosses *per se* is not as equivocal as for extant mosses, although among the latter there were examples of misplacements even in 20th century: the moss genus *Takakia* was referred to hepatics for almost forty years, and Dixon (1932) treated *Haplomitrium* Nees (1833: 109) (as *Calobryum* Nees in Gottsche, Lindenberg & Nees (1846: 507)) as a moss. In extinct groups, the protosphagnalean genus *Vorcutannularia* Pogorevich ex Neuburg (1960: 66) was originally classified as a horsetail, the type species of *Polyssaievia* Neuburg (1956: 322) was originally described as a gymnosperm, and *Diettertia* J.T. Brown & Robison (1974: 170) was thought to be a moss until Schuster & Janssens (1989) found a bilobed structure in its leaves and therefore transferred it to hepatics. Ignatov & Shcherbakov (2011b) described the Triassic mosses *Atrichites* Ignatov & Shcherbakov (2011b: 73) and *Palaeosyrrhopodon* Ignatov & Shcherbakov (2011b: 77) based on leaf fragments, but a subsequent study based on rich collections from the same locality revealed that both genera in fact are different parts of the leaves of a minute, presumably aquatic lycopod that lack stomata (Gomankov 2020).

At the same, the hundreds of cases of erroneous placements of extant mosses at genus, family, order and subclass level have been disclosed in the last two decades, after molecular phylogenetic methods became widely applied to moss taxonomy (Vanderpoorten *et al.* 2002, Goffinet & Buck 2004, Ignatov *et al.* 2007, Goffinet *et al.* 2009, Frey & Stech 2009, Kučera *et al*. 2019).

Despite the mentioned difficulties, the reconstruction of bryophyte phylogeny moves forward, and the aim of the present paper is to provide an overview of moss fossils (excluding spores) that may help to calibrate dated phylogenetic trees. We attempt to summarize all data on Paleozoic and Mesozoic fossils. Cenozoic records are more numerous, and for the Eocene we select for discussion only records that can be identified to genus or family, and otherwise just list publications with taxa that can be identified less precisely. The main part of the present review is compiled from Jovet-Ast (1967), Miller (1980, 1984), Krassilov & Schuster (1984), Oostendorp (1987) Wang & Wu (2007), Ignatov (2013), and Tomescu *et al.* (2018). Brief comments are given in the list below for (putative) moss fossils, along with abbreviations indicating the level of certainty of taxonomic placement, i.e. whether a given fossil is still in need to be proved to be a moss [*****] or can be assigned to division Bryophyta [!****] or any of its classes/subclasses [!!***], orders [!!!**], families [!!!!*], or genera [!!!!!], respectively.

Fossil records overview

1. Pre-Carboniferous records are limited to two mosses. They are so much apart from other fossil moss records that additional confirmation is needed to decide whether *Parafunaria* is indeed a moss, and whether the inferred age of the *Sphagnum* remains, dated as Ordovician, is correct.

***** ***Parafunaria*** R. D. Yang, J. R. Mao, W. H. Zhang, L. J. Jiang & H. Gao (2004: 181) with one species, *Parafunaria sinensis* R. D. Yang in Yang *et al.*, 2004: 181), was described rather briefly from Mid-Cambrian of China. *Parafunaria* has a thallus (2 cm) and whorled leaves at its edges [in mosses, a possible parallel could be with thallose protonema of *Sphagnum*, but the latter is usually less than 1 mm]. Leaves are described as 15 mm long and 5 mm wide, i.e. much larger than in most moss species. The only other exceptionally large-leaved fossil species is the Permian protosphagnalean *Vorcutannularia plicata* Pogorevich ex Neuburg (1960: 67) with leaves up to 16 × 8 mm. Another unusual feature for mosses is the presence of numerous leaf veins (called “costae”), but no costa as it is usually understood in mosses (“no mid-costa” in description). The only fossil comparable in terms of multiple veins could be the Permian protosphagnalean *Polyssaievia* Neuburg (1956: 322). The associated algal flora characterizes the habitat as inappropriate for mosses (Tomescu *et al.*, 2018).

[!!!!!–???] ***Sphagnum*** L. (1753: 1106). Remains that do no substantially differ from the extant species of the genus *Sphagnum* where described by Cardona-Correa *et al.* (2016) from calcareous rocks of Late Ordovician (455–454 Ma) of Wisconsin, USA. Tomescu *et al.* (2018) evaluated this finding with a “reservation of caution” because of the too big gap, of over 100 million years, between these remains and the next moss record in the Visean (Hübers &

Kerp 2012, Hübers *et al.* 2013). The next fossil record of an unequivocal *Sphagnum* occurs also after a big gap in Lower Jurassic (Reissinger 1950), more than 250 Ma after the Ordovician record, and after that there is still a third considerable gap, for more than 100 Ma up to Late Cretaceous, when *Sphagnum* was found in Greenland (Arnold 1932) and Wyoming (Wilson & Webster, 1946). There is a single record of *Sphagnum* in Paleocene (Boulter 1994). Only in Eocene *Sphagnum* records became more numerous, representing plant fragments and even peat bog deposits (Kuc 1973b, Riegel & Wilde 2016). Interestingly, there are two findings of *Sphagnum* in Eocene amber (Frahm 2009, Ignatov *et al.* 2019), which can be assumed as only a moderately rare element of coniferous forests of early Tertiary with temperate epiphytic flora. The enigma with Ordovician (and Jurassic as well?) *Sphagnum* remains unanswered. If at that time plants of the *Sphagnum* lineage already had the structure of modern (=Cenozoic) *Sphagnum*, they likely grew in a different habitat not appropriate for easy fossilization. Mosses placed in or near Sphagnopsida from Carboniferous (Hübers & Kerp 2012, Hübers *et al.* 2013), Protosphagnalean Permian mosses (Neuburg 1958a,b, 1960, Ignatov 1990, Maslova *et al.* 2012a,b, Ivanov 2018, etc.) and Triassic *Sphagnophyllites* likely have no apparent relationship to extant *Sphagnum* (see below).
***** **Calyptra hairs.** Kodner & Graham (2001) found a high similarity of hairs from calyptras of extant *Polytrichum* Hedwig (1801: 88) with some Silurian and Early Devonian debris (Welleman, 1995). Hairy calyptras are known in Bryophyta in Polytrichopsida and in many families of the subclass Bryidae, but are absent in more basal lineages (Sphagnopsida, Takakiopsida, Andreaeopsida, Andreaeobryopsida, Tetraphidopsida, Oedipodiopsida), thus a proof of the calyptral origin of these Devonian hairs could be an important evidence that mosses originated substantially earlier than Devonian.

2. Lower Carboniferous records were considered to be candidates for the most ancient moss, but they are too incompletely preserved and poorly understood even for being unequivocally referred to mosses.

***** ***Muscites plumatus*** Thomas (1972: 159), from UK, is a densely foliate plant, with lanceolate leaves having a broad costa and elongate cells of unistratose laminae near leaf margin; it has nothing that would distinguish it from some Dicranidae. Hübers *et al.* (2013) suggested that the leaf areolation is not shown with enough detail, and Tomescu *et al.* (2018) marked it as a moss with question mark. The only scarcely seen areolation requires some caution, although the probability that it is a moss is rather high.
***** **Visean cuticles**. Hübers & Kerp (2012) and Hübers *et al.* (2013) described cuticle fragments obtained from the bulk maceration, from Germany. These cuticle fragments had an excellent cellular preservation. They were classified in seven types that could be grouped in three major types. Unfortunately, these fragments were small-sized and did not show whole leaf shape, except one putative leaf of type B-1. This narrow lanceolate leaf lacks a costa and somewhat resembles Permian genus *Viledia* (see below) However, minute pores of ca. 4 µm in diameter, in numbers of 30–50 per cell, evenly scattered in both elongate and subisodiametric, broadly rhombic cells make this structure difficult to refer to any known moss type. Pores of much larger size occur in type B-3, which was compared with *Sphagnum*, but unlike any extant *Sphagnum* species, one large pore in positioned in the center of a short cell in this type. Type B-2a has large rounded-hexagonal cells and can be referred, at best, to liverworts, whereas type B-2c comprises a bistratose structure and its placement in Protosphagnales is difficult to understand. Although some of the obtained fragments may belong to mosses, none of them can be assigned to any moss taxon, either extant or fossil.

3. Upper Carboniferous records are also few and limited to the genus *Muscites*.

!****** ***Muscites polytrichaceus*** Renauld & Zeiller (1885: 662), from France, looks more like Mniaceae or Racopilaceae due to its leaf shape than to *Polytrichum*, as the species epithet suggests. However, its cells are not discernible (see also Renauld & Zeiller 1888).
!****** ***Muscites bertrandii*** Lignier (1914: 129), from France, is represented by a single stem transverse section surrounded by rhizoids that have oblique cell walls, a unique trait for mosses.
!****** ***Muscites amplexifolius*** Ottone & Archangelsky (2001: 220) is a widespread moss in river delta environments in Argentina, having erect spreading leaves to 5 mm long, with large isodiametric laminal cells. The absent (or very inconspicuous) costa provides a difficulty for its taxonomic placement, as extant polytrichoid or bryoid mosses with a similar plant habit usually have costae. The large isodiametric cells may suggest the placement in leafy hepatics, although a more or less apparent spiral leaf arrangement makes this unlikely.

4. Permian protosphagnalean mosses possess traits that are absent in any other mosses and therefore are classified here as an extinct group, which descendants cannot be recognized among other moss taxa, both extant and fossil. They are referred to mosses due to rhizoids with oblique walls between cells, unistratose leaf laminae, plant habit and its variation, and comparable dimensions of stems, leaves and cells. Thus, all the genera included in this group are estimated as pertaining to Bryophyta (**!******): *Junjagia* Neuburg (1960: 64)*, Vorcutannularia* Neuburg (1960: 66)*, Protosphagnum* Neuburg (1960: 75)*, Syrjagia* Fefilova (1973: 87)*, Intia* Neuburg (1958a: 101)*, Salairia* Neuburg (1960: 44)*, Kosjunia* Fefilova (1973: 85)*, Uskatia* Neuburg (1960: 45)*, Polyssaievia, Bajdaievia* Neuburg (1958a: 103)*, Bachtia* Neuburg (1960: 58)*, Rhizinigerites* Meyen in Gomankov & Meyen (1986: 28)*, Palaeosphagnum* Ignatov (1990: 177), and *Bulbosphagnum* Maslova & Ignatov in Maslova *et al.* (2016: 330). One small leaf fragment from Neuburg collection was described as *Muscites uniformis* Neuburg: 1960: 60; it may represent one of the genera described by her, treated here as protosphagnalean, but the fragment is too small for any definite decision. The main publications on Protosphagnales include: Neuburg (1956, 1958b, 1960), Fefilova (1978), Gomankov & Meyen (1986), Ignatov (1990), Maslova *et al.* (2012a, b, 2016); Maslova & Ignatov (2013), and Ivanov *et al.* (2018).

