Journal of Palaeosciences 71(2022): 219–233
0031–0174/2022

The first discovery of mosses (Bryopsida) in the Lower Jurassic of Eastern Siberia, Russia

ANDREY O. FROLOV[1*], SERGEI G. KAZANOVSKY[2] AND ILYA V. ENUSHCHENKO[3]

[1]*Institute of the Earth's Crust, Russian Academy of Sciences, 128, Lermontova str., Irkutsk, 664033, Russia.*
[2]*Siberian Institute of Plant Physiology and Biochemistry, Russian Academy of Sciences, 132, Lermontova str., Irkutsk, 664033, Russia.*
[3]*All–Russian Plant Quarantine Center, 77, Krasnoyarskaya str., Irkutsk, 664023, Russia.*
[*]*Corresponding author: frolov88–21@yandex.ru*

(Received 11 October, 2022; revised version accepted 13 December, 2022)

ABSTRACT

Frolov AO, Kazanovsky SG & Enushchenko IV 2022. The first discovery of mosses (Bryopsida) in the Lower Jurassic of Eastern Siberia. Journal of Palaeosciences 71(2): 219–233.

Most of the known diversity of Jurassic mosses comes from the Upper Jurassic of China, Mongolia, and Asiatic Russia. The Early Jurassic mosses are not known in Siberia. According to the study of shoots of bryophytes from the Prisayan Formation (Early–Middle Jurassic) of the Irkutsk Coal Basin (Eastern Siberia), two new species of mosses are established: *Bryokhutuliinia ignatovii* sp. nov. and *Palaeodichelyma kiritchkovae* sp. nov. The stem microstructures of *B. ignatovii* distinguish it clearly from other representatives of *Bryokhutuliinia* Ignatov from the Jurassic and Cretaceous of Mongolia and Transbaikalia. *P. kiritchkovae* is the only known representative preserved with sporophytes of *Palaeodichelyma* Ignatov & Shcherbakov.

Key–words—*Palaeodichelyma, Bryokhutuliinia*, Sporophyte, Gametophyte, Lower Jurassic, Irkutsk Coal Basin.

INTRODUCTION

BRYOPHYTES are one of the most primitive and ancient groups of land plants (embryophytes). This perspective, based on comparative anatomy data, has recently been confirmed by the results of molecular phylogenetic studies (Shaw *et al.*, 2003; Goffinet & Buck, 2004; Newton *et al.*, 2007). The oldest fossil records of mosses are from the Lower Carboniferous (Visean) of eastern Germany (Hübers & Kerp, 2012). However, such a long history (~346 Ma) of the moss evolution is not well understood. This is partly due to the rare occurrence of moss fossils in the pre–Cenozoic rocks. Approximately 13,000 extant mosses are known to date (Goffinet *et al.*, 2009), and many of the abundant Cenozoic bryophyte are assigned to extant families, genera, and species (e.g., Miller, 1984; Taylor *et al.*, 2009). There are more than 200 species of pre–Cenozoic mosses (Tomescu *et al.*, 2018), which is in sharp contrast with the diversity of Cenozoic mosses. Hence, each new discovery of pre–Cenozoic mosses is of great value for understanding the diversity and evolutionary trends of this class in the geological period.

The assignment of Palaeozoic and Mesozoic mosses to extant taxa is of great difficulties. Nevertheless, the similarity of some fossils with modern taxa makes it possible to reveal the diversity of fossil mosses and the evolution of this plant group. For example, the cellular details of type B–IIa leaves from the Lower Carboniferous (Visean) of eastern Germany resemble representatives of the extinct order Protosphagnales Neuburg (Hübers *et al.*, 2013), and are possibly the ancestors of both *Sphagnum* and non–*Sphagnum* mosses. *Baigulia* Ignatov *et al.* and *Bryokhutuliinia* Ignatov, which are discovered in the Upper Jurassic of Transbaikalia (Russia), have highly branched gametophytes (Ignatov *et al.*, 2011). Among them, *Bryokhutuliinia crassimarginata* Ignatov *et al.* has sporophytes that develop on reduced lateral shoots of gametophytes (Ignatov *et al.*, 2012). These fossils, together with the Cretaceous genus *Vetiplanaxis* N.E. Bell (Bell & York, 2007; Hedenäs *et al.*, 2014), are supposed to be pre–Cenozoic bryophytes related to pleurocarpous mosses.

To date, the diversity of Jurassic mosses is limited to 13 genera, including 17 species (Table 1) (Ignatov, 2013; Ignatov & Maslova, 2021). Among them, only a few preserved diagnostic features to be assigned to extant families. For example, isolated capsules of *Kulindobryum* Ignatov from the Middle or Upper Jurassic of Transbaikalia (Russia) are comparable to some modern species of *Tayloria* Hooker (Splachnaceae) (Mamontov & Ignatov, 2019). *Heinrichsiella* Bippus *et al.* from the Upper Jurassic of Argentina probably belongs to the family Polytrichaceae or Timmiellaceae (Bippus *et al.*, 2019), while the *Stachybryolites* Wu *et al.* from the Lower Jurassic of China belongs to Dicranaceae s.l. (Wu *et al.*, 2000). The information available to date is not sufficient to understand the taxonomic diversity and evolution of Jurassic mosses.

