

BULBOSPHAGNUM, A NEW FORM GENUS FOR BROOD BODIES OF MOSSES OF THE PALAEozoic ORDER PROTOSPHAGNALES

***BULBOSPHAGNUM* — НОВЫЙ ФОРМА-РОД ДЛЯ ОРГАНОВ ВЕГЕТАТИВНОГО РАЗМНОЖЕНИЯ ПАЛЕОЗОЙСКИХ МХОВ ПОРЯДКА PROTOSPHAGNALES**

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Abstract

Spheric to ovoid or bulb-like brood bodies are found in Upper Palaeozoic mosses of the order Protosphagnales. They developed on stems and leaf costae, and putatively also on the apical parts of leaves. Their surface was smooth or, more commonly, rough due to short rhizoid initials densely covering their surface all around. It seems that rhizoids developed especially after brood bodies started growth, becoming larger and then forming stem. Rhizoids on brood bodies and on stems growing out of them have oblique cell walls, characteristic to all other mosses. They definitely belong to species of Protosphagnales, wherefrom they were not reported earlier. However, as the taxonomy of the genera of protosphagnalean mosses is based primarily on leaf characters, a new form-genus *Bulbosphagnum* is described to accommodate numerous brood bodies themselves and also brood bodies with leafless stem bases. In the extant flora, the most similar brood bodies are known in *Oedipodium* where they also may form on various parts of plants and have similar shape and size, although differ in fewer rhizoid production as compared with *Bulbosphagnum*.

Резюме

У верхнепалеозойских мхов порядка Protosphagnales обнаружены специализированные органы вегетативного размножения. Небольшие, б.ч. от 400 до 800 μm , округлые или овальные выводковые тела образовывались на стебле, жилке листа и, возможно, на выростах верхушки листа. На поверхности они были гладкими, или, чаще, покрыты щеткой ризоидов или их инициалей. По-видимому, ризоиды развивались вместе с началом роста выводковых тел и их прорастания с образованием стебля. Ризоиды на выводковых телах и на растущих из них стеблях имеют косые перегородки между клетками, что однозначно подтверждает принадлежность округлых темных тел с малоразличимой поверхностной структурой ко мхам. Более того, можно показать их принадлежность к порядку Protosphagnales, в котором ризоиды считались отсутствующими. Вместе с тем, роды протосфагновых различаются по признакам листьев, которые в данных остатках отсутствуют или крайне неполны. Поэтому мы описываем новый форма-род *Bulbosphagnum* для выводковых тел и проксимальных частей безлистных стеблей. Обсуждается сходство в строении выводковых тел с современным родом *Oedipodium*, у которого также есть выводковые тела, сходные с ископаемыми телами по форме, размерам и образованию на разных частях растения, но никогда не имеющие столь густых ризоидов.

KEYWORDS: mosses, fossils, vegetative reproduction, propagation, Bryophyta, Palaeozoic, Permian, Angaraland, Protosphagnales

INTRODUCTION

Moss evolution is poorly documented by fossils. The collections are much fewer, as compared with vascular plants, insects and diatoms, and even if specimens exist, their interpretation and referring to a definite group is usually problematic. The main reason is a limited number of

characters available for study in fossil state. Another important reason is a quite plastic morphology of mosses, so even identification of extant moss collections is usually considered as difficult. General recommendation for practical identification is to begin studies with comprehensive collections of numerous large specimens, to clarify species variation

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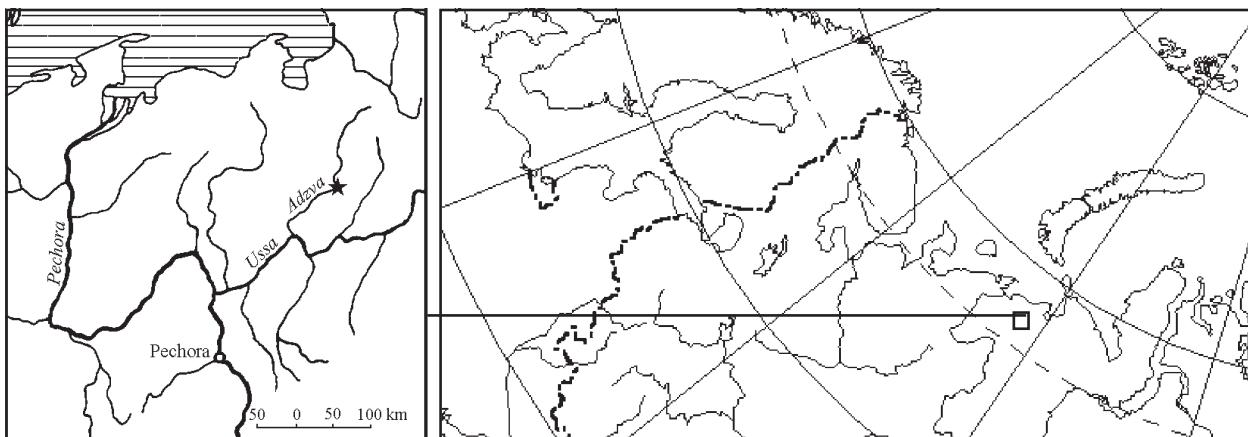


Fig. 1. Collecting locality of fossil material of Protosphagnales (star).

patterns and thereafter be able to identify any specimen. Unfortunately, working with fossils, bryologists have to be satisfied with the available material, which is usually scarce.

The exceptional place providing abundant material for mosses in Palaeozoic was the Angaraland in the uppermost Lower Permian and throughout Upper Permian, ca. 275–250 Ma ago. Mosses were found in Kuznetsk, Tunguska and Pechora Coal Basins; they were described in nine genera by Neuburg (1960), on the basis of numerous specimens. Three genera were segregated by Neuburg (1960) in a separate order Protosphagnales. These genera, *Protosphagnum*, *Junjagia* and *Vorcutannularia*, are characterized by the peculiar differentiation of leaf lamina cells, so the darker cells forming a net and lighter cells situated in the loops of this net resemble the modern *Sphagnum* (Fig. 2 B). In addition to the protosphagnalean genera, Neuburg described six genera which she classified in the Bryales: *Intia*, *Salairia*, *Uskatia*, *Bajdaievia*, *Polyssaievia* and *Bachtia*. Despite their placement in different orders, Neuburg (1960) noted that there is a rather gradual transition from *Intia* to *Protosphagnum*. However, she preferred to keep them not only in different genera, but in different orders, considering the latter as a further level of the evolutionary lineage started with *Intia*.

Subsequent studies revealed that the differences between three genera of Protosphagnales sensu Neuburg and other co-occurred genera are vague (Fefilova, 1978; Gomankov & Meyen, 1987; Ignatov, 1990). At the same time, all these fossil mosses have many characters unknown in modern mosses. Therefore, contrary to referring *Protosphagnum* to Bryopsida, Maslova *et al.* (2012b) suggested to expand the volume of Protosphagnales to accommodate other Permian mosses, including *Intia*, *Kosjunia*, *Salairia*, and also possibly *Uskatia*, *Bajdaievia*, *Polyssaievia* and *Bachtia*.

The broader data on the distribution of protosphagnalean mosses, in this broad circumscription, have also been accumulated since their description by Neuburg (1960). They were found in the adjacent areas of the Subangaraland in the Russian Platform (Ignatov, 1990), and

also in the territories now representing the Russian Far East and NW China (Wu *et al.*, 2000; Meyen, 1982).

However, their taxonomy remains quite uncertain, mostly due to enormous variation of areolation, sometimes within just one leaf (Maslova *et al.*, 2012b; Maslova & Ignatov, 2013; Ivanov *et al.*, 2015). Studies on the systematic position of *Protosphagnalean* mosses are still in progress, so we use their tentative names as in the previous publication (Maslova *et al.*, 2012b).

METHODS AND MATERIALS

Origin of Material

The material for the present study was collected in 2009 by three junior authors from the Pechora Coal Basin, Adzva River key section (Fig. 1), from two localities, #32 and #41; the flora of the former locality is approximately 4–5 ma younger than that of #41.

Outcrop No. 32 of A.A. Chernov, layers 197–199.
Numbering of layers follows Pukhonto (1998).

The plant-bearing deposits consist of green-grey fine-grained loamy siltstones and mudstones containing thin lenses of coal. According to Pukhonto (1998) and identifications of I.A. Ignatiev, along with the mosses cordaitanthaleans are buried: *Cordaites candaleensis* (Zal.) S.Meyen, *Cordaites clercii* Zal., *Rufloria* sp.; cardiolepidians: *Phylladoderma arberi* Zal., *Permotheca* sp., *Cardiolepis piniformis* Neub., *Tundrodendron petschorense* Zal.; supposed peltasperms: *Pursongia paimboica* Pukh., *Lopadiangium* sp., *Sporophyllithes* sp.; dispersal seeds of *Bardocarpus superus* Neub., various *Zamiopteris* and some other plant megafossils.

This plant assemblage is typical for the upper part of Talbeiskaya suite of the Pechora series. The age of the deposits has been determined as Upper Kazanian of the Upper Permian of East European Regional stratigraphic scale (Menning *et al.*, 2006).

The studied plant burials were probably formed under conditions of the low, partly waterlogged flood plain. The moss remains occur in the form of mass accumulations gathered together on the bottom of flat hollows, oxbow lakes and pools, which become covered with fine-grained deposits during the floods.