Protosphagnalean mosses, as they are circumscribed here, were diverse and abundant in Lower to Upper Permian in Angaraland (localities in NE European Russia, southern and middle Siberia) and Mongolia (Durante 1976), and in Subangaraland: *Uskatia* was reported from NW China (Liu & Yan 1996), and *Intia* from Primorsky Territory of the Russian Far East (reported of Burago in Meyen 1982). In most places they form pure deposits, and thus they should be likely interpreted as forming mires.

Among 58 fossil mosses listed by Tomescu *et al.* (2018) for Permian, as many as 30 are referred here to protosphagnalean, which require explanation on the content of the group. Neuburg (1960) placed her genera described from Permian in two orders, Bryales and Protosphagnales, the latter including three genera with clearly dimorphic laminal cells: *Junjagia*, *Vorcutannularia*, and *Protosphagnum*. Neuburg also noted that the areolation in the genus *Intia*, though referred to Bryales, has the specific pattern of *Protosphagnum* (Fig. 1). Subsequently, Fefilova (1973, 1978) described the genus *Syrjagia*, which has in its proximal part a *Protosphagnum* leaf structure while distally it is indistinguishable from *Intia* (Fig. 1B). Ignatov (1990) showed that this pattern is in fact common, and similar transitions were demonstrated later (Maslova *et al.* 2012a, Ivanov *et al.* 2018).

The expression of cell dimorphism within the single lamina is very diverse for different species: the dimorphism can be regular across the leaf or conversely, be greatly variable within the leaf (Figs. 1, 4), and the level of differentiation correlates with the level of regularity and differentiation of cell rows. Occasionally darker laminal cells are arranged in conspicuous rows; presumably, they worked as a conductive system within the leaf (Fig. 2). Leaves of protosphagnalean mosses were attached to the stem by a narrow zone almost equal to the width of the costa (Fig. 2). Ignatov (1990) interpreted one leaf in *Protosphagnum nervatum* as raised on a stalk (described as paraphyllium in Gomankov & Meyen 1986), but that was found later to be based on an artifact. Ultimately expressed, a putative conductive system has a 'net venation' represented in the genus *Polyssaievia* (Fig. 3). Also, the pathways of leaf cell differentiation in protosphagnalean mosses included a pattern unknown in extant mosses: the meristematic zones with just divided cells 4–5 μm wide that in extant mosses occur near leaf base (Schimper 1860, Potier 1925, Frey 1970), in protosphagnalean mosses occurred in the mid leaf (Fig. 4A–D), at apex (Fig. 4E) or at base (Fig. 4FG), as described by Maslova *et al*. (2012a).

Oblique cell rows are known in some extant mosses, e.g. in Mniaceae, but in protosphagnalean mosses the pattern is unique in that the oblique cell rows consist of two alternated cell types, in which one of two neighboring rows has twice the number of cells (Fig. 1D), i.e. one cell in one row and two cells from the neighboring row form triads, that further may develop a sphagnoid areolation pattern (for details see Ivanov *et al.* 2018). A sphagnoid areolation pattern may appear within a leaf here and there (Figs. 1, 2. 4, 5). Its presence, combined with leaf attachment to stem by the costa only and the presence of a peculiar border (Fig. 1B) are common characters of mosses referred here to Protosphagnales. In some genera with longer cells, e.g. *Uskatia*, the sphagnoid areolation pattern may be difficult to note, but the similarity of leaf attachment to stem, and the identical structure of the border, place them into the 'core Protosphagnales'. The border is absent in *Rhizinigerites*, however, the sphagnoid areolation pattern is well expressed in at least some parts of the leaves (Fig. 5C) and probably is responsible for parts of the laminal cells falling off regularly (Fig. 5A). *Rhizinigerites* adds one more character to this group, namely the occasional presence of leafless axes that are either totally naked or bear clusters of rhizoids (Fig. 5D, E). In addition, protosphagnalean mosses comprised in the form-genus *Bulbosphagnum* developed tubers, which propagate into broad stems (Fig. 6). This differs from any propagule of extant mosses, where organs of vegetative reproduction propagate by means of a single apical cells and have a constriction at the joint of propagules and subtending stem, which is absent in *Bulbosphagnum* (Maslova *et al.*, 2016). In conclusion, no Protosphagnales can be recommended for the age calibration of extant subdivisions of the division Bryophyta.

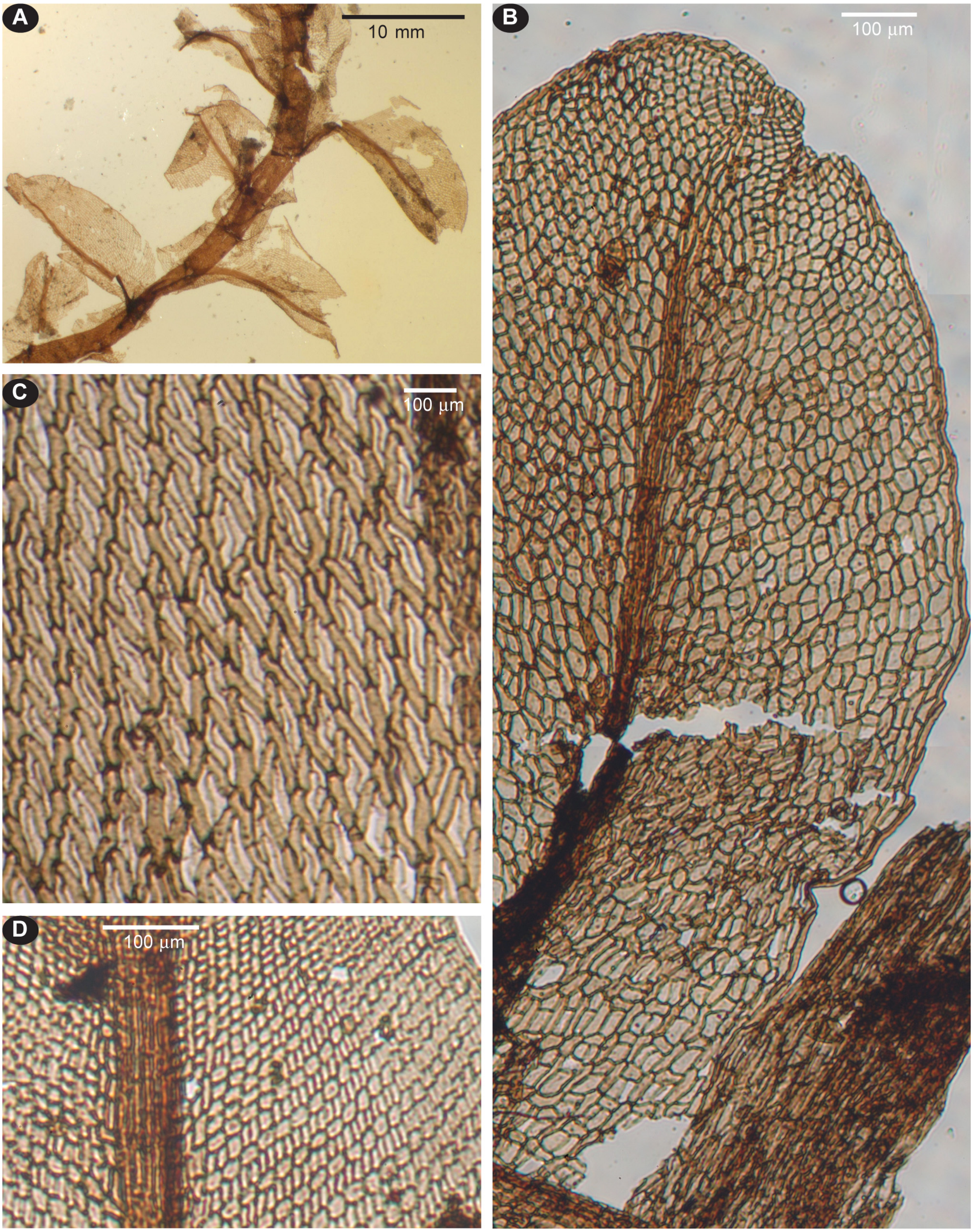

FIGURE 1. Protosphagnalean mosses showing various degrees of expression of sphagnoid areolation pattern. *Protosphagnum nervatum* Neuburg (1960: 75) habit (A). *Intia variabilis* Neuburg (1958a: 101), leaf, with more or less expressed sphagnoid areolation pattern near leaf base (B). *Protosphagnum nervatum,* median laminal cells (C). *Kosjunia* sp., median laminal cell, showing slightly developed sphagnoid areolation pattern (D). Collections: A: Viled (see Gomankov & Meyen, 1986), Upper Permian, GIN 3774/3B-7); B–D: Adzva (MHA: see Maslova *et al*., 2012a), Upper Permian: B: 7643–7646 (32M_11_8_1); C: 5353 (32M_7_3_1); D: 6872 (32M_9_6_4).

