

NEW *BRYOKHUTULIINIA* SPECIES (BRYOPHYTA) WITH SPOROPHYTES
FROM THE UPPER JURASSIC OF TRANSBAIKALIA

НОВЫЙ ВИД *BRYOKHUTULIINIA* (BRYOPHYTA) СО СПОРОФИТАМИ
ИЗ ВЕРХНЕЙ ЮРЫ ЗАБАЙКАЛЬЯ

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Abstract

A new species of the moss genus *Bryokhutuliinia*, *B. crassimarginata* is described from the Upper Jurassic deposits from the Olov, Transbaikal Area of South Siberia. Its excellent preservation demonstrates that the leaves were not only complanate, but truly distichous. In addition to anatomically preserved gametophytes, sporophytes on short lateral branches were found, although carbonized and not exhibiting structural details. Possible relationships with pleurocarpous mosses and with Fissidentaceae are discussed.

Резюме

Из верхнеюрских отложений местонахождения Олов (Забайкальский край, Чернышевский район) описан новый вид мха из рода *Bryokhutuliinia*, *B. crassimarginata*. Превосходная сохранность, позволяющая видеть детали анатомии этого растения, позволила уточнить структурные особенности данного рода, в частности, его листорасположение, которое было не просто уплощенным, но истинно двурядным, что является редким признаком и у современных мхов, известным лишь у 5 родов. Помимо гаметофита, в коллекции представлены остатки коробочек на верхушках коротких латеральных побегов, однако сохранность образцов не позволяет видеть детали их строения. Приводится сравнение с современными бокоплодными мхами и Fissidentaceae.

KEYWORDS: mosses, fossil, sporophyte, Upper Jurassic, Transbaikalia, Olov, leaf cell structure

INTRODUCTION

A considerable number of Upper Jurassic and Lower Cretaceous bryophytes have been recognized in several localities of the Transbaikal region of Siberia, Amur River Basin in Russian Far East and Mongolia; these include Umalta-Makit, a Bureya River tributary (Krassilov, 1973), Ingoda and Samkhak (Srebrodolskaya, 1980), Erdeni-Ula (Krassilov, 1982), Khutuliin-Khara (Ignatov, 1992), Unda and Daya (Ignatov & Shcherbakov, 2007), Baigul (Ignatov *et al.*, 2011), and Khasurty (Ignatov & Shcherbakov, 2011).

The most widespread and abundantly represented genus in these collections is *Bryokhutuliinia*, which so far includes three species (Srebrodolskaya, 1980; Ignatov, 1992; Ignatov & Shcherbakov, 2011; Ignatov *et al.*, 2011). This genus is usually easy to recognize by its relatively large, 3-6 mm long, lanceolate to ovate-oblong leaves, spreading from the stem at an angle close to 90° and being often shallowly reflexed, ecostate and with a distinct dark border all around the margin. In most collections cell outlines can be seen. The unistratose lamina

lacks stomata, supporting that these plants are mosses. Lamina cells are elongate-rectangular, becoming wider towards the leaf base.

The new collections from Olov represent plants which differ from the previously described taxa of *Bryokhutuliinia*, and are therefore described here as a new species. The outstanding preservation of the specimens expands a set of structural details available for study and completing the genus description. Moreover, one gametophyte is provided with structures likely representing sporophytes, and some other gametophytes are provided with similar, but poorly preserved structures.

LOCALITY AND AGE

Specimens were collected in Eastern Transbaikalia, Olov Depression, 52°27'N–116°43'E; Late Jurassic, lower part of Ukurey formation; coll. S.M. Sinitsya, 2009, and deposited in the Borissiak Paleontological Museum of the Russian Academy of Sciences (PIN #5424) in Moscow.

The specimens were collected on the right bank of the river Olov, 1.2 km downstream of the Bagulnaya in finely laminated tuffaceous mudstones. The moss speci-

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mens are associated with the crustacean *Prolepidurus schewija* (Notostraca); the conchostraca *Paleoleptestheria savinaensis* Oley and *Palaeolynceus tshernyshevi* Oley; various insects including a dragonfly larvae of Iso-phlebiidae, beetles and larval caddis cases *Folindusia* sp.; and shoots of the horsetail *Equisetum undense* Srebr.

This composition includes index-species *Prolepidurus schewija* Tchern. – *Paleoleptestheria savinaensis* – *Palaeolynceus tshernyshevi* – *Equisetum undense*, indicating the same age with Glushkovo formation of Unda-Daya depression.

The composition of the fossil insect fauna points to a Late Jurassic or Early Cretaceous age (the Proameletus-Iso-phlebiidae assemblage after Sinitshenkova, 1999). The palynological assemblage from the stratotype of the Ukurey formation also agrees with an assemblage of the Glushkovo formation being attributed to the middle-upper Jurassic, proven by the absolute age of vulcanite series (Bashurova, 2005).