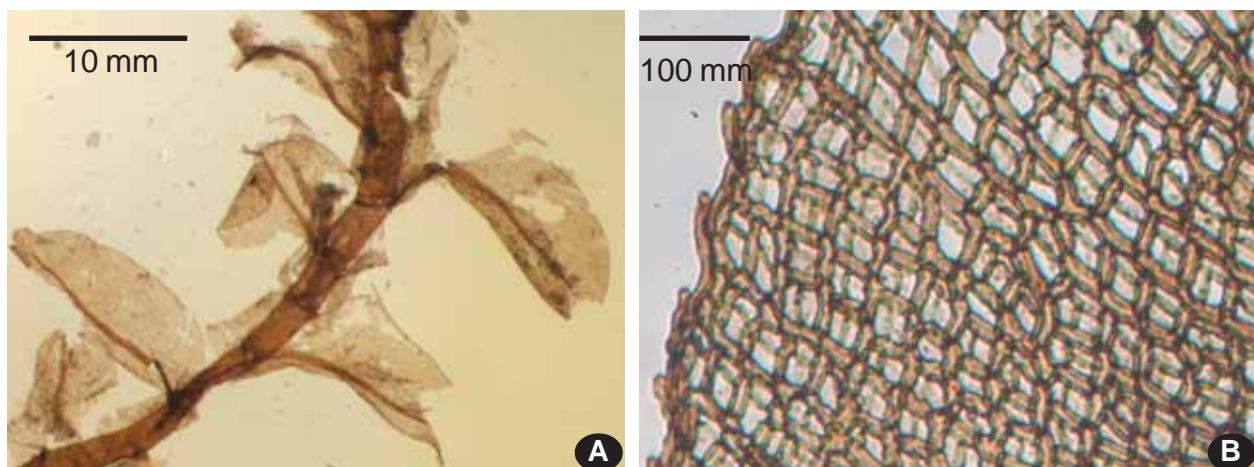


Fig. 2. *Protosphagnum nervatum* Neub. A: Viled, Tatarian Stage of Upper Permian, GIN 3774/3B-7; B: typical areolation of protophagnalean moss, from Adzva 32, #6841.

The transportation of plant remains was presumably short, i.e. the burials are hypoautochthonous. It is evident from: a) the morphological integrity of plant remains, including the preservation of moss leafy shoot fragments; b) the absence of unilateral orientation of plant remains, as well as c) the absence of traces of their differential sorting.

Reconstructions of parent flood-plain vegetation (Ignatiev & Ignatiev, 2001) show the existence of two main types of forest-shrub communities: a) the cordaitean forests occupying more disturbed sites of fluvial plain; b) *Phylladoderma* shrubs on the hydrodynamically more stable waterlogged sites of living flood plain. Judging from recurring association of the moss remains with *Phylladoderma* leaf fragments, mosses preferred the same waterlogged sites, where soils, as evidenced by the buried palaeozoic profiles, were quite often poor in organic matter.

Mosses from this outcrop were identified as *Intia angustifolia* Neub., *I. variabilis* Neub., *Vorcutannularia* sp., *Protosphagnum nervatum* Neub., *Junjagia glotophylla* Neub. and *Kosjunia* sp.

Outcrop No. 41 of A.A. Chernov, layer 12. Numbering of layers follows Tchalyshev & Variukhina (1968).

The plant-bearing deposits consist of 7 m thick pack-
et of fine-grained sandstones, passing into siltstones,
which are covered by grey mudstones and coaly clays
with clay-carbonate concretions. In the upper part of the
layer, mainly in concretions, numerous plant remains
were found. Among them there are dispersal cordaitean
leaves and scales of *Cordaites singularis* (Neub.)
S.Meyen, *Rufloria loriformis* (Neub.) S.Meyen, *R. recta*
(Neub.) S.Meyen, *Nephropsis* sp., *Sulcinephropsis* sp.,
seeds *Samaropsis frigida* Neub., *S. elegans* Neub., as well
as solitary remains of *Rufloria obovata* (Neub.) S.Meyen
and *R. synensis* (Zal.) S.Meyen leaves. The ferns are rep-
resented mainly by *Pecopteris anthriscifolia* (Goepp.) Zal.
and *P. heleneana* Zal. Sphenopsids *Paracalamites* sp.
and *Annulina* sp. are not numerous. The solitary leaf frag-
ments of *Callipteris* type are also discovered. The moss

remains are quite numerous and represented by dispersed leaves and little shoot fragments.

The presence of not numerous remains of *Callipteris*, *Rufloria obovata* and *R. synensis* on the background of typical for the Pechora basin “Vorcutian” assemblage of cordaitians, ferns and sphenopsids allows attributing the plant-bearing deposits to the lowest part of Seidinskaya suite of the Pechora series of Regional stratigraphic scheme of the Pechora coal Basin. This interval may be correlated with the upper part of Sheshmian horizon of the Ufimian stage of the Upper Permian of the East Europe Regional stratigraphic scale (Menning *et al.*, 2006).

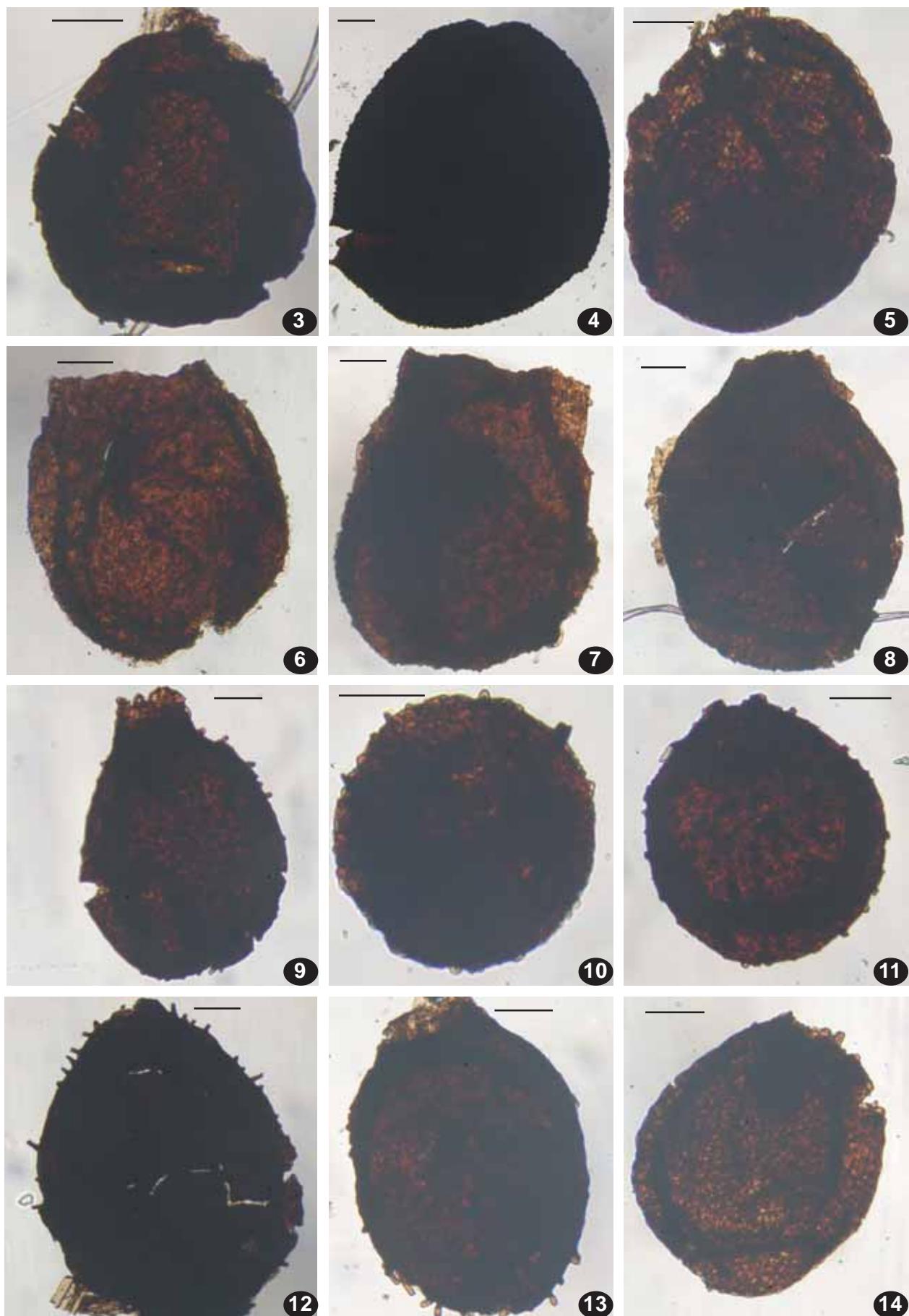
The plant-bearing deposits are alluvial in their genesis and were accumulated in the flood-plain conditions. The predominance of leaves and scales of cordaitians suggests that the parent association was a flood-plain forest, with the upper layer composed by cordaitean trees. Their leaf roofs in the outcrop are numerous, and any signs of significant transportation of material are absent. Sphenopsids were probably not a part of this forest vegetation, but they could be water and semi-water macrophytes.