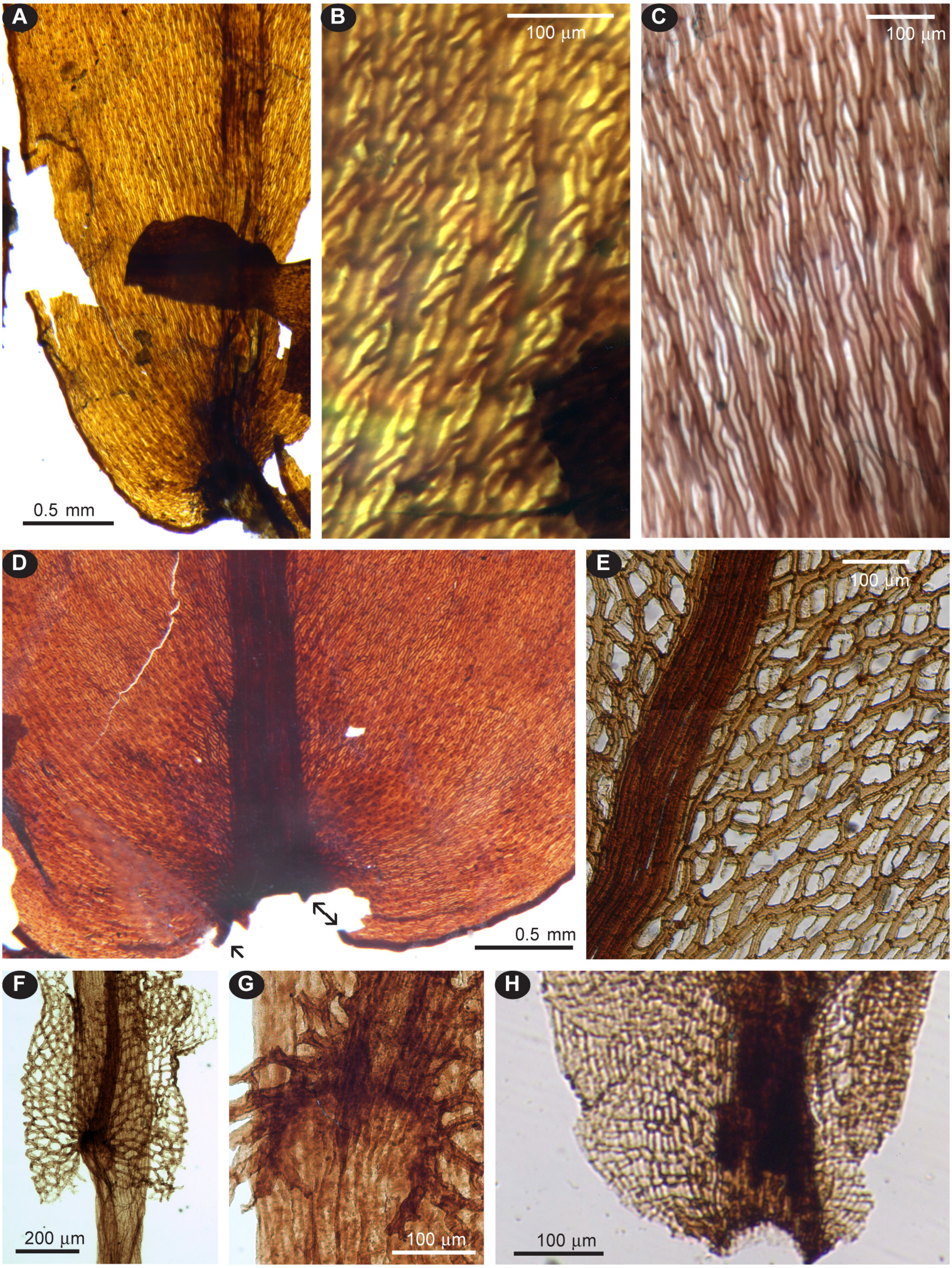

FIGURE 2. Protosphagnalean mosses, showing areolation patterns in leaves putatively responsible for conducting functions (A–C, E) and leaf attachment to stem by a narrow zone almost equal to costa width (D, F–H). *Intia vermicularis* (A–D, in D arrowed are border fragments, showing their adjoining almost to costa and therefore lacking decurrencies); *Protosphagnum nervatum* (E–G); *Intia* sp. (H). Collections: A–D: Pechora, Upper Permian (Neuburg, 1960), GIN #231; E–H: Adzva (MHA: see Maslova *et al.*, 2012a), Upper Permian: E: 38669 (32M_5_36_6); F: 32M_A_1; G: 32M_A_2; H: 4574 (32M_1_27_2).

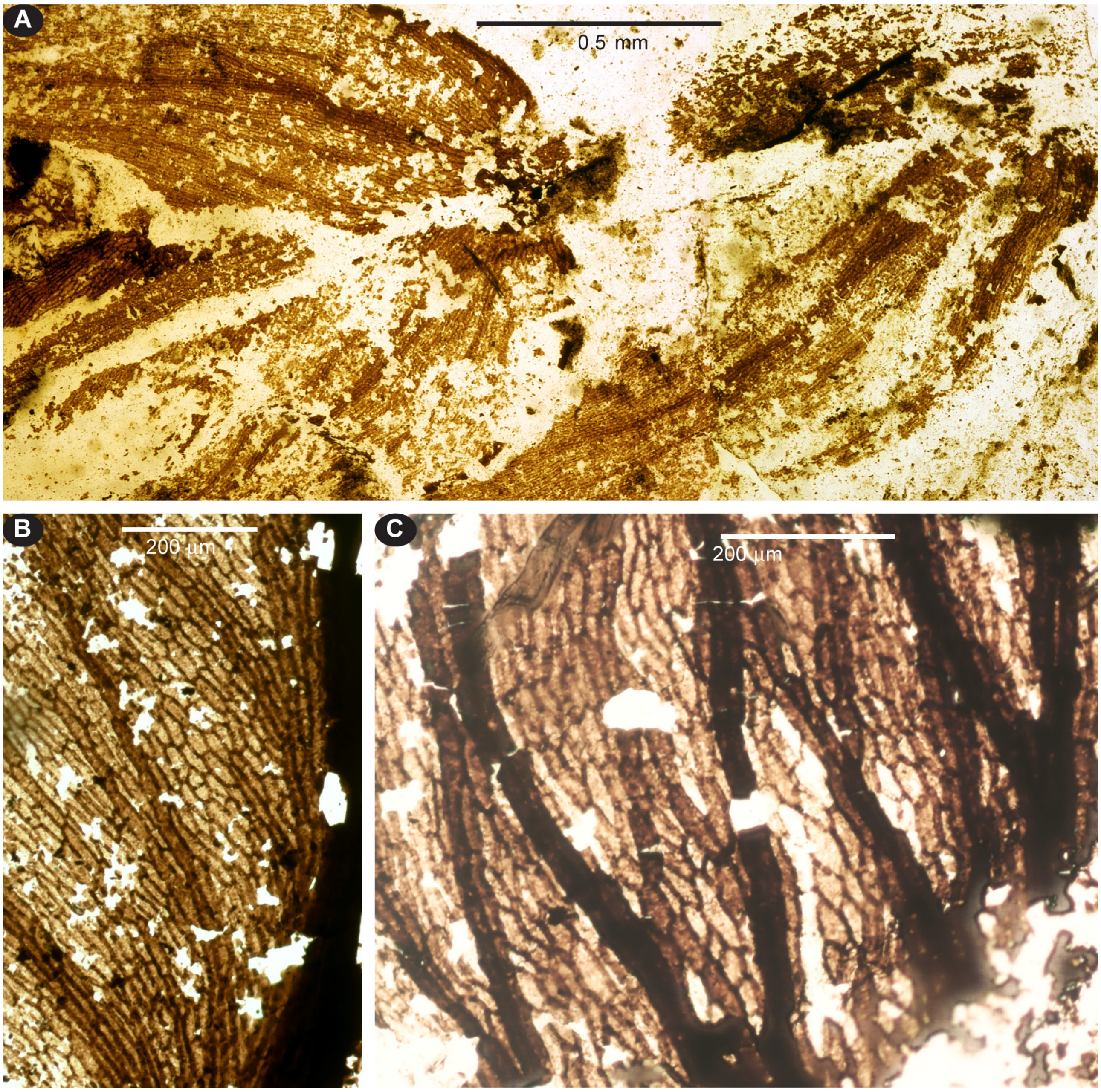

FIGURE 3. *Polyssaievia deflexa* Neuburg (1960: 55). Leaves and their parts with "net venation" (A–C). Collections: Pechora coal basin (see Neuburg, 1960), Upper Permian, GIN: 3041_151c.

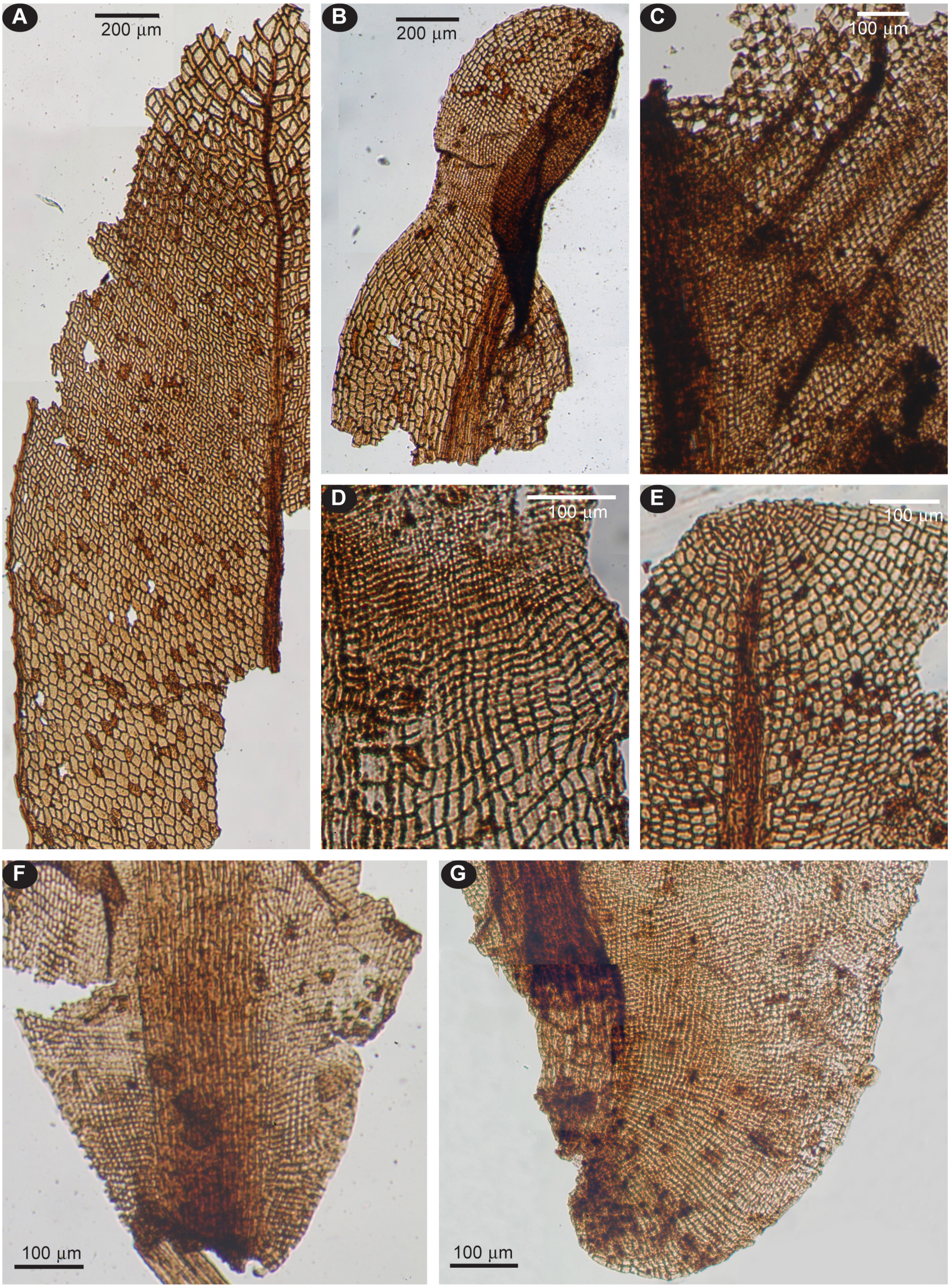

FIGURE 4. Protosphagnalean mosses, showing variation within their leaves and position of meristematic zones. *Vorcutannularia sp.* (A). *Intia sp.* (B, D, E, F). *Junjagia glottophylla* (C, G). Collections: Adzva, Upper Permian (MHA: see Maslova *et al.*, 2012a), Upper Permian: A: 5903 (32M_4_35_1); B: 1759-1762 (32M_5_21_2); C: 5893-5894 (32M_4_24_1); D: 5572-5575 (32M_6_20_6); E: 7685 (32M_11_28_3); F: 5584-5586 (32M_6_22_9); G: 6421-6431 (32M_2_39_1).