MATERIAL AND METHODS

The plant material is attached to the surface of aleurolites and fine argillites, allowing observation of the leaf cell structure at places on sole slabs, while the piece #7 represents leaves with preserved areolation on almost all shoots due to exceptionally fine whitish material. Multi-layered structures, such as stem and sporophytes are strongly coalified, hence, the cell structure can not be recognized.

The mosses were photographed with Olympus SZX16 stereomicroscopes, mostly in dry condition. When the rock surface was not completely flat, several digital images were produced and combined using the software Helicon Focus 4.50 (Kozub *et al.*, 2008: <http://www.heliconsoft.com>).

TAXONOMY

Genus **Bryokhutuliinia** Ignatov, J. Hattori Bot. Lab. 92: 379. 1992.

Description. Plants robust. Stem pinnately branched at an angle of (25-)50-80°. Leaves distichous, patent to reflexed, ovate to ovate-lanceolate, apex acute to broadly rounded; margin entire, bordered; costa absent; laminal cells elongate rectangular, with transversal cell walls more or less perpendicular to leaf length, alar cells shorter and broader than central basal cells. Sporophytes terminal on short lateral branches with strongly reduced leaves.

Type species: *Bryokhutuliinia jurassica* Ignatov, Upper Jurassic, Mongolia.

The genus includes four species from the Upper Jurassic to Lower Cretaceous of South Siberia and Mongolia.

Bryokhutuliinia crassimarginata sp. nov.

Figs. 1-29

Holotype: Olov, PIN 5424/7*. Upper Jurassic. Figs. 11 & 27. The slab comprises dozens of shoot and leaf fragments (Figs. 4, 5, 9, 18-25, 27). The shoot with clearly visible sporophytes is chosen as the holotype, while the other plant fragments should be treated as paratypes. They

allow describing several gametophytic characters, which are not seen in the fertile holotype.

Description. Plants in loose wefts. Stem creeping or floating, >15 mm long, 0.15-0.70 mm wide, cells in lateral view rectangular, 50×15 μm; leaves complanate and clearly distichous, loosely to densely inserted along the stem; shoots irregularly pinnately branched, branches deviating from stem at (25°-)50-75°(-100°), straight, clearly to often poorly differentiated from stem in width and foliage, or with leaves more densely arranged, complanate, with a more acute angle with branch axis compared to associated stem leaves; proximal branch leaves much smaller and more crowded or only slightly differentiated, branch bases without foliose structures. Stem leaves loosely to densely arranged, distance between them between 300 μm and 2 mm, deviated from stem at broad angle with the stem (55-80°), above patent to gradually reflexed and sometimes abruptly reflexed, up to 150°(-180°) with stem or sometimes reflexed from their bases, mostly 3.0-4.0×1.0-1.3 mm, but some leaves larger, to 6.0 mm long, 2.1 mm wide, ovate-oblong to ovate-lanceolate, gradually tapered distally to obtuse apex, rounded towards cordate or clasping base, plane or concave in basal part; margin entire, bordered throughout, border dark, 150-200 μm wide near leaf base, 60-100 μm wide above, formed by darker cells only slightly differentiated from lamina cells in length and width. Cells irregularly rectangular, 60-100×11-20 μm, 4-6(-7):1, shorter and broader in wider leaves, to 3-4:1, broader towards leaf base (up to 1.5-3:1, and to 25-30 μm wide). Proximal branch leaves smaller, from 0.5×0.15 mm to 3.3×1.0-1.2 mm and further so to stem leaf size, relatively narrower and less reflexed, otherwise similar to stem leaves. In some cases proximal part of branches more or less leafless, likely due to decomposition of thinner smaller leaves.

Sporophytes terminal on short lateral branches, regularly situated in some distance to a few leaves (1-1.5 mm), alternating on both sides of stem. Sporophyte-bearing branches 0.7-1.0 mm long, with strongly reduced leaves, narrower than proximal branch leaves; upper perichaetial leaves surrounding the capsule 0.6 mm long, narrowly lanceolate, stiff. Capsule sessile, erect; young capsules narrowly ellipsoid, mature capsule cup-like to shortly cylindrical, urn 0.7 mm long and 0.7 mm wide at mouth, not constricted below mouth. Operculum conic and shortly rostrate, 0.5 mm long.

Material: *Bryokhutuliinia crassimarginata* is found as compression fossil on 13 rock slabs, where plants are lying one upon another (Figs. 1-5). Some slabs (mostly of argillites) have shoots lying in a parallel ways, with tops from one side (Figs. 1-3), indicating their rapid simultaneous embedment. The remains in finer argillite (Figs. 4-5) are less regular in their arrangement on the rock surface. The longest shoots are 15 mm long (Figs. 2, 3), and their stems have diameters of up to 600(-700) μm.