Most of the known Jurassic bryophytes come from the Upper Jurassic of China, Mongolia, and Asiatic Russia (Table 1). Bryophytes of the Early Jurassic are not known in Siberia. This work describes two new Early Jurassic species of mosses *Bryokhutuliinia ignatovii* sp. nov., and *Palaeodichelyma kiritchkovae* sp. nov., which are discovered in Siberia (Irkutsk Coal Basin) for the first time. To date, these are the only two reliably known species of the bryophyte flora that lived in the Early Jurassic within the Siberian palaeofloristic region.

GEOLOGICAL SETTINGS AND AGE

The Irkutsk Coal Basin is located in the south of the Siberian Platform and extends along the Eastern Sayan Mountains. The Early–Middle Jurassic sediments of the basin are subdivided into Cheremkhovo, Prisayan and Kuda formations (Skoblo *et al.*, 2001; Frolov & Mashchuk, 2018). The fossil materials come from the Prisayan Formation, which is an alluvial megacycle that begins with channel sediments (Lower Subformation), passes into predominantly floodplain (Middle Subformation) and ends with lacustrine–marsh ones (Upper Subformation). According to palaeobotanical and palynological data, the age of Prisayan Formation ranges from the upper Pliensbachian to the Aalenian (Frolov *et al.*, 2022).

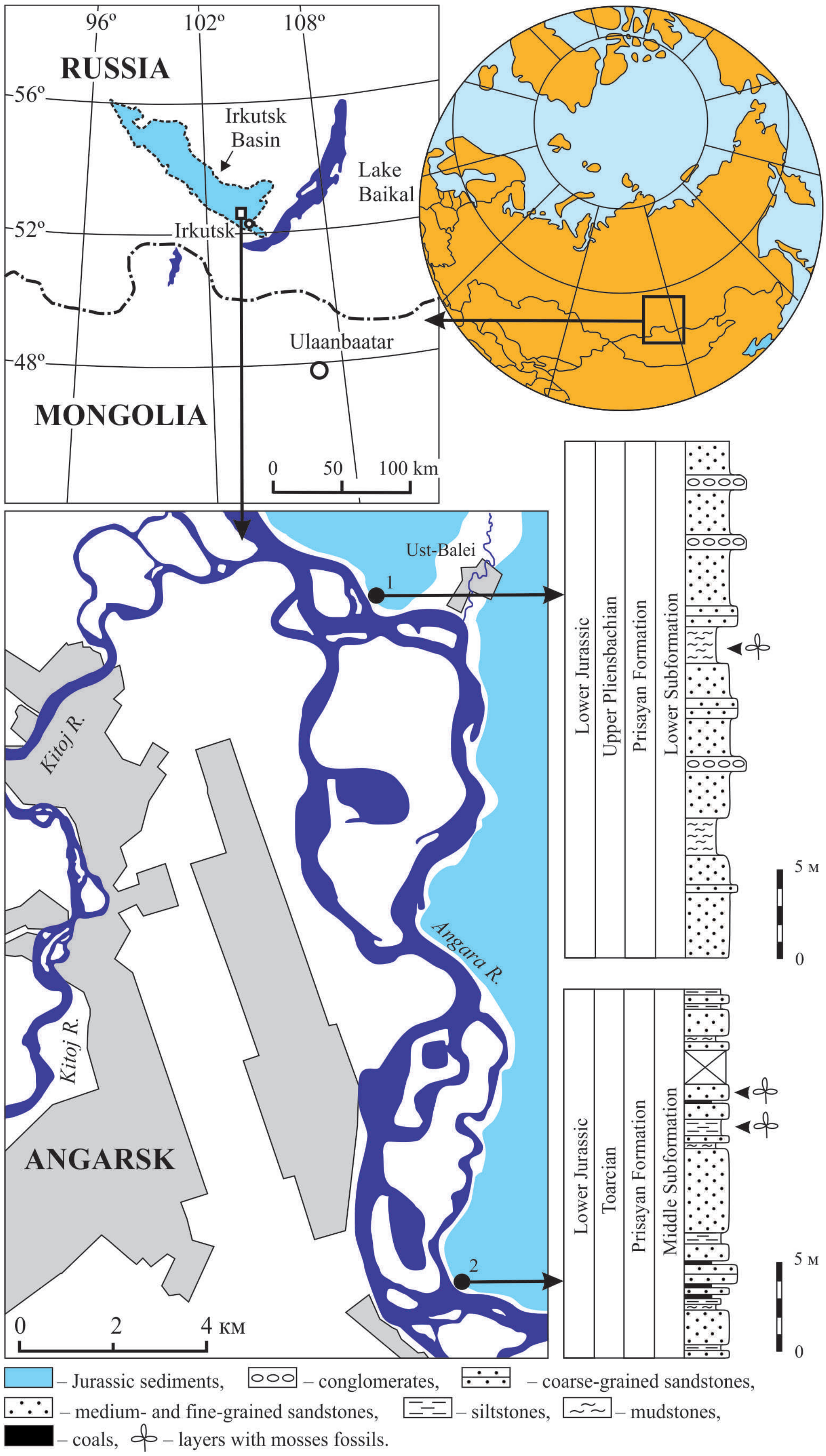
Palaeodichelyma kiritchkovae is collected from the natural outcrop of the Lower Subformation of Prisayan Formation, located on the right bank of Angara River, near the Ust–Baley Village (52°37'34" N, 103°58'07" E) (Fig. 1). Here, the subformation consists of a thick (up to 20 m) sequence

Table 1—Diversity of Jurassic representatives of Bryophyta.