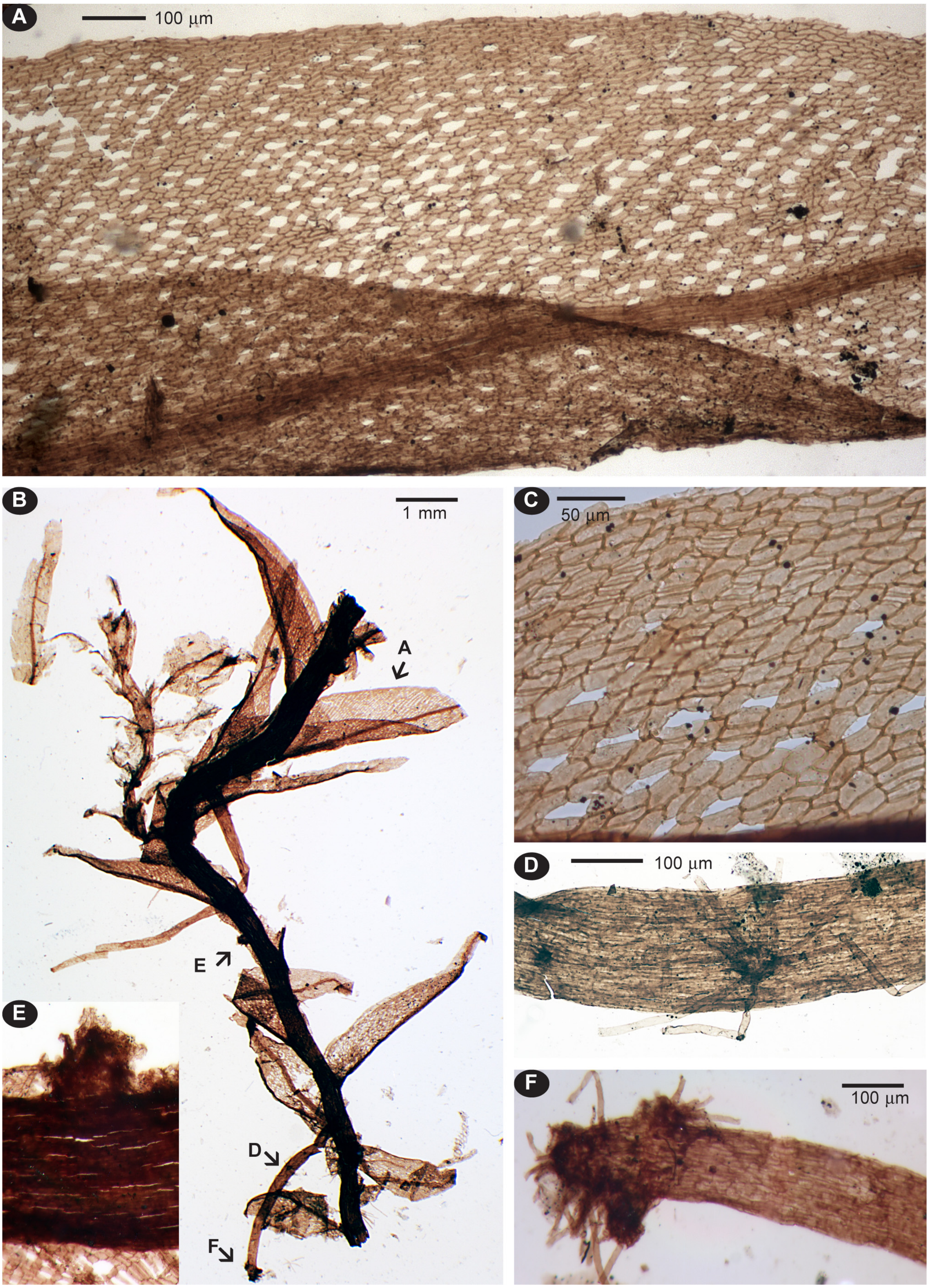

FIGURE 5. *Rhizinigerites neuburgae* S.V. Meyen in Gomankov & Meyen (1986: 28). Part of leaf (A); shoot with rhizoidophores (B); areolation with sphagnoid areolation pattern (C); rhizoidophor with rhizoid cluster (D, F); primordium of branch or perianth (E). Collections: Viled (see Gomankov & Meyen, 1986), Upper Permian, A–B & D–F: 3774/3B-10; C: 3774/3B-5).

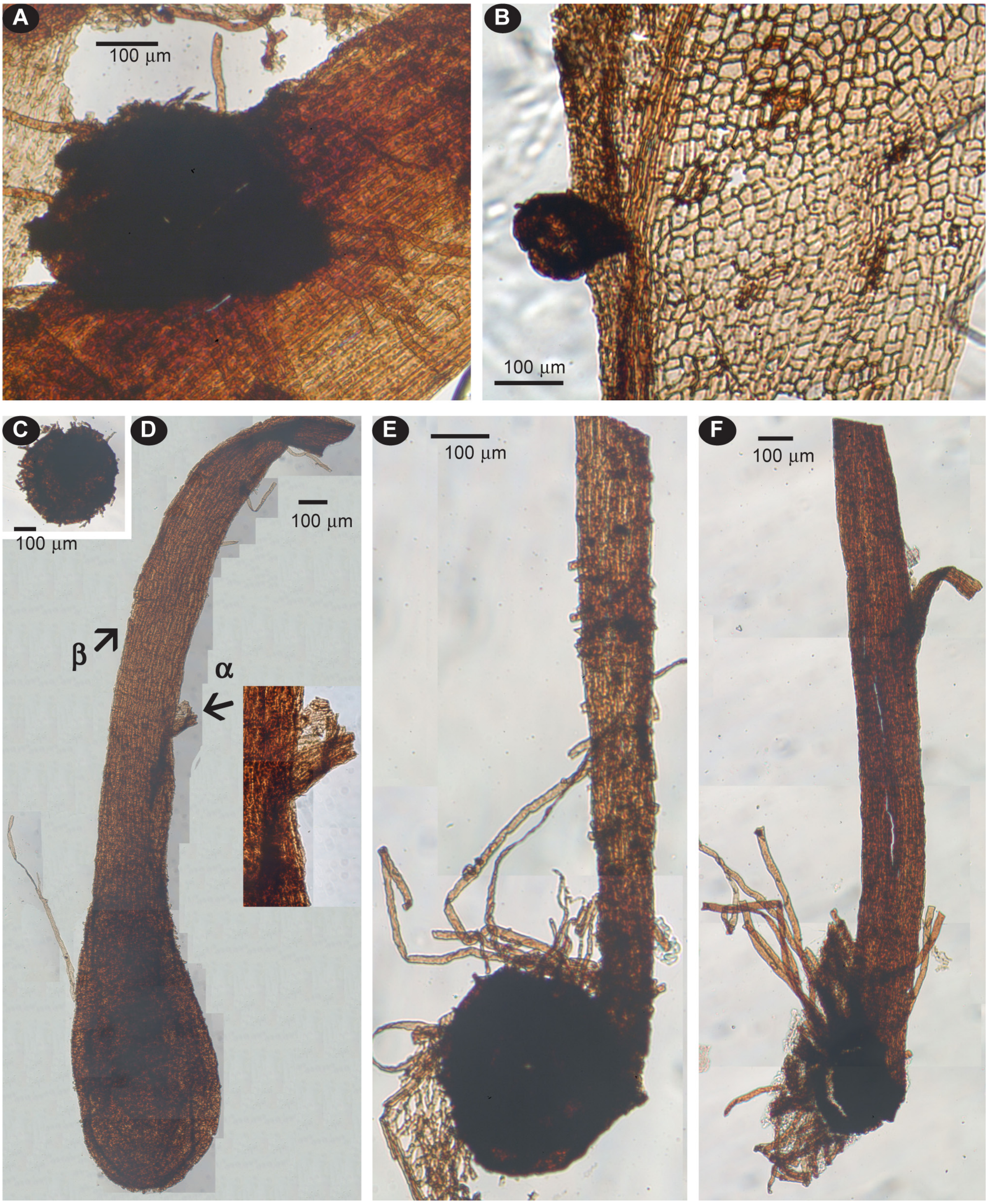

FIGURE 6. Brood bodies of *Bulbosphagnum* cf. *polyrhizon* Maslova & Ignatov in Maslova *et al.* (2016: 330), developed on stem (A) and leaf (B). Separate brood body of *B. polyrhizon* (C). Brood bodies and stems grown from them of *B. sublaeve* Maslova & Ignatov Maslova *et al.* (2016: 330) (D [α and β leaf remains]); *B. polyrhizon* (E); and a protosphagnalean stem base with rhizoids (putatively *B. polyrhizon*, but brood body indistinct, largely decomposed). Collections: Adzva (Upper Permian, Maslova *et al.*, 2012a). A: 11367 (32M _16_6_2); B: 9093 (32M_12_4_6); C: 11257 (32M_16_1_11); D: 10742 (32M_12_20_1); E: 8567 (32M_12_1_7); F: 8667-71 (32M_12_2_3).