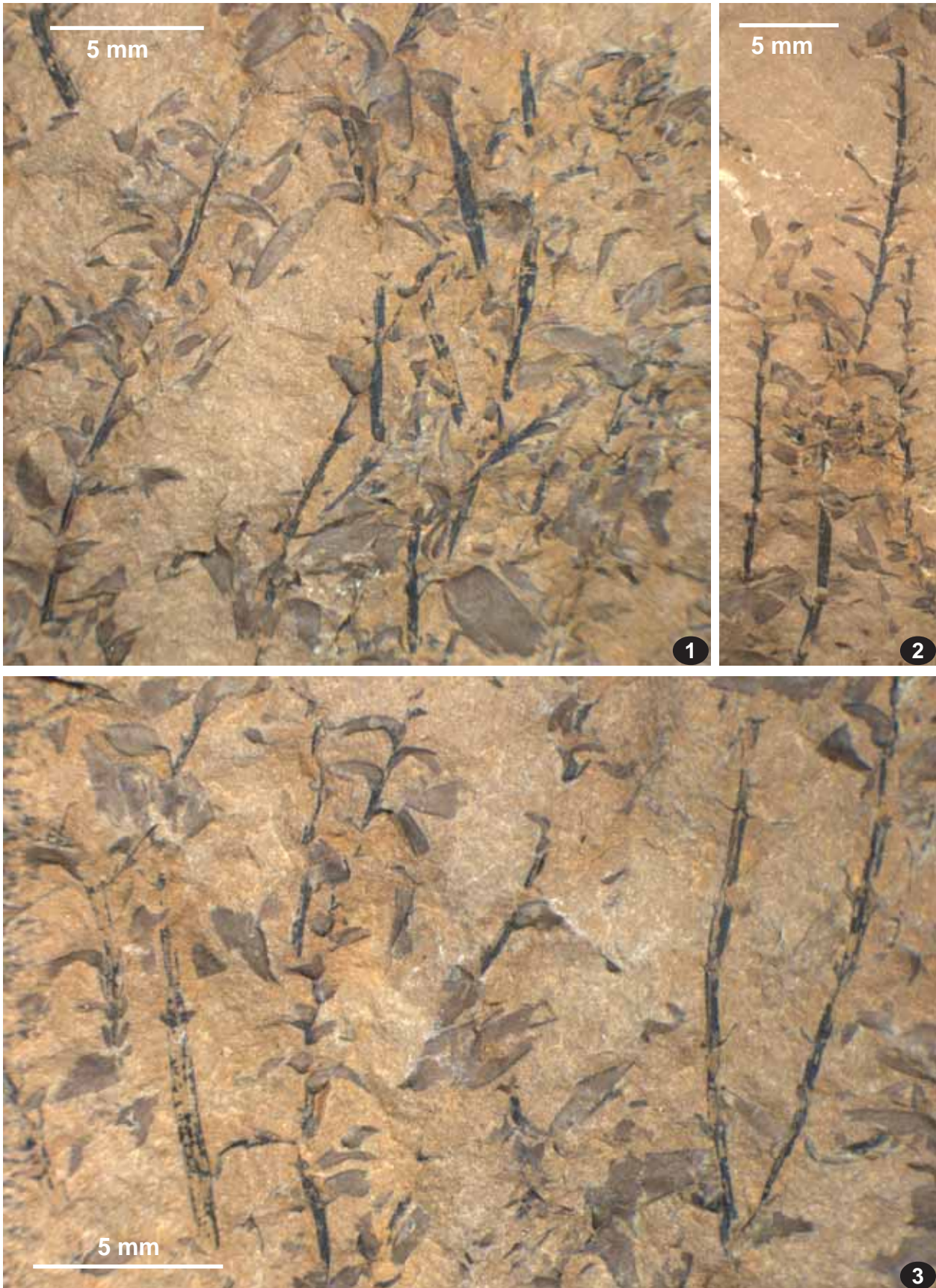
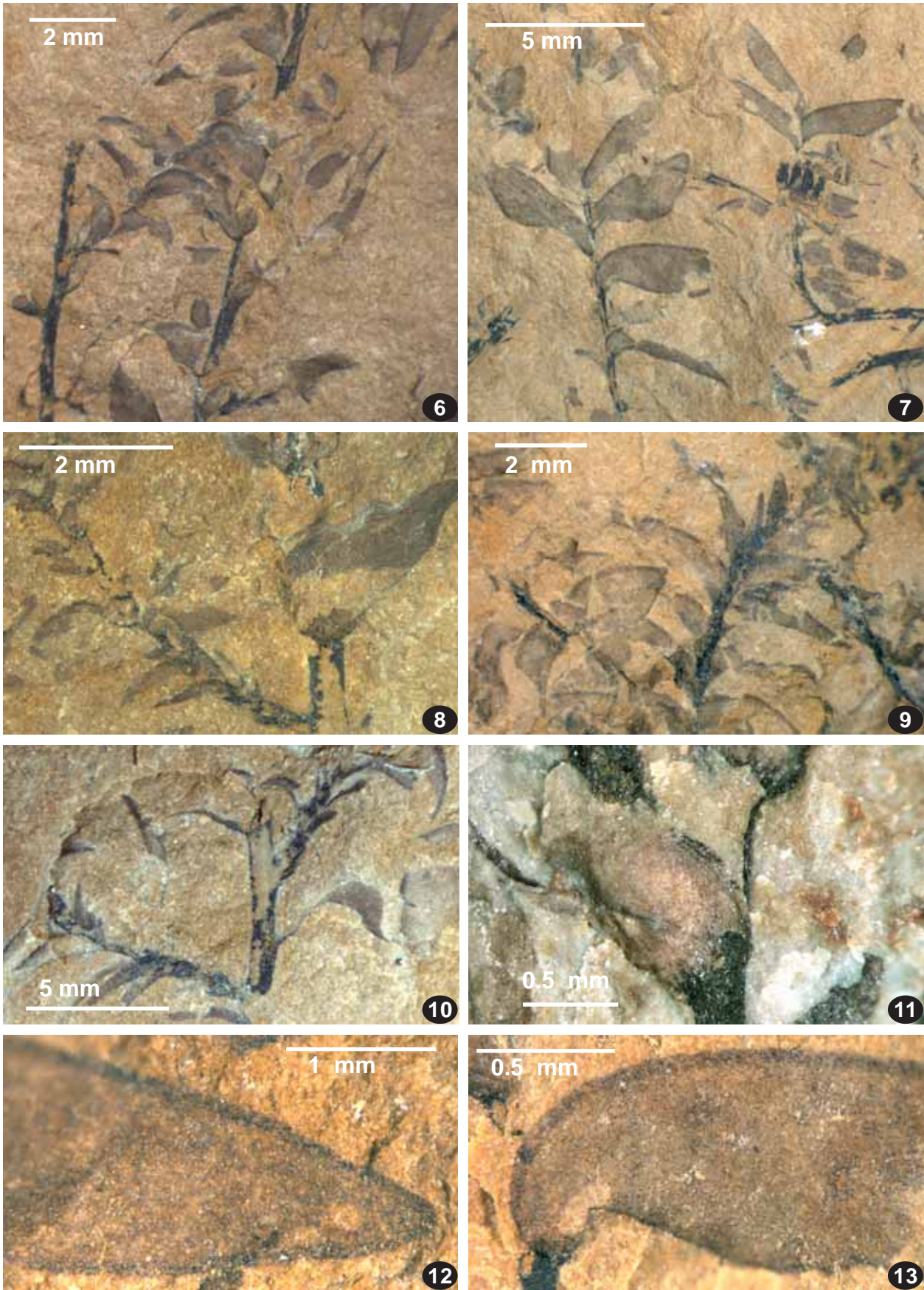