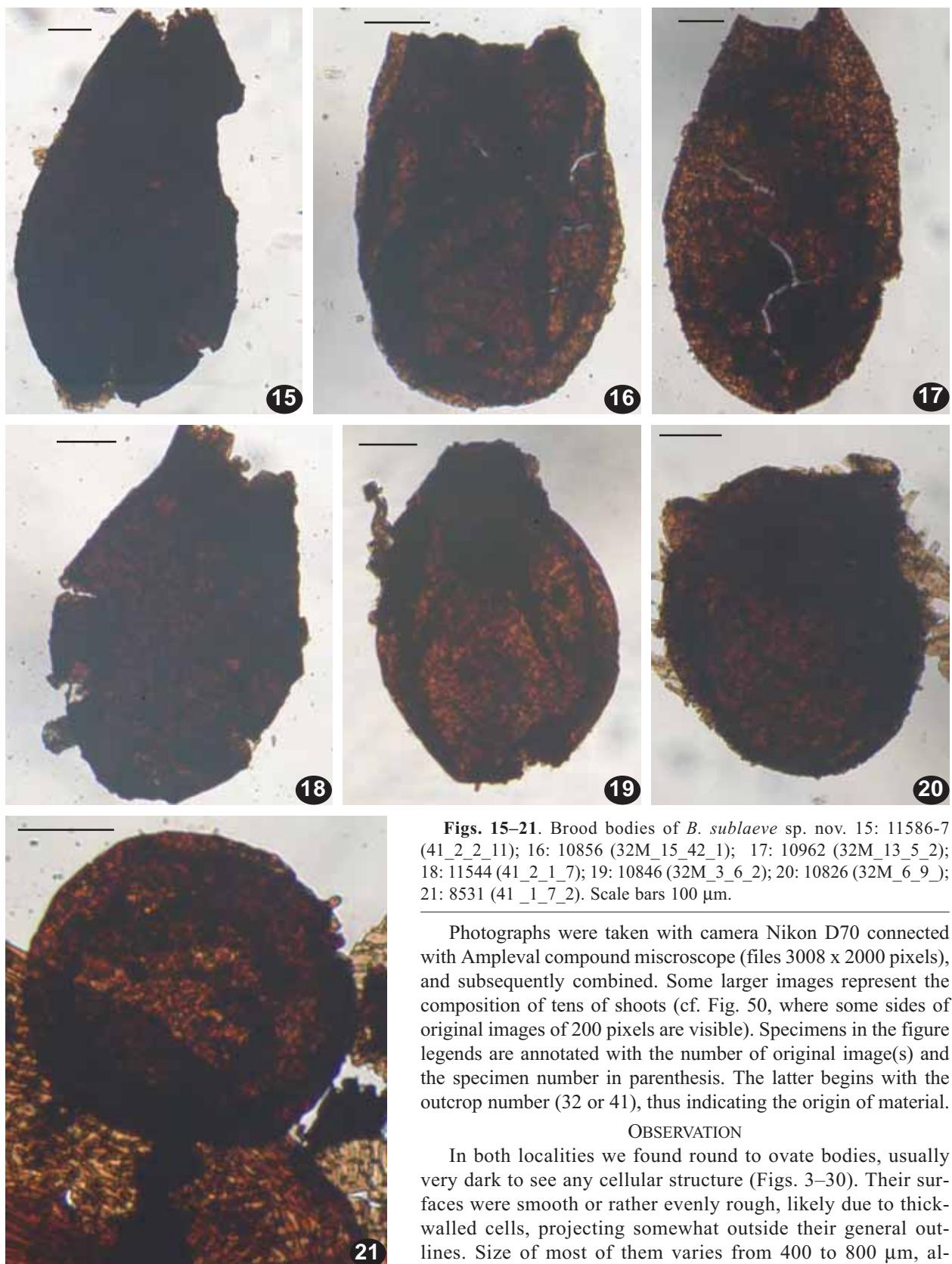
Mosses from this outcrop were identified as *Intia variabilis*, *Protosphagnum nervatum*, *Salairia* sp. and *Vorcutannularia* sp.

Preparation, photography and presentation of data

To extract moss and other plant remains from inorganic matter, the standard bulk-maceration method was used (Andrews, 1961; Darrah, 1960). The fragments of rock were placed into 50% fluoric acid during 14 days or more. The duration of the procedure was determined and controlled by experience. The products of bulk-maceration were washed by distilled water. The moss remains were extracted by infiltration through geological sieve with the mesh diameter 250 μm and then mounted in permanent glycerin-gelatin slides. The material is kept in the Main Botanical Garden of the Russian Academy of Sciences (Moscow), collections Adzva32 and Adzva41.

Such preparation allows clear vision of cellular struc-
ture, but the size of specimens rarely exceeds 2–4 mm.





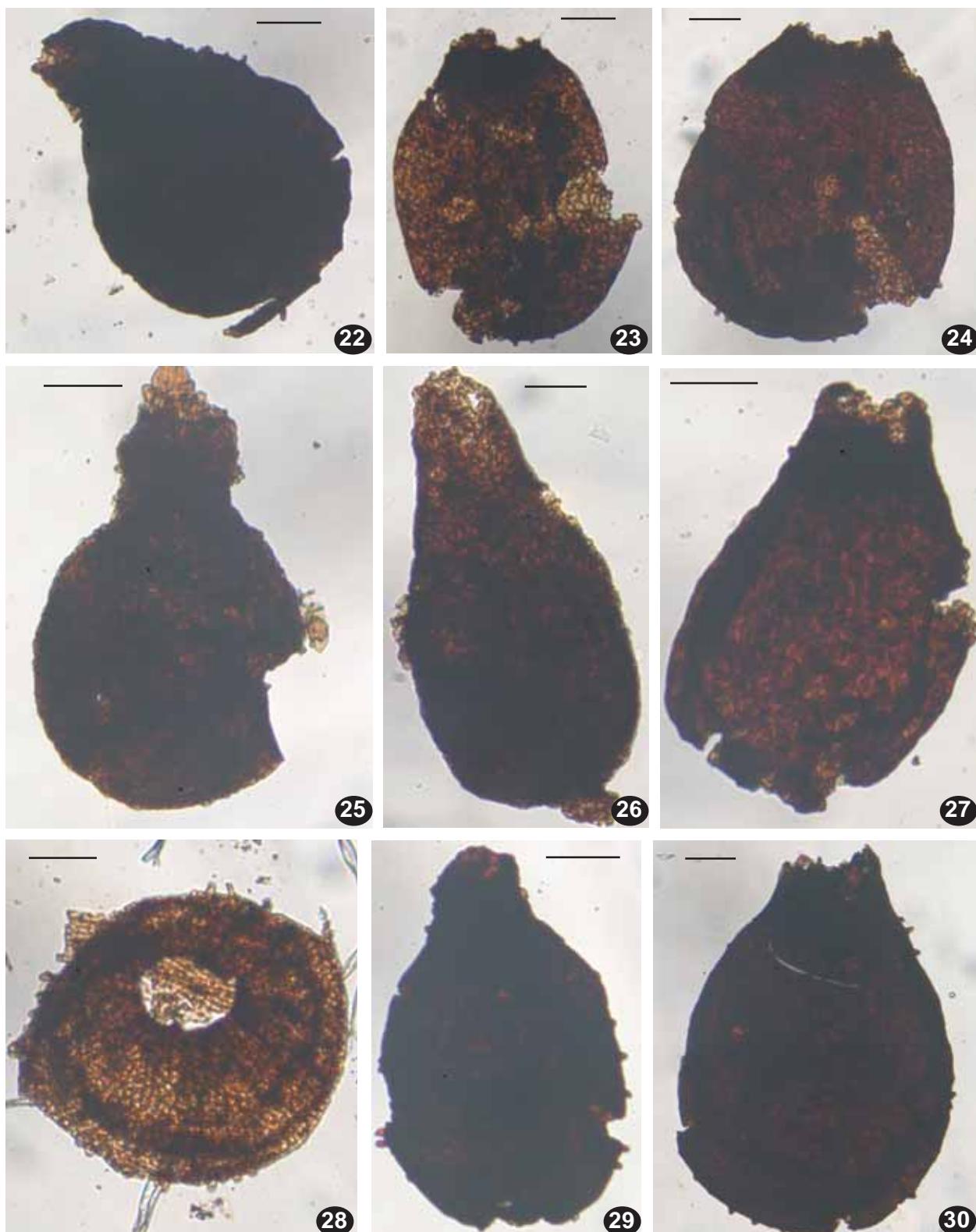
Figs. 15–21. Brood bodies of *B. sublaeve* sp. nov. 15: 11586-7 (41_2_2_11); 16: 10856 (32M_15_42_1); 17: 10962 (32M_13_5_2); 18: 11544 (41_2_1_7); 19: 10846 (32M_3_6_2); 20: 10826 (32M_6_9_1); 21: 8531 (41_1_7_2). Scale bars 100 µm.

Photographs were taken with camera Nikon D70 connected with Ampleval compound microscope (files 3008 x 2000 pixels), and subsequently combined. Some larger images represent the composition of tens of shoots (cf. Fig. 50, where some sides of original images of 200 pixels are visible). Specimens in the figure legends are annotated with the number of original image(s) and the specimen number in parenthesis. The latter begins with the outcrop number (32 or 41), thus indicating the origin of material.