5. Permian true mosses. About half of Permian mosses were described as having no features contradicting their placement in mosses, and in some cases they are comparable with one or several extant moss groups. The level of confidence is different between taxa with discernible leaf areolation and those where cell shape and size remain unknown, which are discussed separately.

5.1. Permian true mosses with known laminal areolation

5.1.1. Gondwana

!**** ***Merceria*** Smoot & Taylor (1986: 1684), *M. augustica* Smoot & Taylor (1986: 1684), from Antarctica, consists of transverse sections of stem and leaves. It is characterized by a moderately homogeneous costa in transverse section, leaves up to 2.5 mm wide, and cells elongate-rhomboidal to linear, ca. 60–160 × 10–15 μm (average 80 × 11 μm). The authors' suggestion of an affinity with Bryales (now equivalent of acrocarpous Bryidae) is most likely due to the oblique laminal cell ends.

!**** ***Palaeocampylopus*** Ignatov & Shcherbakov (2009: 209) with one species, *P. buragoae* Ignatov & Shcherbakov (2009: 209), from the Russian Far East, is a compression of erect shoots with cup-like terminal rosettes of short and broad leaves, similar to, e.g., perigonial leaves of Polytrichaceae (*Polytrichum* Hedw.) and perichaetial leaves in Dicranaceae (*Campylopus* Brid.). Leaf shape and fine striolation on the dorsal leaf side are characteristic of *Campylopus*, thus both Dicranidae and Polytrichopsida could be considered.

!**** ***Talchirophyllites*** Chandra (1995: 24), with one species *T. indicus* Chandra (1995: 24) from India, is compared, among extant mosses, with *Atrichum* P. Beauv. and *Pogonatum* P. Beauv., which agree with the leaf length of 8 mm. Laminal cells are reported as rectangular, although from the illustration they may more likely be considered as almost quadrate, supporting the affinity to Polytrichaceae.

!**** ***Yguajemanus*** Christiano de Souza, Ricardi Branco & Leon Vargas (2012: 236) with one species *Y. yucapirus* Christiano de Souza, Ricardi Branco & Leon Vargas (2012: 236), from South Brazil, is a moss superficially resembling the Upper Carboniferous *Muscites amplexifolius* from Argentina, but differs from it in having a distinct costa, well differentiated leaf margins, and considerably smaller leaves. The cells were not described, although the original Fig. 5H in Christiano de Souza, Ricardi Branco & Leon Vargas (2012: 236) illustrates rectangular cells 2–3:1 (ca. 20 × 10 μm). The authors compared the species with extant Mniaceae, but their cell areolation is not similar.

5.1.2. Angaraland

!**** ***Arvildia*** Ignatov (1990: 150) includes two species, from NE European Russia. Both have small, lanceolate to oblong leaves with stout costa and thick-walled subquadrate cells, smooth or with shallow papillae. Rhizoids are also present. *Arvildia elenae* Ignatov (1990: 150) has narrowly acuminate leaves, while in *A. obtusifolia* Ignatov (1990: 155) the leaf is broadly rounded. This genus was originally compared with Pottiaceae (e.g. *Didymodon* Hedw.), although similar structures are known in other Dicranidae. Regular cell rows and papillae are similar with *Andreaea* Hedw., but the only moderately thick-walled cells do not support this affinity.

!**** ***Aristovia*** Ignatov (1990: 157) includes two species, *A. subcordata* Ignatov (1990: 157) and *A. microcellulata* Ignatov (1990: 159), from NE European Russia. They are represented by few almost complete, excellently preserved leaves distinguished from each other by cell size. Leaves are ovate-lanceolate, unbordered, the costa ends shortly below apex, and the cells are isodiametric and smooth.

!**** ***Gomankovia*** Ignatov (1990: 156), with one species, *G. latifolia* Ignatov (1990: 156), from NE European Russia, is represented by one complete, excellently preserved leaf, comparable with Funariaceae (Funariidae) or *Splachnobryum* (Pottiaceae).

!**** ***Ignatievia*** Ignatov (1990: 164), with one species, *I. papillosa* Ignatov (1990: 164), from NE European Russia, combines fragments of broad leaves with a costa and strongly prorate (or papillose) distal cell ends, resembling, e.g., Bartramiaceae, thus suggested to be a member of Bryidae.

!**** ***Protoochyraea*** Ignatov (1990: 160), with one species, *P. polymorpha* Ignatov (1990: 160), from NE European Russia. Leaves are variable in shape from lanceolate to broadened and lobate (similar to leaves around discoid perigonium in, e.g., Bartramiaceae), with a broadened costa of indistinct outlines, long rectangular laminal cells and unbordered, entire margins.

!**** ***Servicktia*** Ignatov (1990: 181), with four species that differ in leaf shape: *S. acuta* Ignatov (1990: 181), *S. longifolia* Ignatov (1990: 181), *S. undulata* Ignatov (1990: 181), and *S. vorcutannularioides* Ignatov (1990: 181), from NE European Russia. All species of the genus have small, moderately thick-walled isodiametric cells and a peculiar border of one row of rather large, elongate cells with oblique walls between its cells, resembling the border structure of some species of extant *Fissidens* Hedw. However, their placement into any extant order remains problematic.

!** *Viledia*** Ignatov (1990: 163), with one species, *V. minuta* Ignatov (1990: 163) from NE European Russia, is known by a single lanceolate leaf with a thin costa and narrow, oblong cells with length to width ratio >5:1.

5.1.3. Euramerica

******* Moss cuticles** (Busche, 1968) from Germany, consisting of fragments of unistratose laminae, probably of mosses.

5.2. Permian true mosses without discernible cellular structure.

5.2.1. Gondwana

!** *Dwykea*** J.M.Anderson & H.M. Anderson (1985: 95) includes two species having densely foliate stems with spirally arranged, erect, appressed narrow leaves to 5 mm long. *Dwykea goedehoopensis* J.M.Anderson & H.M. Anderson (1985: 95), from South Africa, has leaves 5 mm long and 0.15 mm wide. *Dwykea araroii* Ricardi-Branco, Costa, Cristiano de Souza, Rohn, Longhim & Faria (2013: 344), Brazil, was described from periglacial tundra habitats. It has leaves 1.40–4.19 mm long × 0.11–0.38 mm wide (measured on compression), and one lateral structure was interpreted as a sporophyte, with a capsule only 0.2 mm long, which is somewhat odd for a large plant (unless that it was a very young sporophyte). Besides, the description of leaf areolation is unclear. Amaral *et al.* (2004) and Ricardi-Branco *et al.* (2013, 2016) referred *D. araroii* to Upper Carboniferous, while a possibly Permian age was suggested by Christiano de Souza *et al.* (2012), an opinion endorsed by Tomescu *et al.* (2018). No systematic placement has been suggested for the genus; while the habit points to Dicranidae, Bryidae and Polytrichopsida cannot be excluded.

!** *Buthelezia*** Lacey, van Dijk & Gordon-Gray (1975: 411) with one species, *B. mooiensis* Lacey, van Dijk & Gordon-Gray (1975: 411), from South Africa. Leaves up to 7 mm long, ovate, thus the plant can be compared to modern Mniaceae or Permian Protosphagnales. However, lack of data on leaf areolation makes further comparison too vague.

!** *Saksenaphyllites*** Chandra (1995: 28), with one species, *S. saksenae* Chandra (1995: 28), from India. It was compared, among extant mosses, with *Anoectangium* Schwägr. (Pottiaceae, Dicranidae). One structure is interpreted as seta with capsule, but leaf-like structures on this "seta" are not explained.

!** *Umariaphyllites*** Chandra (1995: 29), with one species, *U. acutus* Chandra (1995: 29), from India. It was compared, among extant mosses, with *Macromitrium* Brid. (Orthotrichaceae, Bryidae) due to immersed large capsule-like structures. However, other groups with immersed capsules that are known in many families could not be excluded.

!** *Capimirinus*** Christiano de Souza, Ricardi Branco & Leon Vargas (2012: 231) with once species, *C. riopretensis* Christiano de Souza, Ricardi Branco & Leon Vargas (2012: 231), from Brazil, is a compression of moss with erect-spreading, oblong leaves, 1.1–2.1(–4.9 [perichaetial?]) × 0.5 mm (in average 1.4 × 0.5 mm), with a single costa and unbordered margins. The areolation was not described. The sporophyte is described as lateral, seta slightly more than 1 mm, capsules erect, straight, 0.4 × 0.2 mm. The sporophyte position is not very well seen, but it does not contradict the placement of this plant into acrocarps, where many groups have lateral-looking sporophytes (*Racomitrium* Brid*., Molendoa* Lindb*., Fissidens*). The affinity with Dicranidae seems most likely. At the same time, the lack of capsule details and its unusually small size make the interpretation of a single capsule-like structure questionable. Such small capsules are known in extant mosses, but in small plants (e.g. in *Schistostega* D. Mohr), but in mosses with leaves up to 2 mm long the capsules are of larger size, most commonly 1–2 × 0.5 mm.

6. Triassic.

In contrast to 100% costate leaves in Permian mosses, many Triassic mosses are ecostate.

!** *Muscites guescelinii*** Townrow (1959:10), from South Africa, is a moss with densely foliate stems, ecostate leaves with short and very thick-walled cells (cell wall width 11 μm), arranged in longitudinal and obliquely transverse rows. Townrow (1959) compared this moss with Leucodontaceae. However, quadrate cells are against its placement in pleurocarps. The absence of a costa and the quadrate cells may indicate an affinity with: (1) Dicranidae with broad costa, thus looking ecostate, like, e.g., *Octoblepharum* Hedw. (Leucobryaceae), or (2) *Andreaea*. The latter placements seem possible, as cells are arranged in conspicuous rows and are thick-walled; however, the even, not sinuose cell thickening is not in favor of such an affinity.

!** *Muscites brickiae*** Moisan, Voigt, Schneider & Kerp (2012: 35), Kyrgyzstan. This plant is characterized by branched, remotely sub-complanately foliate stems, with widely spreading, oblong leaves 2–2.5 mm long and 0.6–0.8

mm wide, without a costa, with elongate-rectangular cells arranged in distinct longitudinal rows. Its habit reminds of Jurassic and Cretaceous *Bryokhutuliinia*, but the latter genus has a distinct border that is absent in *M. brickiae.*

!** *Muscites*** sp. Moisan, Voigt, Schneider & Kerp (2012: 35, and plate II, 4–7), Kyrgyzstan, has appressed narrow leaves, having superficially a Dicranidae habit.