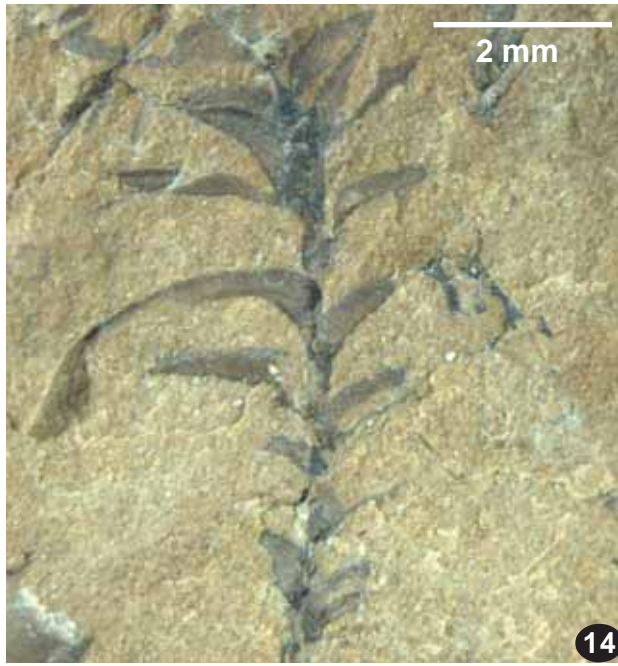
Fig. 1-3. *Bryokhutuliinia crassimarginata* sp. nov. (Olov, PIN 5424/104 (##1, 3) and PIN 5424/102 (#2). Upper Jurassic or Lower Cretaceous). Plant habit and general view on collection. Note the principally parallel direction of shoots.