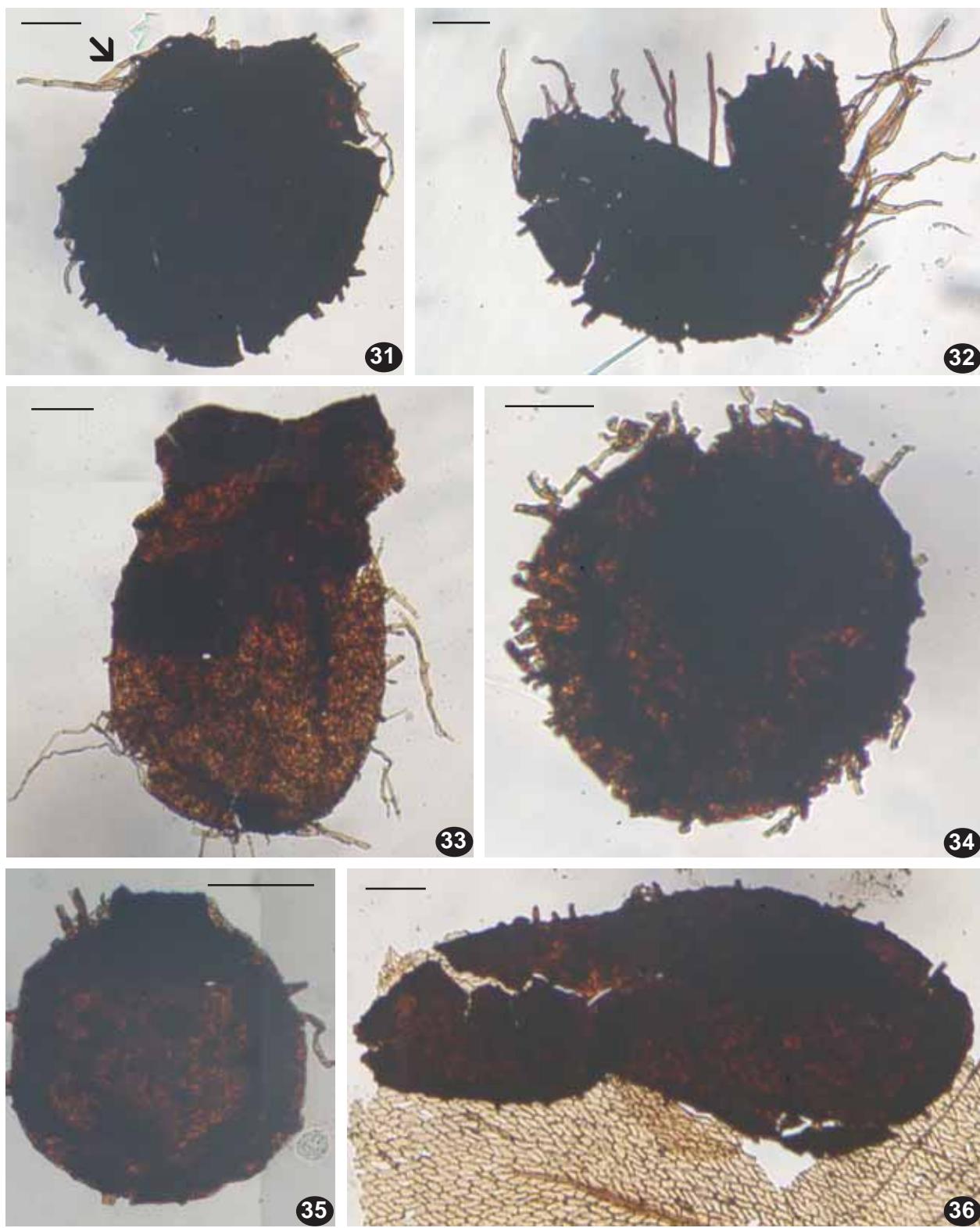
OBSERVATION

In both localities we found round to ovate bodies, usually very dark to see any cellular structure (Figs. 3–30). Their surfaces were smooth or rather evenly rough, likely due to thick-walled cells, projecting somewhat outside their general outlines. Size of most of them varies from 400 to 800 µm, al-

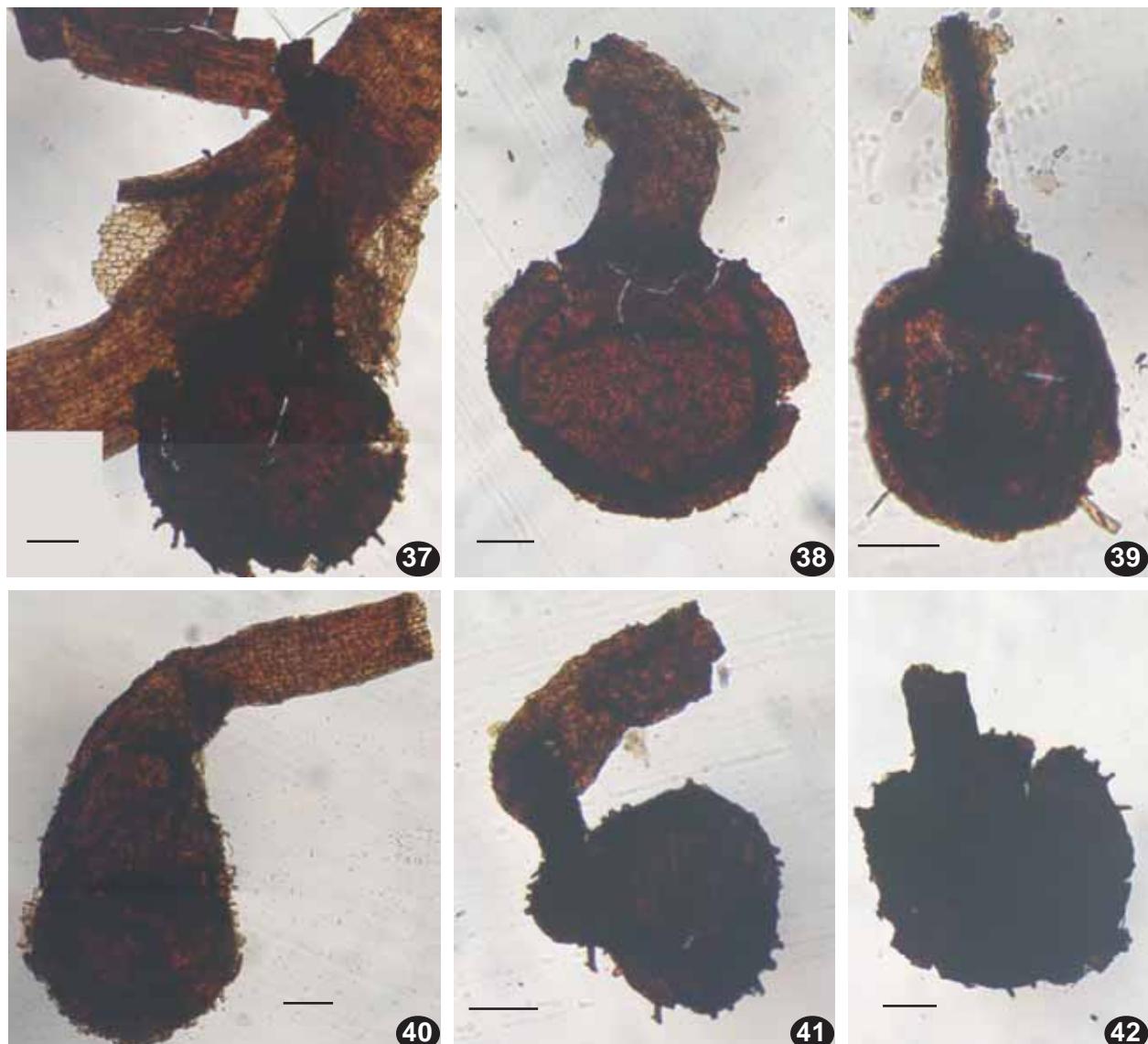
Figs. 3–14 (page 317). Brood bodies of *Bulbosphagnum polyrhizum* sp. nov. [3,4,5,8, 9,10,11,12,13,14] and *B. sublaeve* sp. nov. [6,7]. 3: 10819 (32M_5_7_1); 4: 10820-21 (32M_13_8_1); 5: 8387 (41_1_5_15); 6: 10824 (32M_12_5_1); 7: 10917 (32M_5_5_1); 8: 11555 (41_2_1_14); 9: 8372 (41_1_5_1); 10: 8190 (41_1_2_5); 11: 8260 (41_1_3_12); 12: 10774 (32M_12_17_3); 13: 11596 (41_2_3_3); 14: 11554 (41_2_1_13). Scale bars 100 µm.



Figs. 22–30. Brood bodies of *Bulbosphagnum polyrhizon* sp. nov. [22,25,28?,29,30] and *B. sublaeve* sp. nov. [23,24,26,27]. 22: 11761 (41_2_8_2); 23: 10837 (32M_3_6_1); 24: 11779 (41_2_10_9); 25: 11566 (41_2_2_5); 26: 11771 (41_2_10_1); 27: 11703 (41_2_5_8); 28: 11368 (32M_16_6_3); 29: 11565, (41_2_2_4); 30: 11667 (41_2_4_16). A partly broken epidermal layer of brood bodies in Figs. 23 and 24 allow clear view of cell outlines. Fig. 28 illustrates a fragment of distal part of the brood body with stem totally decomposed: round hole in the middle indicates the place of its junction with the brood body. This specimen is referred to *B. polyrhizon* with question mark, because of small epidermal cells, more characteristic to *B. sublaeve*, which differs in overall shape of brood body. Scale bars 100 µm.



Figs. 31–36. Brood bodies of *Bulbosphaignum polryhizon* sp. nov. [31–32; 34–36] and *B. sublaeve* sp. nov. [33]. 31: 11361 (32M_16_5_14); 32: 11473 (32M_17_1_1); 33: 10753-54 (32M_5_28_1); 34: 11257 (32M_16_1_11); 35: 10939-40 (32M_1_100_2); 36: 10854-55 (32M_14_31_2). Oblique cell wall in rhizoid arrowed in Fig. 31. Fig. 36 shows brood body of irregular shape, apparently having started propagation [to the left in picture]; leaf fragment belongs to *Intia variabilis*. Scale bars 100 µm.



Figs. 37–42. Brood bodies and stems derived from them of *Bulbosphagnum polyrhizon* sp. nov. [37–39; 41–42] and *B. sublaeve* sp. nov. [40]. 37: 10851-53 (32M_14_31_1); 38: 11314 (32M_16_4_10); 39: 11324 (32M_16_4_19); 40: 10831-32 (32M_5_3_1); 41: 11320 (32M_16_4_16); 42: 11483 (32M_17_2_1). Scale bars 100 µm.

though the smallest bodies were less than 200 µm.

It would be difficult to refer such specimens to mosses at all, and initially they were not picked up intentionally from the bulk macerated material, as we concentrated mostly on moss leaves.