!** *Muscites uralensis*** Turutanova-Ketova (1958: 677), described from the Ural Mountains in Russia. The illustration gives no clue to the species affinity.

!** Moss cuticles** (Bomfleur *et al.* 2014, Fig. 2 and 4A–F) from East Antarctica. They represent at least five different mosses, as illustrated and briefly discussed in the publication, but none shows apparent affinities to extant groups of mosses.

******* Moss cuticles** (Bomfleur & Kerp 2010, Plate 16, Figs. 1–3) from Late Triassic of Antarctica are represented by unistratose fragments, putatively bryophytes. Cells are irregularly round-hexagonal, 15–20 µm, comparable with areolation of acrocarpous mosses. However, no costa or leaf border is seen, thus the width between costa and leaf border is no less than 2 mm, which means that the leaf was at least 5 mm wide. Such a size makes an attribution to mosses unlikely.

******* *Sphagnophyllites*** D.D. Pant & N. Basu (1976: 346) with one species, *S. triassicus* D.D. Pant & N. Basu (1976: 346), from India, is difficult to evaluate. The leaf size, 3.8 mm long × 2.5 mm wide exceeds the size known in extant *Sphagnum*, and hyaline cells are described as isodiametric, ca. 100 µm, surrounded by 4–6 dark cells to 88 µm long × 42 µm wide. This combination of characters may suggest to place Sphagnophyllites into protosphagnalean rather than into sphagnalean mosses, but a protosphagnalean affinity is rejected by the absence of a costa.

!** *Tricostium triassicum*** Ignatov & Shcherbakov (2011b: 78), from Mongolia (Yamanus). Leaves are oblong, with a strong central costa and weaker submarginal costae reaching 0.8 leaf length; laminal cells ca. 13 µm wide, quadrate to short rectangular, thick-walled.

!** *Yamanusia crassicostata*** Ignatov & Shcherbakov (2011b: 68), from Mongolia (Yamanus). Leaf broadly ovate, with small isodiametric cells and a strong costa.

The Lower Triassic *Atrichites triassicus* Ignatov & Shcherbakov (2011b: 75) and *Palaeosyrrhopodon grossiserratus* Ignatov & Shcherbakov (2011b: 77) from Yamanus, Mongolia, were re-evaluated by Gomankov (2020) using additional Upper Permian specimens from the same locality, who demonstrated that both collections, originally described by few leaf compressions on one slab, belong to Lycophyta (despite the fact that the leaves lack stomata).

7. Jurassic and Cretaceous. These two periods are combined in this review, as many records are from their border. Lower Jurassic records are few: *Sphagnum* leaf fragments (Reissinger 1950), discussed above with the Ordovician *Sphagnum*, and Chinese *Stachybryolites* and *Mnioites* without discernible cellular structure. For the Jurassic and Cretaceous periods, we arrange genera by the degree of the certainty in a fossil moss placement: from those that can be referred to genus, to those which may be placed in the division Bryophyta.

7.1. Genus level

!!!!! *Campylopodium* (Müller [1848: 429]) Bescherelle (1873: 189), comprises 4 good and few more dubious extant species as well as one fossil species, *C. allonense* Konopka, Herendeen & Crane (1998: 715), Upper Cretaceous, USA. The latter shows a perfectly preserved peristome with “classical” dicranoid striolation shown with SEM images.

!!!!! *Cynodontium* Bruch & Schimper in Schimper (1856: 12) includes about 30 extant species, one Eocene fossil (see below) and also *C. luthii* Bippus, Rothwell & Stockey (2021), from Upper Cretaceous of Alaska, USA. Cross sections of permineralized fossil show a complex stricture of costa and bistratose margins that fit morphology of some extant species.

7.2. Family level

!!!!* *Calymperites burmensis* Heinrichs, Schäfer-Verwimp, Hedenäs, Ignatov & A.R. Schmidt (2014c: 261), from Myannar, mid-Cretaceous amber, is known from rich collections, showing a gametophyte structure that is similar to extant Calymperaceae by attenuate leaf tips.

!!!!* *Eopolytrichum* Konopka, Herendeen, Merrill & Crane (1997: 490) with one species, *E. antiquum* Konopka, Herendeen, Merrill & Crane (1997: 490), from USA, Upper Cretaceous. Both gametophyte and sporophyte (perfect preservation allowed SEM images as well) are obviously of Polytrichaceae, although with a combination of characters not known in any extant genus. Phylogenetic analyses of Bippus *et al.* (2018) found *Eopolytrichum* to be nested within *Polytrichum*, thus for the calibration purposes the age of this fossil can be applied for the clade *Polytrichum* + *Eopolytrichum*.

!!!!* *Kulindobryum* Ignatov in Mamontov & Ignatov (2019: 351), with the only species *K. taylorioides* Ignatov in Mamontov & Ignatov (2019: 352), Middle or Upper Jurassic, Transbaikalia, Russia. A morphotaxon for dispersed capsules, some having 32 peristome teeth, contorted and loosely appressed to capsule wall from outside, a conic to shortly rostrate operculum and a mitrate-cucullate calyptra. The species epithet refers to the similarity of peristome structure with some species of extant genus *Tayloria* Hooker (1816: 144) in the **Splachnaceae**.

!!!!* *Meantoinea* Bippus, Stockey, Rothwell & Tomescu (2017: 585), with one species, *M. alophosioides* Bippus, Stockey, Rothwell & Tomescu (2017: 585), Lower Cretaceous of Canada (Vancouver Island). Cross sections of permineralized fossil show a moss with brood bodies and typical structure of **Polytrichaceae**, very similar to *Alophozia* Cardot ex Sérgio, a Macaronesian endemic and the most basal genus in Polytrichaceae phylogeny. An additional expanded discussion of the phylogenetic position of *Meantoinea* was published by Bippus *et al.* (2018).

!!!!* *Muscites* sp. 1–**3** (Kadlecová, 2020: 39; 2020: 40; 2020: 41), from Cretaceous of James Ross Island in Antarctica and from Czech Republic. The fossils comprise shoots with remote small leaves ca. 1 mm long, with a stout costa, and overall similarity to genera of Mniaceae: *Rhizomnium* (Mitt. ex Broth.) T.J. Kop*., Cinclidium* Sw. or *Cyrtomnium* Holmen (the geniculate stem in upper part is especially similar to the latter genus).

!!!!* *Tricarinella* Savoretti, Bippus, Stockey, Rothwell & Tomescu (2018: 1276), with one species, *T. crassiphylla* Savoretti, Bippus, Stockey, Rothwell & Tomescu (2018: 1276), Lower Cretaceous, Canada (Vancouver Island). Cross sections of permineralized fossil, showing homogeneous costa in transverse section. Consistence with other characters of Grimmiaceae suggested the placement in this family.

7.3. Order level

!!! Unnamed Leucobryaceae** Tomescu (2016: 5), Lower Cretaceous of Canada (Vancouver Island). The anatomically preserved material, comprising both surface and transverse sections, shows a leucobryoid structure and was compared with some genera of the Leucobryaceae, namely *Leucobryum* Hampe (1839: 42), *Cladopodanthus* Dozy et Molk. (1846: 79), *Holomitriopsis* H. Rob. (1965: 75), and *Steyermarkiella* H. Rob. (1965: 75) (Tomescu, 2016). Transverse section in distal part of leaves, however, comprise a triangular, not quadrate shape of chlorocysts, which suggest affinity to Leucophanaceae s.l., especially to *Octoblepharum* (sometimes separated to its own family Octoblepharaceae, nom. illeg.). Thus despite a highly specific leucobryoid leaf structure, its presence in more than one family allows the placement of these fossils only up to the ordinal level, in Dicranales.

!!! *Livingstonites*** Vera (2011: 123), was described with one species, *L. gabrielae* Vera (Vera, 2010), Lower Cretaceous, South Shetland Islands (Antarctica). This is a small moss, known from both habit and cross sections, with stem ca. 150 µm in diameter, with central strand, leaves narrowly linear to subulate, ca. 5×0.2 mm, showing elongate laminal cells and complex costa differentiation, thus allowing placement in Dicranales (former Dicranaceae s.l.). Affinity to other groups are less likely because of the following structural differences: Grimmiales have a simpler costa structure; Timmiales have a complex costa anatomy, but are larger plants with distally isodiametric and mamillose cells; Bryales have either shorter cells in the distal lamina (e.g. in Bartramiales, Meesiaceae) or broader leaves (Mielichhoferiaceae), while setaceous leaves with long laminal cells are known in many genera of Dicranales. Recently, *Livingstonites* sp.1 and sp.2 were reported from Cretaceous of James Ross Island in Antarctica and from Czech Republic (Kadlecová 2020), although both habit and the very distant localities make the placement of these fossils in *Livingstonites* highly doubtful.

!!! *Vetiplanaxis*** N.E. Bell (2007: 518) includes four species from mid-Cretaceous amber, Myanmar: *V. espinosus* Hedenäs, Heinrichs & A.R. Schmidt (2014: 8), *V. longiacuminatus* Hedenäs, Heinrichs & A.R. Schmidt (2014: 7), *V. oblongus* Hedenäs, Heinrichs & A.R. Schmidt (2014: 6), and *V. pyrrhobryoides* N. E. Bell (2007: 518). All have narrow lanceolate leaves, a percurrent costa and subquadrate laminal cells, and are thus referred to Hypnodendrales.

7.4. Class/superorder level

!!* *Krassiloviella*** Shelton, Stockey, Rothwell & Tomescu (2016: 693), with one species, *K. limbelloides* Shelton, Stockey, Rothwell & Tomescu (2016: 693), from Lower Cretaceous of Canada (Vancouver Island), was referred to the family Tricostaceae (class Bryopsida, subclass Bryidae, superorder Hypnanae, order level *incertae sedis*), described for the genus *Tricosta* from the same deposits. Like in *Tricosta*, the leaves are tricostate, but *Krassiloviella* differs by more delicate, erect, concave leaves up to 5 mm long, with wider and thicker costae converging in the apex; laminal cells are mostly isodiametric; and rhizoids at leaf base both abaxial and adaxial.

!!* *Palaeodichelyma*** Ignatov & Shcherbakov (2007: 327) with one species, *P. sinitzae* Ignatov & Shcherbakov (2007: 327), from three localities in Russia, Transbaikalia (first and second: Upper Jurassic or Lower Cretaceous; third: Lower Cretaceous). Short branches that are either juvenile vegetative branches or inflorescences indicate its pleurocarpous affinity (superorder Hypnanae). The moss has costate leaves, elongate-rectangular laminal cells and short branches.