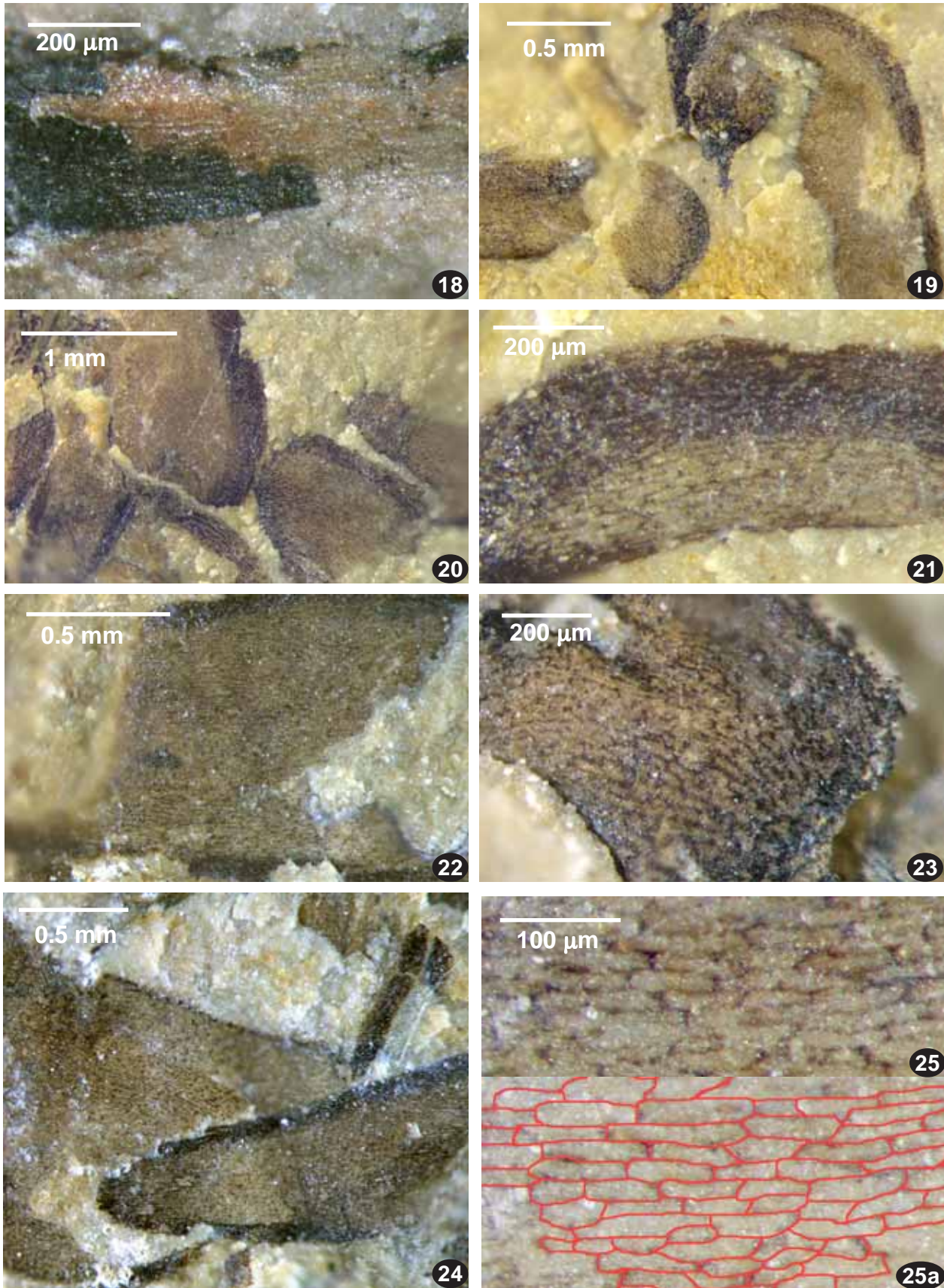
Figs. 4-5. *Bryokhutuliinia crassimarginata* sp. nov. (Olov, PIN 5424/104 (##7: paratypes). Upper Jurassic or Lower Cretaceous). Plant habit, showing variation in leaf shape and size.