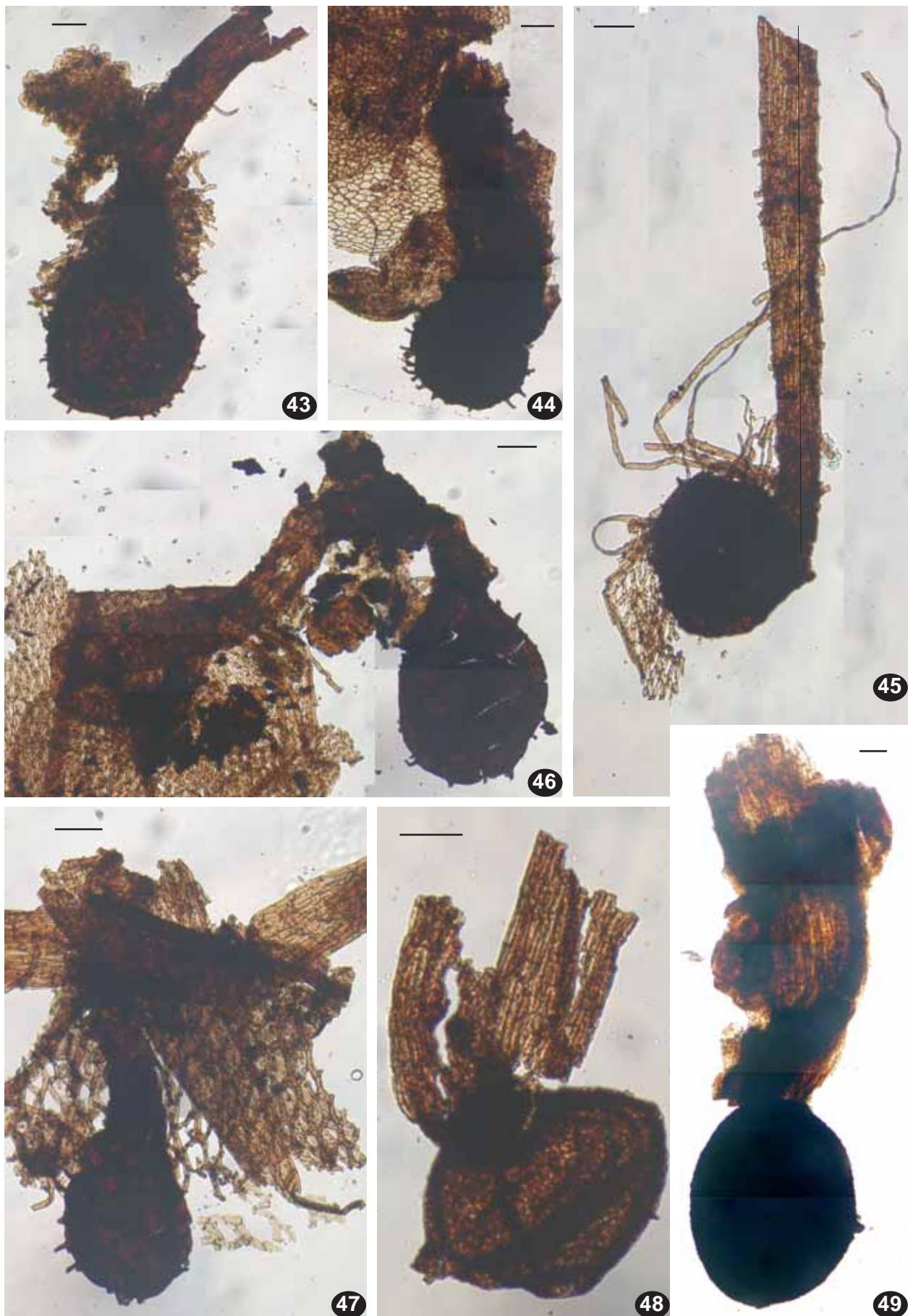
However, when specimens with rhizoids were found (Figs. 31–35), the initial notion about these dark bodies was overturned. The fact that they belong to mosses became unequivocal. Moss rhizoids are so characteristic in oblique pattern of cell walls, that just one stem cross section with such rhizoids has once been described by Lignier (1914) as a separate species, *Muscites bertrandii* Lign., from the Upper Carboniferous.

Rhizoids with such oblique cell walls are not numerous in specimens with short rhizoids (Figs. 31, 34). Numerous folds in fossil material is a common problem, thus solitary observation in this case can not be reliable.

Fortunately, in our collection specimens with rhizoids are represented by tens (Figs. 66–77), and in some of them oblique cell walls are clearly visible (Figs. 78–83). At moment there are 155 relatively complete brood bodies, including those with the proximal parts of stems, as in Figs. 43–46, but not including stems with rhizoids (cf. Figs. 66–77), without brood bodies.

Soon it became clear that the more common type of bodies is not simply round to ovate, as it seemed at superficial look (Figs. 3–30). Most of them have a mark of a broken part, which can be about as wide as the whole body (Figs. 6–7, 16–18), or otherwise narrower, making the specimen flask-shaped (Figs. 9, 25, 29), i.e. with a definite stalk.

Further observation revealed tuber-like bodies with stems, indicating their functioning as brood bodies, as they will be called hereafter. Basically they appear in two





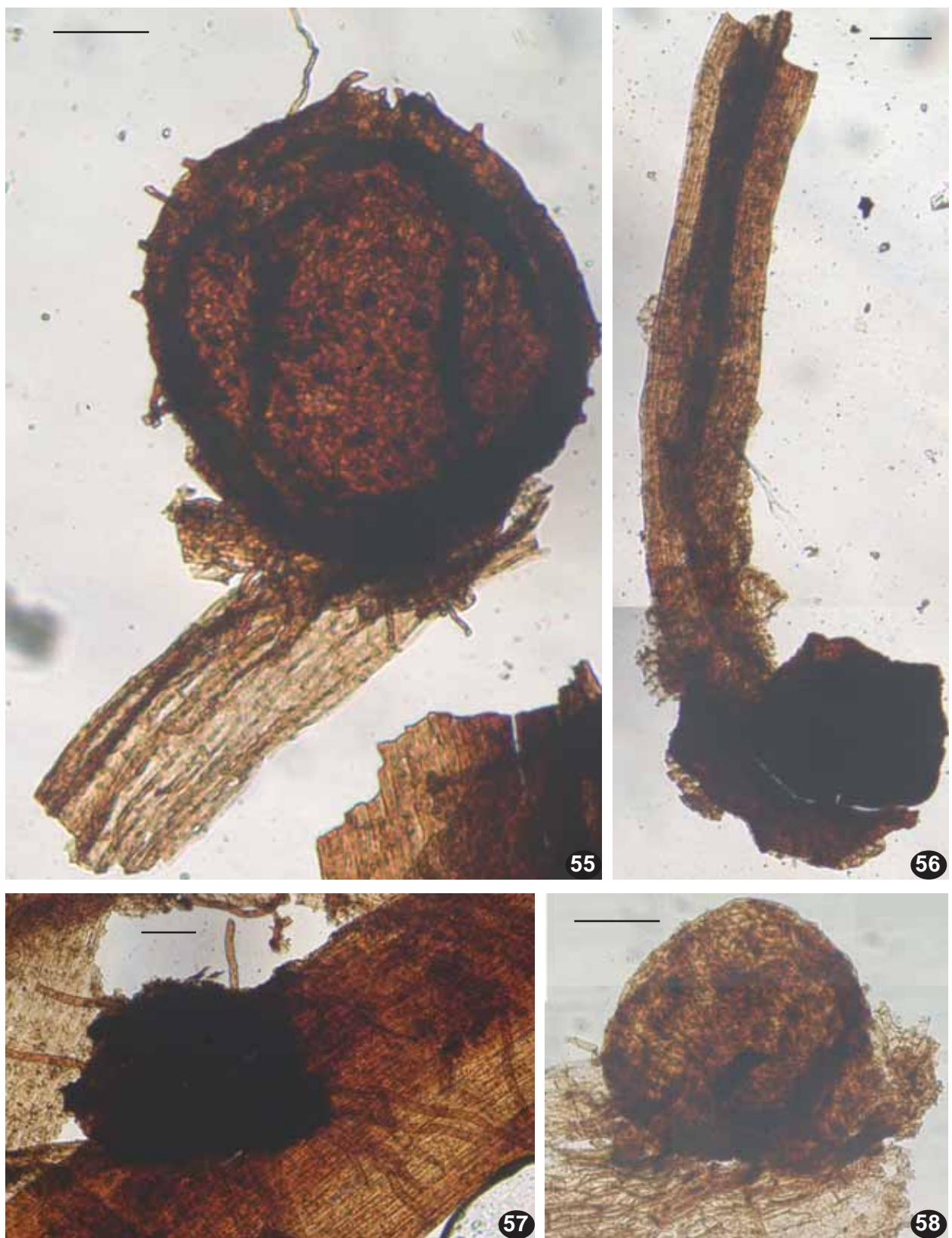
Figs. 50–54. *Bulbosphaignum sublaeve* sp. nov.: brood bodies and stems grown from them. 50: 10742 (32M_12_20_1); 51: 10891 (32M_15_41_1); 52: 10808-11 (32M_15_25_1); 53: 10899-901 (32M_5_23_1); 54: 11424-6 (32M_16_8_3). Scale bars 100 µm.

variants: either (1) bulb- or tuber-like brood bodies give rise to growth of stems (Figs. 37–54), or (2) they appear as more or less hemispheric excrescence upon the stem (Fig. 57) or pieces of indefinite tissue, which are more likely fragments of the stem cortical layer (Fig. 55, 58). In the second case, the bodies have more or less numerous rhizoids coming out from their stem-faced sides. It is