!!* *Tricosta*** Shelton, Stockey, Rothwell & Tomescu (2015: 1886), with one species, *T. plicata* Shelton, Stockey, Rothwell & Tomescu (2015: 1886), from Lower Cretaceous of Canada (Vancouver Island). Excellent preservation allowed the authors a complete reconstruction of a fossil moss gametophyte, including gametangia and details of branch primordia, which place them to Superorder Hypnanae, without placement in any definite order. The genus *Tricosta* was segregated in a separate family Tricostaceae (class Bryopsida, subclass Bryidae, superorder Hypnanae, order level *incertae sedis*), that is characterized by three stout costae up to 0.9 leaf length, and mostly rhombic mid-leaf cells and elongate, to 5:1, basal leaf cells.

7.5. Division level

!** *Baigulia*** Ignatov, Karasev & Sinitsa (2011: 53), with one species, *B. complanata* Ignatov, Karasev & Sinitsa (2011: 61), from Upper Jurassic of Transbaikalia, Russia, is a large, branched plant with ecostate, unbordered leaves to 5 mm long, and with rectangular laminal cells. Cell structure is against its pleurocarpous affinity and resembles the sympatric genus *Bryokhutuliinia*, which, however, differs by bordered leaves.

!** *Baiguliella*** Ignatov, Karasev & Sinitsa (2011: 63), with only *B. minuta* Ignatov, Karasev & Sinitsa (2011: 63), from Upper Jurassic of Transbaikalia, Russia, is a small plant with remotely arranged linear-lanceolate leaves spreading at about 90° angle; costa absent or weak and indistinct; laminal cells narrowly linear.

!** *Bryiidites*** Barclay, Duckett, McElwain, van Es, Mostaert, Pressel & Sageman (2013: 2453), with one species, *B. utahensis* Barclay, Duckett, McElwain, van Es, Mostaert, Pressel & Sageman (2013: 2453), from Middle Cretaceous of USA (Utah). Filaments on leaf surface, considered to represent an epiphyllous moss.

!** *Bryokhutuliinia*** Ignatov (1992: 379) includes four species (overview in Mamontov & Ignatov 2019): *B. jurassica* Ignatov (1992: 379), Upper Jurassic or Lower Cretaceous, Mongolia; *B. crassimarginata* Ignatov, Karasev, Sinitsa & Maslova (2013: 70), Middle or Upper Jurassic, Transbaikalia, Russia; *B. ingodensis* (Srebrodolskaya [1980: 27]) Ignatov (1992: 385), Upper Jurassic or Lower Cretaceous, Transbaikalia, (also Ignatov *et al.* 2011); *B. obtusifolia* Ignatov & Shcherbakov (2011a: 20), Lower Cretaceous, Transbaikalia. All of them consist of large plants with stems irregularly to regularly pinnately branched, rather loosely terete to complanate foliate. Leaves ovate-oblong to ovate-lanceolate, broadly rounded above or gradually tapered to the blunt apex, costa absent, limbidium distinct all around the leaf, lamina cells rectangular, border cells linear, thick-walled. Sporophytes on short lateral branches. Capsules immersed to slightly emergent, ovate, with conic operculum. A position of *Bryokhutuliinia* in the Dicranidae was considered most likely (Mamontov & Ignatov 2019), although affinity to pleurocarpous mosses in the Superorder **Hypnanae** is only a little less likely.

!** *Heinrichsiella*** Bippus, Savoretti, Escapa, García Massini & Guido (2019: 884), with one species, *H. patagonica* Bippus, Savoretti, Escapa, García Massini & Guido (2019: 884), from Jurassic of Argentina, possesses features of Polytrichaceae or Timmiellaceae.

!** *Mnioites*** X.-W. Wu, X.-Y. Wu & Y.-D. Wang (2000: 170), with one species, *M. brachyphylloides* X.-W. Wu, X.-Y. Wu & Y.-D. Wang (2000: 170), from Lower Jurassic of Xinjang, China, has broadly ovate leaves, resembling extant *Mnium* Hedw., although without sufficient details for certain placement in Bryidae.

!** Moss gametophytes #1-2** Drinnan & Chambers (1986) from Lower Cretaceous of SE Australia do not provide enough details, one of them is more or less similar by habit to Orthotrichaceae.

!** *Muscites antarcticus*** Cantrill (2000: 158) from Lower Cretaceous of Snow Island, Antarctica is represented by numerous imprints, without apparent cellular structure.

!** *Muscites cretaceus*** Ettingshausen & Debey (1859: 185), from Cretaceous of Germany, small fragment of shoot with costate, lanceolate leaves.

!** *Muscites drepanophyllus*** S.Q. Wu (1999: 9) from Upper Jurassic or Lower Cretaceous of China, has an erect stem to 3 cm high, with an acrocarpous habit due to branches divergent at acute angle; leaves are erect at base, gradually reflexed in the middle, to 4 mm long and 0.8 mm wide, oblong, obtuse at apex; in some leaves the costa can be interpreted as broad and then the plant can be compared with *Oligotrichum* DC. (Polytrichaceae). However, abundant branching alternatively suggests aquatic Dicranidae, e.g. *Scouleria* Hook. or *Dialytrichia* (Schimp.) Limpr.

!** *Muscites fontinalioides*** Krassilov (1973), from Upper Jurassic of the Russian Far East (Bureya River), has stem with leaf fragments and a sessile ovoid capsule, ca. 0.5 mm long, which is shorter than what is usual in *Fontinalis* Hedw.

!** *Muscites gracilis*** Mays & Cantrill in Mays *et al*. (2015: 1047), Late Cretaceous of Chatham Islands (east of New Zealand), was left without class assignment, but Fig. 5D shows a stem terminating in which seems a wide, plate-like perigonium with several subterminal innovations, somewhat similar to those in *Philonotis* Brid. or *Bryum* Hedw.; thus we suggest its affinity to Bryidae, as in Dicranidae such branching is less common.

!** *Muscites kujiensis*** T. Katagiri in Katagiri *et al.* (2013: 297) from Upper Cretaceous amber of Japan, has small leaves with strong costa and large isodiametric cells, and attenuate leafless stem apices.

!** *Muscites ostracodiferus*** Krassilov (1982: 6), from Lower Cretaceous of Mongolia. Aquatic moss with branched stem, remotely arranged leaves to 6 mm long, with a long single costa.

!** *Muscites samchakianus*** Srebrodolskaya (1980: 28), from Upper Jurassic of Transbaikalia, Russia, somewhat similar to *Bryokhutuliinia* from about the same age and regions, but twice as small. Costa absent, cells indiscernible.

!** *Muscites tenellus*** S.Q. Wu (1999: 9), from Upper Jurassic or Lower Cretaceous of China, has erect stem 3–4 cm high, with filiform leaves to 3 mm long, similar to some Dicranidae, e.g. *Flexitrichum* Ignatov & Fedosov, or Bryidae, e.g. *Bartramia* Schwägr.

!** *Muscites* sp.** Passalia (2007: 567), from Upper Cretaceous of Argentina, is a large moss with loosely arranged, broadly oblong leaves, 1.4–2,5 mm long × 0,8–1,2 mm wide, with a strong costa. It may relate to Bryidae (e.g. Mniaceae or Bryaceae) or Dicranidae (e.g. Scouleriaceae).

!** *Muscites* sp.** Puebla, Mego & Prámparo (2012: 226), from Lower Cretaceous of Argentina, comprises imprints of narrowly lanceolate leaves near the ovate capsule that is open and shows more or less apparent, incompletely preserved (ca. 16?) peristome teeth. Plants were compared with *Hypnodontopsis* Z. Iwats. & Nog., a common moss in Eocene amber, but its placement in Dicranidae seems to be the most likely option.

!** *Muscites* sp. 1–3** Ignatov & Shcherbakov (2011a), from Lower Cretaceous of Transbaikalia, Russia, are mosses with narrow appressed leaves, most similar to Dicranales, without apparent cellular structure.

!** *Ningchengia*** Heinrichs, X. Wang, Ignatov & M. Krings (2014b: 51), with one species, *N. jurassica* Heinrichs, X. Wang, Ignatov & M. Krings (2014b: 51), from Upper Jurassic of China, is a tuft with several cylindrical capsules on long setae; leaves are lanceolate with long single costa. Although the gross morphology suggests an affinity with Pottiaceae, Ditrichaceae, Dicranaceae or Rhabdoweisiaceae, its position in other families, including nematodontous Tetraphidopsida and Polytrichopsida, cannot be ruled out.

!** *Stachybryolites*** X.-W. Wu, X.-Y. Wu & Y.-D. Wang (2000: 168), with only *S. zhoui* X.-W. Wu, X.-Y. Wu & Y.-D. Wang (2000: 169), from Lower Jurassic of China, Xinjang, has a habit of extant *Campylopus* or other large Dicranaceae s. l., with crowded, narrow leaves and proximal parts of plants almost leafless.

!** *Taimyrobryum*** Ignatov, Heinrichs, Schäfer-Verwimp & Perkovsky (2016b: 26), with one species, *T. martynoviorum* Ignatov, Heinrichs, Schäfer-Verwimp & Perkovsky (2016b: 26), from Upper Cretaceous amber of North Siberia, is one shoot, resembling *Archidium* Brid. in habit, although the cell pattern allows pleurocarpous affinities as well.

!** *Tricostium*** Krassilov (1973: 100) was described for one species, *T. papillosum* Krassilov (1973: 100) from Upper Jurassic or Lower Cretaceous deposits of Russian Far East (Bureya River), later referred to Jurassic (Krassilov & Schuster, 1984) for leaves from bulk maceration, which in addition to a strong median costa have intramarginal costae to 0.5–0.9 leaf length; leaves of 1.2–1.8 mm long × 0.5–1.3 mm wide, cells 15–18 µm wide, polygonal to short rectangular, with 8–10 small papillae. Lower Cretaceous compressions from Transbaikalia include *T. longifolium* Ignatov & Shcherbakov (2011a: 34), represented by separate leaves and foliate shoots, with similar laminal cells and costae, but longer (4–6 mm) leaves; cell papillosity could not be discerned in compressions. *Tricostium triassicus* Ignatov & Shcherbakov from Lower Triassic of Yaman-Us in Mongolia was described based on one incompletely preserved leaf, which is similar to *T. longifolium* in shape and dimensions, but the intramarginal costae are weaker.