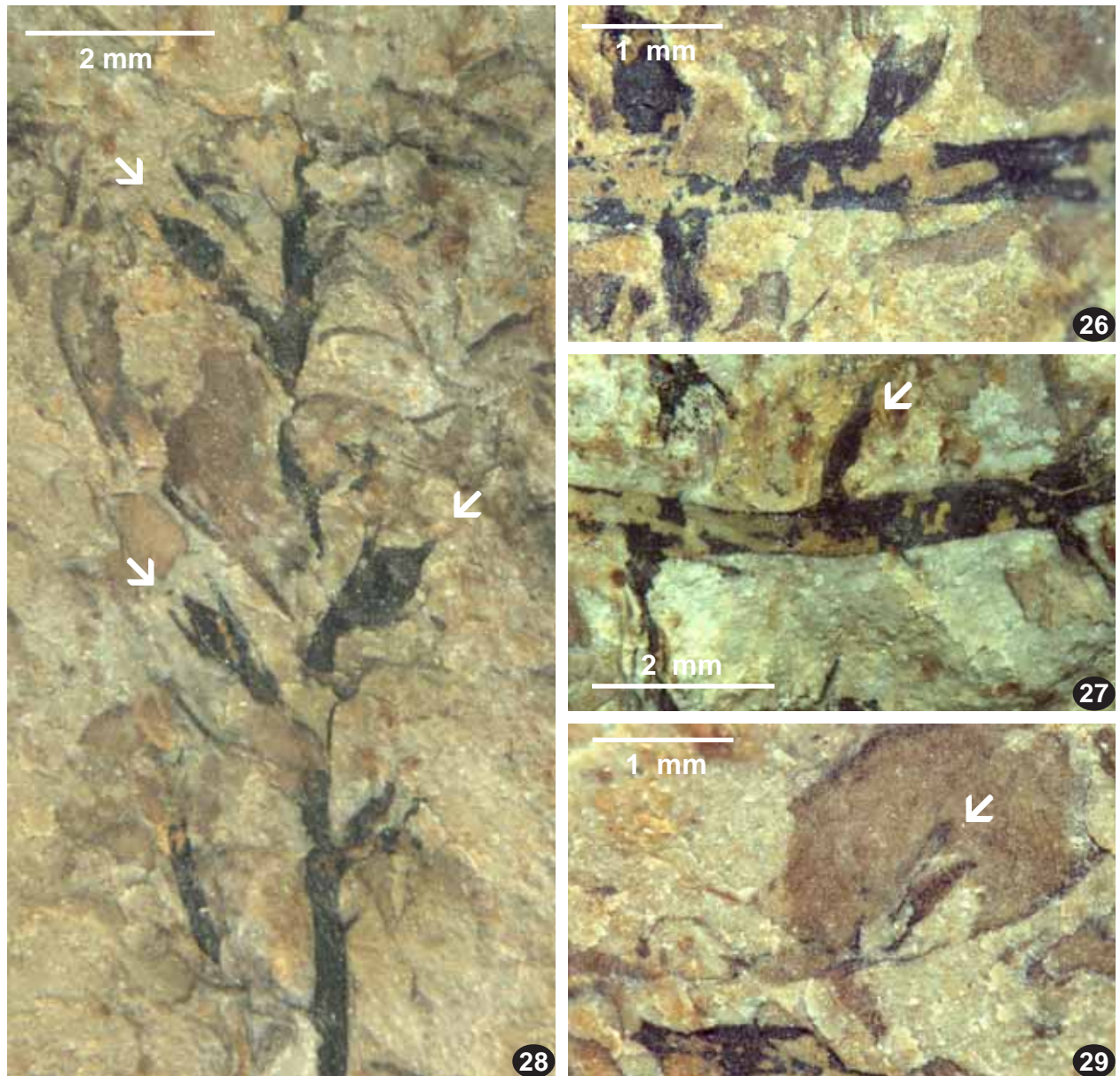
Figs. 6-13. *Bryokhutuliinia crassimarginata* sp. nov. (Olov, PIN 5424/104, 108, 111, 107, 104, 107 (from holotype), 102, 108 – respectively; Upper Jurassic or Lower Cretaceous). Plant habit, showing variation in leaf shape and size.



Figs. 14-17. *Bryokhutuliinia crassimarginata* sp. nov. (Olov, PIN 5424/104,110, 101, 103 respectively; Upper Jurassic or Lower Cretaceous). Distichous phyllotaxis, clearly seen by lines of leaf insertions in #16, and supported by clearly two-rowed leaf arrangement in loosely leaved shoots in # 14, 15, 17.



Figs. 18-25. *Bryokhutuliinia crassimarginata* sp. nov. (Olov, PIN 5424/107, paratypes); Upper Jurassic or Lower Cretaceous). Leaf fragments, showing lamina areolation in different parts of leaves, leaf border and its areolation; # 25 is from middle part of leaf (25a is same as 25 with outlined cells).



Figs. 26-29. *Bryokhutuliinia crassimarginata* sp. nov. (Olov, PIN 5424/107, 28 – holotype; 26-27 and 29 – paratypes). Upper Jurassic or Lower Cretaceous). 26-27: stems with short lateral branches, possibly gametangia-bearing; 28: shoot with capsules (arrowed); 29: upper parts of two small leaves, underlying by a large leaf; arrangement in relation to stem allow considering them representing short lateral branch similar to that in #27.