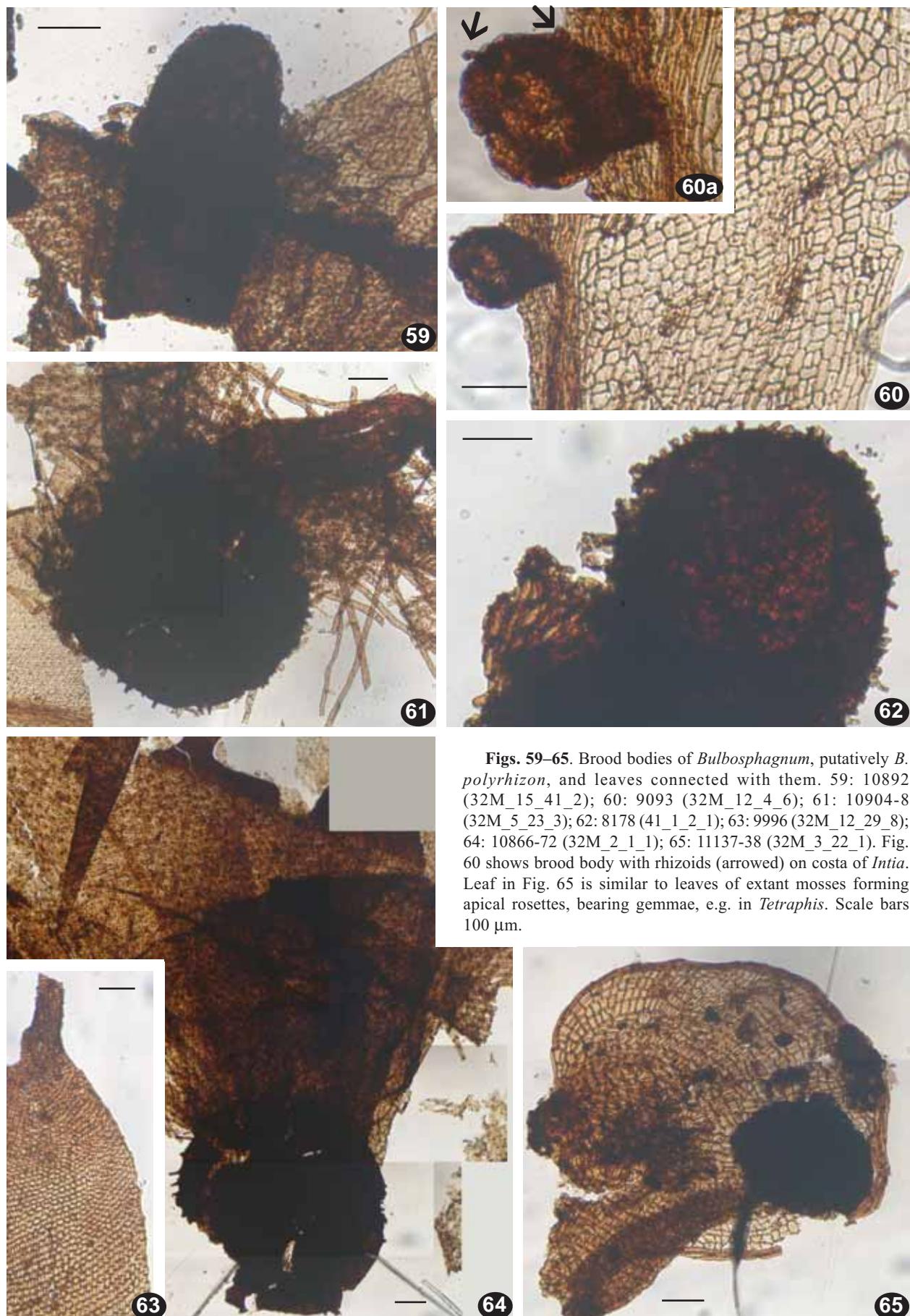
rather obvious that in the first case propagated brood bodies are at hand, while in the second case earlier stages of their development are represented.

The specimen shown in Fig. 28 is interpreted as a distal part of brood body, *i.e.* faced to the stem. The size and shape of the specimen are the same as of other complete brood bodies. In addition, isodiametric cells of ca.

Figs. 43–49 (page 322). Brood bodies and stems grown from them of *Bulbosphaignum polyrhizon* sp. nov. 43: 11252-4 (32M_16_1_8); 44: 11417-23 (32M_16_8_2); 45: 8567 (32M_12_1_7); 46: 11245-50 (32M_16_1_6); 47: 11239-40 (32M_16_1_3); 48: 10762 (32M_1_89_2); 49: 10957-61 (32M_13_5_2). Note a bud on the stem in Fig. 49. Scale bars 100 µm.



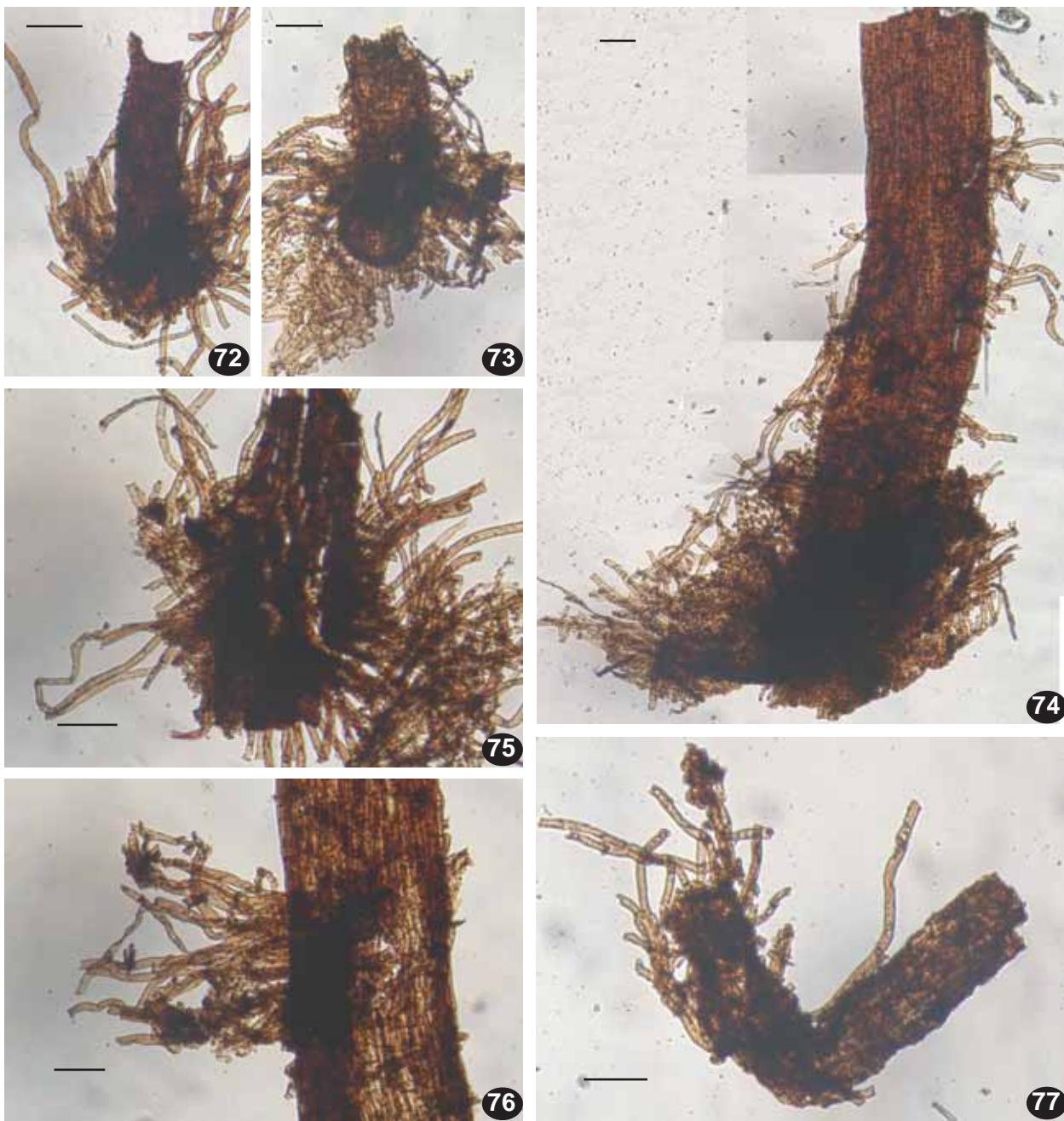
Figs. 55–58. Brood bodies of *Bulbophyllum*, putatively *B. polyrhizon*, developing on stem (Fig. 57) or indefinite tissues, likely stem cortex fragments. 55: 11370 (32M_16_6_4); 56: 10864-5 (32M_14_25_2); 57: 11367 (32M_16_6_2); 58: 11123-31 (32M_5_20_1). Scale bars 100 µm.



Figs. 59–65. Brood bodies of *Bulbosphagnum*, putatively *B. polyrhizon*, and leaves connected with them. 59: 10892 (32M_15_41_2); 60: 9093 (32M_12_4_6); 61: 10904-8 (32M_5_23_3); 62: 8178 (41_1_2_1); 63: 9996 (32M_12_29_8); 64: 10866-72 (32M_2_1_1); 65: 11137-38 (32M_3_22_1). Fig. 60 shows brood body with rhizoids (arrowed) on costa of *Intia*. Leaf in Fig. 65 is similar to leaves of extant mosses forming apical rosettes, bearing gemmae, e.g. in *Tetraphis*. Scale bars 100 µm.



Figs. 66–71. Rhizoids of protosphagnalean mosses (stem without leaves or leaves are too incomplete for a genus identification). 66: 8667-71 (32M_12_2_3); 67: 11140-1 (32M_6_8_1); 68: 11788-9 (41_2_11_2); 69: 8684 (32M_12_2_7); 70: 10157-60 (32M_3_13_2); 71: 8955-58 (32M_12_6_1). Note juvenile shoot near the stem base in Fig. 69. Small leaves on stem in 67 and their close up in 67a have arrangement typical for proximal branch leaves surrounding a branch initial; note that the shape of proximal branch leaves is similar to those in Fig. 49. Proximal branch leaves have distinct border, which is differentiated early in some protosphagnalean mosses, cf. Fig. 65. Scale bars 100 µm.