!** *Yorekiella*** Krassilov (1973: 101), with one species, *Y. pusilla* Krassilov (1973: 101), from Lower Cretaceous of Russian Far East (Bureya), has shoots with leaves 0.2–0.4 mm only, terete to complanate, leaves acute, unbordered, ecostate, cells isodiametric.

8. Paleocene and Eocene. Tomescu *et al.* (2018) listed 102 mosses from the Eocene and two from the Paleocene. Most of them are amber inclusions. Comments on all of them would be only moderately informative, as many taxa that look rather similar to extant genera could also be placed in other genera and often, also to other families. For this reason, some authors published such fossils under "Moss pleurocarpous #xxx" or under the name of a superficially similar moss genus with suffix '-ites'. However, the names of extant genera and even species are also used in about the same situation. In most cases such an "identification" means that there are no characters that would contradict such a placement, but they do not exclude other alternative placements either. To facilitate the overview, Eocene taxa are ranked here into four groups by the level of similarity to extant taxa.

8.1. Mosses with a combination of traits that is unknown in extant genera. Such mosses are common in Paleozoic and Mesozoic, but in Cenozoic there is only one: *Pottiodicranum papillosum* Ignatov, Schäfer-Verwimp, Perkovsky & Heinrichs (2016c: 234), from Ukraine.

8.2. Mosses that can be placed in an extant genus are as follows:

Genus	Reference
Aptychella (Broth.) Herzog	Frahm, 2004a, 2010
Atrichum P. Beauv.	Frahm, 2004a, 2004b, 2010
Arrhenopterum Hedw. (as *Aulacomnium heterostichoides* Janssens, D.G. Horton & Basinger)	Janssens *et al.*, 1979
Brothera Müll. Hal.	Frahm & Gröhn, 2013
Calliergon (Sull.) Kindb.	Kuc, 1973b
Campylopodiella Cardo*t*	Frahm, 2004a, 2010
Campylopus Brid.	Frahm, 2004a, 2010
Cynodontium Bruch & Schimp.	Ignatov *et al.*, 2016a
Ephemeropsis K.I. Goebel	Köck, 1939
Fabronia Raddi	Weitschat &Wichard, 2002; Frahm, 2010
Grimmia Hedw.	Frahm & Gröhn, 2013
Haplocladium (Müll. Hal.) Müll. Hal.	Frahm, 2004a, 2010
Herpetineuron (Müll. Hal.) Cardot	Grimaldi *et al.* 2018 Fig. 4F
Hypnodontopsis Z. Iwats. & Nog.	Frahm, 2004a, 2010; Ignatov & Perkovsky, 2011, 2013a
Isopterygium Mitt.	Ignatov & Perkovsky, 2011
Pyrrhobryum Mitt.	Frahm, 2010; Heinrichs *et al.*, 2014a
Sarmentypnum Tuomik. & T.J. Kop. (as *Drepanocladus* cf. *exannulatus* (Schimp.) Warnst.)	Kuc, 1973b
Sphagnum L.	Frahm, 2010; Ignatov *et al.*, 2019; Kuc, 1973b; Riegel & Wilde 2016
Trachycystis Lindb.	Frahm, 2004a, 2010; Ignatov & Perkovsky, 2013a

8.3. Mosses which could be places to an extant family are as follows:

Family	Species, Reference
Mniaceae	*Rhizomnium dentatum* Heinrichs, Hedenäs, Schäf.-Verw., Feldberg & A.R. Schmidt (2014a: 114)
Neckeraceae	Grimaldi *et al.* 2018 Fig. 4D–E; *Neckerites pusillus* Ignatov & Perkovsky (2011: 7)
Polytrichaceae	*Polytrichites pogonatoides* Frahm (2010: 23).

8.4. Many specimens of the order Hypnales from Eocene amber faced difficulties in identification up to even family level. Recent molecular phylogenetic revisions resulted in species referred in mid-20th century to the genus *Drepanocladus* (Müll. Hal.) G. Roth now being classified in three families, and species of *Hypnum* Hedw. in eight families (Kučera *et al.* 2019; Hodgetts *et al.* 2020). For most *Hypnum*-like fossil mosses, it would be difficult to choose the family in their current narrow circumscriptions.

It is highly likely that the European Eocene amber inclusions represent (in addition to families mentioned above) Sematophyllaceae, Pylaisiadelphaceae, Hypnaceae, Pylaisiaceae, Amblystegiaceae, Brachytheciaceae, Meteoriaceae, Leskeaceae, and Myuriaceae. However, all these records may be challenged by detailed evaluations, and for the same reason we do not recommend use for calibration purposes genera such as e.g. *Hypnum*, *Ctenidium* (Schimp.) Mitt., or *Palamocladium* Müll. Hal. Likewise, other Eocene records form North America (Britton 1899, Brown 1962, Kuc 1972, 1974, Wittlake 1968), and from Asia (Ignatov & Perkovsky 2013b, Heinrichs *et al.* 2016) cannot also be assigned to any family with certainty. It is noteworthy, however, that most of them have an undoubtful pleurocarpous habit, while mosses of Dicranales morphology are relatively few, e.g. *Ditrichites* Kuc (1974: 411). The latter cannot be identified to family after parts of *Ditrichum* Timm ex Hampe were segregated not only into different genera, but even different families (Fedosov *et al.* 2016).

9. **Oligocene to Pleistocene.** Comprehensive reviews of Late Tertiary and Quaternary bryophytes were published by Miller (1980, 1984). and Miocene records were summarized by Tomescu *et al.* (2018). However, numerous post-Eocene moss records remain scattered. They are often included in publications that describe whole fossil floras, where mosses are represented by few specimens, often referred to form genera. Their compilation requires a special effort.

There are relatively few publications with illustrations detailed enough for species identification, such as the Late Miocene or Pliocene Beaufort formation bryophytes described by Kuc (1973a). More often illustrations, if available at all, allow alternative interpretations of the represented fossils, and using those names for calibration is dangerous.

Exceptionally excellent preservations, allowing reliable species identification, occur in Dominican amber (Frahm, 1993, 1996, 2001, 2004c, 2008, Frahm & Newton 2005). Many such fossils were identified up to species level, and the provided illustrations leave no doubt in this case. A note of caution with Dominican amber, however, is briefly discussed by Frahm & Newton (2005), as some amber moss specimens may represent extant mosses embedded in copal or even forgeries. To be certain of the age of Dominican amber inclusions, a specimen has to be checked with FTIR spectroscopy. A proper example of such study was Heinrichs *et al.* (2013), which confirmed the Miocene age with the extant and sympatric *Macromitrium richardii* Schwägr. (1826: 70).

General comments

Well-preserved **Late Tertiary** mosses can in many cases be referred to extant species. The selection of genera for calibration has to be done with caution, considering the reliability of the identification and not by just using the published names. The complete preservation of mosses in **Miocene** Dominican amber makes those inclusions prime candidates for phylogenetic tree calibrations.

Eocene mosses are well-represented in amber, comprising mainly subtropical or south-temperate mosses, with prevalence of pleurocarps. Small fragments sizes in most cases preclude their placement into a single family: a specimen may be referred to two or few different families. Nevertheless, 19 extant genera may be recognized in Eocene collections: *Aptychella, Atrichum, Arrhenopterum, Brothera, Calliergon, Campylopodiella, Campylopus, Cynodontium, Ephemeropsis, Grimmia, Haplocladium, Herpetineuron, Hypnodontopsis, Isopterygium, Pyrrhobryum, Sarmentypnum, Sphagnum,* and *Trachycystis.* Families that are likely represented in Eocene fossils include Amblystegiaceae, Aulacomniaceae, Brachytheciaceae, Dicranaceae s.l. (incl. Rhabdoweisiaceae), Grimmiaceae, Hypnaceae, Pylaisiaceae, Leskeaceae, Meteoriaceae, Mniaceae, Myuriaceae, Neckeraceae, Polytrichaceae, Sematophyllaceae s.l., and Sphagnaceae. Eocene mosses almost always fit the combination of traits that is known in extant genera, with probably only two exceptions: the genus *Pottiodicranum* and *Rhizomnium dentatum,* which still can be referred to extant order Dicranales and extant family Mniaceae, respectively.

Some **Cretaceous** fossils can be placed into extant genera (*Campylopodium, Cynodontium, Sphagnum*), while other fossils show combinations of characters unusual for extant genera. Some of them could be placed in existing families, e.g. *Eopolytrichum* in Polytrichaceae; while for *Tricosta* and *Krasiloviella* a new family, Tricostaceae, was established within the superorder Hypnanae. In the case of *Bryokhutuliinia*, the combination of characters is drastically different, precluding placement at even subclass level: most its traits are in favor of Dicranidae, but the placement in Bryidae is only slightly less probable (Mamontov & Ignatov 2019). Upper and mid-**Jurassic** fossils are similar to Cretaceous ones. The mid-Mesozoic seems to be a time when pleurocarpous mosses appeared (Shelton *et al.* 2015, 2016), although acrocarpous records prevail until the Eocene. Therefore, this important event in moss evolution probably happened in approximately the same time as for ferns (Schneider *et al.* 2004) and hepatics (Wilson *et al.* 2007, Heinrichs *et al.* 2007, Villarreal *et al.* 2016), coinciding with angiosperms spreading and diversification on the Earth, i.e. the Cretaceous Terrestrial Revolution. **Triassic** mosses are few, and their placement in extant groups is uncertain.

Permian is the oldest period when fossil mosses are numerous. Half of them (especially those known from the Angaraland) belong to protosphagnalean groups, while the morphology of the other half does not contradict placement in extant classes / subclasses. In most cases Permian fossils cannot be placed in a single class or subclass, as their structure bears not enough characters for a definite choice among several possibilities. Accumulated data support the conclusion of Schuster & Krassilov (1984) that Paleozoic mosses were much more numerous in the temperate (Angaraland and Gondwana) than in the tropical or subtropical realms (Euramerica). Protosphagnalean mosses have many characters unknown in other mosses, both extant and fossil, and have to be considered as an extinct lineage.

Unequivocal mosses are known since **Upper Carboniferous**, but their structure does not help to attribute any of them to a definite class of extant mosses. **Lower Carboniferous** remains may belong to mosses, but proof of their identity is still needed. Pre-Carboniferous records are awaiting proof of either age of fossils or their identity as mosses at all.

Extensive search in the last two or three decades contributed no less than half of all records to the current knowledge; thus new findings in the near future may greatly improve our knowledge of moss evolution.

Author contributions

The section on Protosphagnalean mosses is written and illustrated by MI and EM, the rest of review is done by MI, who is the only responsible for mistakes.

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