Most specimens represent shorter shoot fragments or isolated leaves, with an axis diameter ranging from 200 μm to 300-400 μm . Stems and branches are usually strongly carbonized, without any traces of cell structures, but in some fossils in fine argillite rectangular cells are recognizable in a few sections where the coalified layers were fallen of. In few such sections, they are invariable, ca. 50 \times 15 μm . Sometimes similar outlines are seen on coal layers nearby (Fig. 18), likely due to the cortical cells transmit outline of cells of deeper layers.

The leaves show a considerable variation in size, however, for the time being we consider them to belong to one species. In addition to the co-occurrence of different-

ly sized leaves in one compression, there are a number of branches whose leaves vary in size from the branch base upwards. These observations indicate that a wide range of leaf variation must have occurred in *Bryokhutuliinia crassimarginata*.

The largest leaves are 2.1 mm wide, and measurements of slightly incomplete leaf fragments indicate their length as no less than 6 mm. However, many leaves are 2 to 5 mm long; they are positioned at a distance of 0.3-2.0 mm one from each other on both sides of the stem. Leaves in proximal part of branches are very different: from 0.5 mm long (Fig. 8, 10) to 2 mm long (Fig. 6, 9), and the bigger leaves are, the larger is the distance between them.

One stem has lost some of its leaves (Fig. 16), showing lines of leaf insertions very clearly. This stem unequivocally indicates the distichous phyllotaxis. Subsequent study of foliate stems provided an additional confirmation: places where leaf arrangement is clearly seen never contradict the interpretation of a truly distichous arrangement (Figs. 14, 15, 17).

Taking into consideration the variation among stem and branch leaves and the variation in modern aquatic and subaquatic mosses, all the fragments are referred to as one species, *Bryokhutuliinia crassimarginata*. Well-developed leaves are (1) ecostate; have (2) elongate-rectangular leaf cells, and (3) a dark, even border all around the leaf (Figs. 12-13).

Cells are seen to a certain extent in all slabs, but in aleurolites (Figs. 12-13) they are less clearly seen and can be evaluated for length and width only in a few of the best preserved areas. What is seen there does not contradict better preserved moss remains in whitish argillites (Figs. 18-25). Their length varies from 50 to 100 μm , the width being 11-20 μm . Basal cells are to 30 μm wide and shorter, to 1.5-2: 1 (Figs. 11, 19, 20, 23). The leaf border is better observable in argillite, its areolation is formed by cells not strongly different from nearby laminal cells. A few fragments have an exceptionally wide leaf border (up to 200 μm in proximal parts of leaves, while in distal parts of leaves the marginal border is usually about 100 μm wide).

Fig. 28 illustrates the shoot with dark structures at the top of three short branches, and one similar branch which cannot be observed completely (right side, below in Fig. 28). Two of them have a narrow ellipsoid form, while one is broader and resembles an operculate capsule. A slight difference in color clearly indicates the presence of a conic and shortly rostrate operculum, and a broadly cylindrical or elongate cup-like urn; most part of the latter is hidden in perichaetial leaves. If this interpretation is correct, two other dark structures can be readily interpreted as premature capsules because of their shape and position on similar branches.

The alternative interpretation is that 'capsules' represent just proximal parts of shoots, and carbonized material is simply shaped by rock material to mimic a similar outlines. However this seems unlikely, because the stem of the holotype is 350 μm wide, and the putative capsule-bearing branch is even thinner, so the immediate broadening of the latter to a solid structure 700 μm wide would be difficult to explain. Also, the proximal branch leaves are rather well recognizable even in carbonized state (Fig. 26).

A number of specimens show very small lateral branches with only two leaves. One of them (Fig. 27, arrowed) is seen on the stem, while another one with a better preservation exhibits only upper parts of leaves. Their connection to the short lateral branch can be assumed from their position. The latter leaves are small, narrow and

formed by short cells with a size of 30-50 \times 15-20 μm . Their dark color may be explained by their channeled shape, thus one leaf side is overlaying another part, and this pattern is probably the same as in perichaetial leaves, making them narrower. Interpretation of such short branches as gametangia-bearing structures is possible, although a more definite statement can only be made of gametangia are detected.

Specimens examined: PIN 5424/101-113.

Comparison. *Bryokhutuliinia crassimarginata* differs from other representatives of the genus by its very broad leaf border (200 μm wide near leaf base and 60-100 μm wide above); all other species have marginal borders of 40-50 μm wide. Furthermore, *B. obtusifolia* has widely rounded leaves forming distinct rosettes in apical regions of shoots.