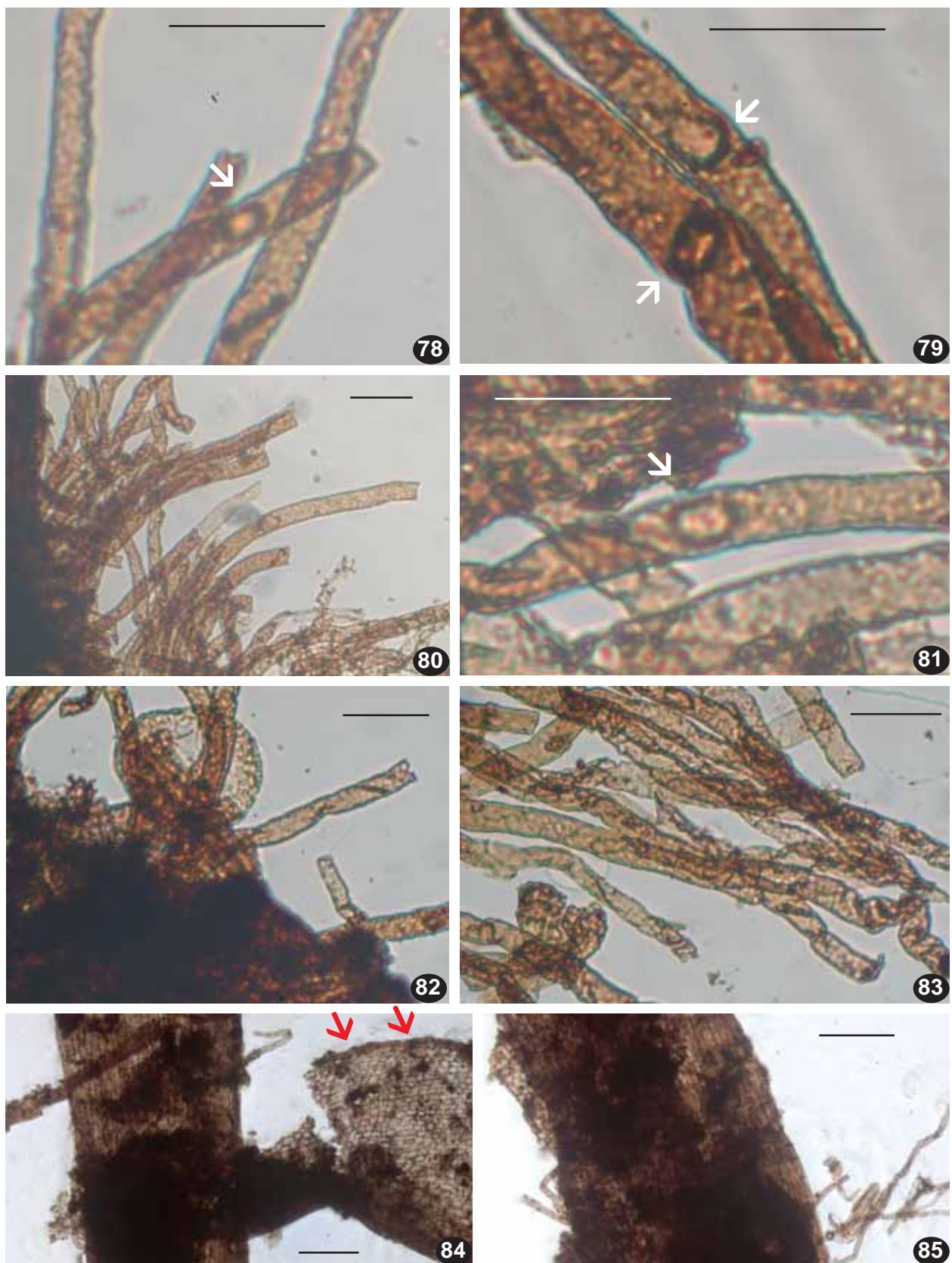


Figs. 72–77. Rhizoids of protosphaignalean mosses (stem without leaves or leaves are too incomplete for a genus identification). 71: 11296 (32M_16_3_16); 72: 11413 (32M_16_7_10); 73: 11072 (32M_2_21_2); 74: 11020, (32M_4_1_1); 75: 11713 (41_2_6_1); 76: 11713 (41_2_6_1); 77: 11073 (32M_2_21_2). Scale bars 100 µm.

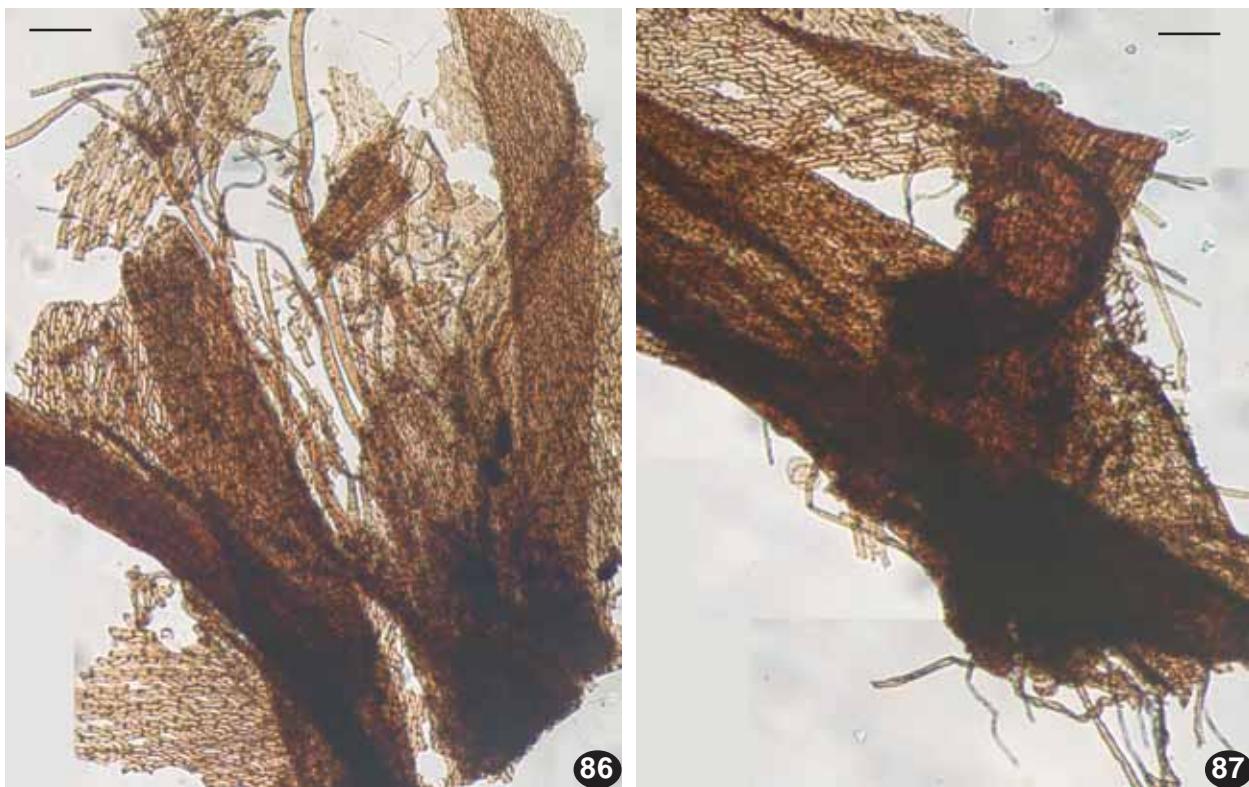
15 µm and short rhizoid initials ensure that a *Bulbosphagnum* is at hand. However, the specimen has a totally decomposed stem and at this place a round hole is seen. Especial similarity can be seen between specimens in Fig. 28 and Fig. 48, where the stem underwent strong maceration and comprises fragments of the stem cortical tissue.

One specimen has a bud on the stem shortly above the junction of stem and brood body itself (Fig. 49). The bud is formed by ca. 5 juvenile leaves surrounding a somewhat raised apical part of the developing shoot. It is similar to buds observed on the developed stems of protosphaignalean mosses. One of them is illustrated in Fig. 67

where juvenile leaves, however, are more distantly spaced. Innovations near stem base are also seen in Fig. 69, were a thin branch is approaching 0.5 mm in length. It is likely that in the case of early development, such proximal buds may result in curvatures, especially conspicuous in a specimen shown in Fig. 41. The axis grown out of a brood body curved abruptly at about a right angle and at this place also became abruptly (more than twice) broader. We may explain this only in a way commonly observed in extant mosses, when a shoot accidentally loses its ability to continue growth due to the apical cell damage, and a dormant bud substitutes it and continues



Figs. 78–85. Rhizoids of Protosphagnalean mosses: 78–83: stem without leaves or with leaves too fragmentary preserves for certain genus identification, and 84–85: *Intia* cf. *variabilis*, two parts of the same shoot (identification is certain, at least to the genus level, due to elongate marginal cells, arrowed, cf. Fig. 2). 78: 11290 (32M_16_3_15); 79: 11783 (41_2_11_1); 80: 11085 (32M_2_21_2); 81: 11435 (32M_16_8_6); 82: 9939 (32M_12_10_5); 83: 9941 (32M_12_4_6); 84: 41_A_1 (41A_1); 85: 41_A_2 (41A_1). Scale bars 200 µm for 84–85; 50 µm for 78–83.



Figs. 86–87. Rhizoids of Protosphaignalean mosses. 84: 8973-6 (32M_12_7_1); 85: 8977-80 (32M_12_7_2). Scale bars 50 µm.

growth. Naturally all such cases are marked by abrupt curving, and the case in Fig. 41 is one of them.

Stems growing from the brood bodies have a width and surface areolation as in foliate stems from the same collection (note that *Protosphaignum* is a loosely foliate moss). The main problem with the present material is that there are no specimens complete enough to represent brood bodies with rhizoids and stem with more or less complete leaves. However, there are a number of reasons ensuring that the discussed brood bodies belong to one and the same group of mosses.

1) First of all, the expedition of 2009 found only two places where mosses were abundantly represented and have excellent preservation. Both places, within 41 and 32 outcrops, have moss leaf remains only of protosphaignalean type (e.g. Figs. 44–47, 59–65). Moss genera composition was subidentical at least at the level of genus.

2) The specimen shown in Fig. 50 has a broadened stem base, similar to that in some ‘brood bodies’ (Figs. 17, 18, 40), rhizoids on both the broadened part and all along the stem, although not abundant. The base of a broken leaf is preserved at about 0.5 mm above the transition from brood body part to stem (arrow α). No parts of other leaves can be seen further up the stem, but at about equal distances above the leaf fragment there are traces of possibly existed leaves. Arrow β in Fig. 50 points to a broken stem surface similar to those observed in other stems, apparently indicating a place of a broken off or decomposed leaf. Arrow γ in Fig. 50 indicates the zone of more numerous rhizoids, which are known to concen-

trate near leaf bases in both extant (Ignatov & Hedenäs, 2007) and Permian mosses (Ignatov, 1990).

3) Stems with leaf fragments in Figs. 66 and 68 have rhizoids at their bases. Although the fragments have only small parts of lamina, the protosphaignalean areolation is apparent although not comprehensive. Larger leaf fragments with unequivocal protosphaignalean areolation are numerous, although stems and leaves are overlaying each other, providing moderately clear views (Figs. 86, 87), except few *Intia variabilis* specimens where complete leaves and stems with rhizoids were found Figs. 84, 85).

4) Brood bodies are developing on stems (Fig. 57, and putatively 55, 56 and 58), and on leaf costae (Fig. 60), and likely on leaf apices (Fig. 63). Although only one small brood body was found on leaf costa (Fig. 60), it is very important. In addition to indicating one of possible places of origin, it allows definite identification of the moss by its leaf areolation. Protosphaignalean structure is clear in this case, and the specimen can definitely be referred to *Intia variabilis* by its cell triad pattern (described in details in Neuburg, 1960, Ignatov, 1990; Maslova *et al.*, 2012a and Ivanov *et al.*, 2015), as well as elongate cells along the leaf margin, a characteristics for all ‘core Protosphaignales’, e.g. *Intia*, *Kosjunia*, *Protosphaignum*, *Vorcuttannularia* and *Junjagia* (Neuburg, 1960, Maslova *et al.*, 2012b).

5) A leaf in Fig. 63 has areolation of young *Kosjunia* and a very characteristic leaf border, definitely indicating that the leaf at hand, despite its overall shape, is unusual. The presence of apical part suggests that more than

half of its width is represented, however any traces of costa are absent. Costa can be short to almost absent in younger leaves of Protosphagnales (Maslova & Ignatov, 2013), but this leaf is apparently not that case, but another type of modification, likely associated with brood body formation. Apical attenuated part is really strange, looking more like stem. The cell bulgings on its surface are similar to those of stems with rhizoids, *e.g.* shown in Fig. 45. Noteworthy, they have approximately the same diameter. Nothing more can be said about such structure until additional material appears.

Being certain that brood bodies belong to protosphagnalean mosses, we still can not attribute them to any genera, which differ mainly in leaf characters. Thus the new form-genus is suggested below to accommodate all these brood bodies. There are some differences among the studied collections, especially in the mode of transition to stems, gradual or abrupt, thus two species are described from them, moreover, some other less apparent differences occur.

Bulbosphagnum Maslova & Ignatov, gen. nov. [form genus, Protosphagnales, Bryophyta]

Type species: *Bulbosphagnum polyrhizon* Maslova et Ignatov, sp. nov. (Upper Permian, Angaraland).

Diagnosis: Multicellular spheric to ovoid brood bodies (100–)400–800(–1200) µm. Epidermal cells thick-walled, quadrate-polygonal, 10–25 µm, smooth, with rhizoid initials or with elongated unbranched rhizoids 15 µm in diameter, with oblique cell walls. Propagated brood bodies tapered to stem gradually to abruptly. Stem smooth or with rhizoids, leafless or with remotely arranged leaf bases.

Etymology: the name refers to bulb-like shape of brood bodies and to *Sphagnum*, most known genus of the lineage where protosphagnalean mosses likely belong.

Bulbosphagnum polyrhizon Maslova & Ignatov, sp. nov.

Holotype: Upper Permian, Angaraland, Pechora coal Basin, 150 km W of Vorkuta, Adzva outcrop #32; collection 32M_16_1_3 (MHA, paleobotanical collection). Fig. 45.

Diagnosis: Brood bodies spheric, abruptly tapered to stems derived from them. Rhizoid rigid, straight. Epidermal cell outlines sharp.

Description: The holotype is the brood body of about spheric shape, 400 µm wide and 350 µm long, abruptly constricted to stem that turned to side, apparently when fossilized. Stem is 1.2 mm long, 100 µm wide at base and to 150 µm wide distally. No traces of leaves are seen. Rhizoids sparse on brood body and stem, the longest being 2100 µm, while most of them are apparently broken, and their length does not exceed 50 µm; rhizoid cells 15 µm wide, about 100 µm long. Stem cells elongate-rectangular, ca. 15 µm wide.

Other specimens range in size of their more or less spheric or shortly ovate brood bodies from 170 µm (Fig. 60) to 750 µm (Fig. 12), being most commonly about

400 µm in diameter. Specimens with partly broken brood bodies allow clear view of irregularly polygonal epidermal cells, 15–25 µm. Rhizoids on brood bodies are absent, few to dense, usually straight, 15 µm wide. Stems at base vary from 100 to 200 µm. Stems in proximal part are leafless, with sparse to numerous rhizoids.

Illustrations of additional specimens: Figs. 3–5, 8, 9–14, 22, 25, 29–32, 34–39, 41–49, 55–58.

Bulbosphagnum sublaeve Maslova & Ignatov, sp. nov. (Upper Permian, Angaraland).

Holotype: Upper Permian, Angaraland, Pechora coal Basin, 150 km W of Vorkuta, Adzva outcrop #32; collection 32M_12_20_1 (MHA, paleobotanical collection). Fig. 50.

Diagnosis: Brood bodies ovate to bulb-shaped, gradually tapered to stems derived from them. Rhizoid slender, flexuose. Epidermal cell outlines unsharp.

Description: The holotype is represented by ovate to oblong brood body, 550 µm wide and 1050 µm long, gradually narrowed to stem that has the same direction as the brood body. Stem is 2 mm long, 250 µm wide all along its length. One leaf base retained at 0.5 mm above the junction from brood body to stem, and traces of two other leaves are moderately apparent. Rhizoids are sparse on brood body and stem, 15 µm wide, the longest being 675 µm long. Stem cells elongate-rectangular, ca. 15 µm wide, and 60–100 µm long. Leaf has narrow and slightly decurrent base, basal cells dimorphous in color, ca. 35 µm long and 20 µm wide (basing on measurement of 3 cells with a more complete shape).

Other specimens range in size of their ovate brood bodies from 350 to 500 µm in width (Fig. 12), being most commonly about 800 µm long (the value is fairly inexact because of very gradual transition to stem). Epidermal cells have unclear outlines. Few places (Figs. 52, 53) allow estimate them as irregularly rounded polygonal, 12–15 µm in diameter. Rhizoids on brood bodies are absent, few to dense, usually flexuose, 15 µm wide. Stems at base are ca. 200 µm wide, with sparse to numerous rhizoids.

Illustrations of additional specimens: Figs. 6, 7, 15–21, 23–24, 26–27, 33, 40, 50–54.

Distribution: Both species of *Bulbosphagnum* occur in both localities; *B. sublaeve* is more rare in both of them: 14 out of 55 in Adzva41, and 21 out of 155 in Adzva32, *i.e.* 15% and 14% correspondingly.

Comparison: the genus *Rhizinigerites* S.V. Meyen was until recently the only rhizoid-bearing moss from the Upper Permian of the Angaraland and Subangaraland (Gomankov & Meyen, 1986). Its main distinction from all other Permian mosses of that area was considered to be the presence of rhizoids. None of those who studied protosphagnalean mosses earlier has ever reported rhizoid presence in this group of mosses (Neuburg, 1960; Fedilova, 1978; Gomankov & Meyen, 1986; Ignatov, 1990).

However, *Rhizinigerites* leaves have no border, have peculiar perforations in proximal part of leaves (Goman-

kov & Meyen, 1986; Ignatov, 1990). No similar plants were found in both Adzva collections.

The specimens from Adzva rarely have rhizoids on stems where fully developed leaves are present, although at least several such specimens were found (Figs. 84–87). Next, brood bodies with rhizoids were found developing on protosphaignalean leaves.

Comparison with extant mosses can hardly be fruitful, considering both age and overall dissimilarity, especially in the leaf areolation in Protosphaignales, which have no parallels in extant groups. The brood bodies in *Bulbosphaignum polryrhizon* are especially similar to those known in *Oedipodium*. In this extant genus, gemmae are forming in different parts of both protonema (which is foliose) and gametophore, on stems, leaf sides, leaf costae and leaf apices. Gemmae of *Oedipodium* are somewhat similar in shape and size to *Bulbosphaignum polryrhizon*, and they propagate into stem in a more or less similar way (Correns, 1899; Ignatov *et al.*, 2015). The main difference is rather few rhizoids on gemmae in *Oedipodium*. A similarity is the areolation of young leaves of protosphaignalean mosses and *Oedipodium* has been discussed by Ignatov *et al.* (2015).

It is rather easy to imagine how a relatively thin stems of *B. polryrhizon* grow from its brood body (although the strange is the fact that the brood body retains its shape, escaping any tissue resorption). The growth of *B. sublaeve* is enigmatic. The growth by means of a single apical cell upon the surface of brood body would unlikely results in so gradual transition to stem. At least superficially *B. sublaeve* resembles the *Rhynia* propagules, described by Kearney *et al.* (2016). Smaller of them had about the same size as *B. sublaeve*, 350–800 µm, were globose to ovate, have rhizoids, albeit few. These propagules have broad blunt apex, corresponding to growth by means of apical meristem, which would be the most obvious guess for *B. sublaeve* as well. However the larger size of propagules in *Rhynia*, to 2 mm long and the presence of tracheids make this similarity too superficial.

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