An important new fact observed in the present study concerns the phyllotaxis. Previous observations indicated distichous leaves, but it was unclear if the arrangement was truly distichous or pseudodistichous. There are many mosses with spiral leaves which have a distinctly distichous appearance, e.g., *Taxiphyllum*, *Phyllocladophora*, *Catagonium*, and *Isopterigiopsis muelleriana*. Truly distichous leaves occur among the extant genera *Fissidens*, *Schistostega*, *Distichium*, *Eustichium*, and *Bryoxiphium* (Goffinet *et al.*, 2009). None of these genera resembles *Bryokhutuliinia*; furthermore, the leaf rosettes of *B. obtusifolia* seemed to indicate a pseudodistichous arrangement. An additional reason for this assumption were the ecostate leaves and the pinnate branching, pointing to a pleurocarpous mosses. In extant pleurocarpous mosses true distichous phyllotaxis is totally unknown, whereas a "pseudodistichous" strongly complanate foliation is rather common.

Although no extant group can be related to *Bryokhutuliinia*, the new facts on phyllotaxis might force us to reconsider its position in pleurocarpous mosses.

Bryokhutuliinia stands out by its distichous phyllotaxis, strong limbidium, rectangular cells with transversal cell walls more or less perpendicular to leaf length, sporophytes on short branches with strongly reduced leaves, and small capsules. It shares these characters with the extant aquatic moss *Fissidens*, especially *F. fontanus*, whose leaves have very similar arrangement and size. However, the latter genus has (1) a costa (although there are ecostate species in the genus, but all of them are very small-sized); (2) a unique "triradiate" leaf structure, and (3) isodiametric upper cells. The very strong variation in leaf size is also in conflict with the concept of *Fissidens*, but more characteristic for pleurocarps.

The balancing of the pro and contra of a position of *Bryokhutuliinia* in pleurocarpous mosses is thus still in favor of 'pro' as the branching and the long lamina cells are difficult to imagine in any acrocarp group. The previously suggested (Ignatov *et al.*, 2011) possible relationship with Hookeriales remains poor, although small cap-

sules are a characteristic of these large plants.

Two Mesozoic plants need to be compared to *B. crassimarginata*.

Among Upper Jurassic mosses from Bureya River (now ca. 1000 km from the Olov locality to the East), Krassilov (1973) described *Muscites fontinalioides*, represented by few shoots and one still operculate capsule of ca. 1 mm long on a shoot with small leaves (0.6–0.8 mm long). Krassilov related the capsule to the extant genus *Fontinalis*, which seems unlikely. Although capsules are submerged in perichaetial leaves in some species of this genus, they are considerably larger, as are the vegetative leaves. Krassilov's material was obtained from balk maceration, a method providing excellent cell structure details. However, bulk maceration also leads to fragmentation of plant material, and bigger parts may vanish from the collection. The small capsules of *B. crassimarginata* resemble those of *M. fontinalioides*; both species have ecostate leaves of similar size and shape, at least on capsule-bearing branches. The putatively three-ranked leaves and the absence of a marginal border, underlined in Krassilov's description, oppose a close relationship, although small leaves of *Bryokhutuliinia crassimarginata* (cf. Fig. 29) may be only indistinctly bordered.

Bryokhutuliinia crassimarginata is one of the oldest moss fossils with preserved sporophytes. However, the state of preservation of these sporophytes does not allow for a detailed systematic treatment. In contrast, the Cretaceous fossils of *Eopolytrichum* and *Campylopodium* (Konopka *et al.*, 1997, 1998), include peristomate sporophytes in a nearly perfect state of preservation, allowing for a thorough classification of these plants. The Permian *Saksenaphyllites saksenae* Chandra from India (Chandra, 1995) and the Brazilian *Capimirinus riopretensis* Christiano de Souza, Branco & Léon (Christiano de Souza *et al.*, 2012) as well as an unnamed moss published by Amaral *et al.* (2004) lack structural details. Being strongly carbonized, the capsules of *B. crassimarginata* also provide little information on its phylogenetic relationships, as lateral position of sporophyte-bearing branches occurs both in extant pleurocarps, as well as in Fissidentaceae, Grimmiaceae and some other acrocarpous groups.

Among the recently described Triassic fossils, there are two mosses resembling *Bryokhutuliinia*. *Muscites brickiaae* Moisan, Voigt, Schneider & Kerp from Kyrgyzia (Moisan *et al.*, 2012) has a rather similar habit, but differs in the smaller size and total absence of a leaf border. Unnamed leaves from the Antarctic (Bomfleur *et al.*, 2013, Fig. 2) have a somewhat similar cell shape, leaf border and laxer areolation towards the base, but the leaves are shorter and the cells are larger.

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Ignatov & Shcherbakov (2011) already noted that fossil mosses often occur as single plants. The present case supports this observation, which was first outlined by Neuburg (1960) for Permian mosses.

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