Genus	Number of species	Locality	Geological age	Reference(s)
Baigulia Ignatov *et al.*	1	Russia (Transbaikalia)	J_3	Ignatov *et al.*, 2011
Baiguliella Ignatov *et al.*	1	Russia (Transbaikalia)	J_3	Ignatov *et al.*, 2011
Bryokhutuliinia Ignatov	3	Mongolia, Russia (Transbaikalia)	$J_{2–3}$	Ignatov, 1992; Ignatov *et al.*, 2012
Heinrichsiella Bippus *et al.*	1	Argentina (Santa Cruz)	J_3	Bippus *et al.*, 2019
Kulindobrium Ignatov	1	Russia (Transbaikalia)	J_3	Mamontov & Ignatov, 2019
Mnioites Wu *et al.*	1	China	J_1	Wu *et al.*, 2000
Muscites Brongniart, 1828	3	China, Russia (Bureja, Transbaikalia)	J_3 or K_1	Krassilov, 1973; Wu, 1999
Ningchengia Heinrichs *et al.*	1	China	J_3	Heinrichs *et al.*, 2014
Palaeodichelyma Ignatov & Shcherbakov	1	Russia (Transbaikalia)	J_3 or K_1	Ignatov & Shcherbakov, 2007
Sphagnum L.	1	Germany	J_1	Reissinger, 1950
Stachybryolites Wu *et al.*	1	China	J_1	Wu *et al.*, 2000
Tricostium Krassilov	1	Russia (Bureja)	J_3	Krassilov, 1973
Yorekiella Krassilov	1	Russia (Bureja)	J_3	Krassilov, 1973

⟶

Fig. 1—Geographical position and lithological structure of Jurassic mosses location on the right bank of the Angara River. (1) outcrop near of Ust–Baley Village; (2) outcrop at Sukhov Cape.



96°
102°
108°
RUSSIA
56°
52°
48°
Irkutsk Basin
Lake Baikal
Irkutsk
Ulaanbaatar
MONGOLIA
0 50 100 km
Ust-Balei
1
2
Kitoj R.
Angara R.
ANGARSK
0 2 4 км
Lower Jurassic
Upper Pliensbachian
Prisayan Formation
Lower Subformation
Toarcian
Middle Subformation
5 м
0
– Jurassic sediments,
– conglomerates,
– coarse-grained sandstones,
– medium- and fine-grained sandstones,
– siltstones,
– mudstones,
– coals,
– layers with mosses fossils.

of coarse–and medium–grained, cross–bedded sandstones containing two lenses of horizontally bedded siltstones and mudstones. Silty lenses contain abundant plant remains, including *Lycopodites tenerrimus* Heer, *L. trichiatus* Prynada emend. A. Frolov & Mashchuk, *Phyllotheca sibirica* Heer, *Coniopteris murrayana* (Brongniart) Brongniart, *Ginkgoites concinna* (Heer) Seward emend. Kostina, *G. sibirica* (Heer) Sew., *Sphenobaiera czekanowskiana* (Heer) Florin, *Sorosaccus gracilis* Harris emend. Liu *et al.*, *Czekanowskia rigida* Heer, *Leptostrobus laxiflora* Heer, *Elatides ovalis* Heer, *Ixostrobus heeri* Prynada, *Carpolithes deplanatus* Prynada, *C. cinctus* Nathorst, *Samaropsis rotundata* Heer. Among them *Phyllotheca sibirica, Coniopteris murrayana* and *Sphenobaiera czekanowskiana* are the dominant species for beds bearing *Coniopteris murrayana* and *Sphenobaiera czekanowskiana*. The age of the Lower Subformation of Prisayan Formation is constrain within the upper Pliensbachian (Frolov *et al.*, 2022).

Bryokhutuliinia ignatovii is collected from the Middle Subformation of the Prisayan Formation, which exposed in the natural outcrop Sukhov Cape (52°30'18.3" N, 103°59'00.6" E), also located on the right bank of the Angara River (Fig. 1). The subformation is represented here by a sequence of fine–grained gently undulating and horizontally layered sandstones up to 20 m thick. Among the sandstones, in the middle part of the section, there are two thin (up to 0.1 m) coal interlayers. In its upper part, there are lenses of siltstones and mudstones with plant remains: *Equisetites lateralis* (Phillips) Phillips, *Coniopteris maakiana* (Heer) Prynada emend. Kiritchkova and Travina, *C. murrayana*, *Lobifolia* sp., *Cladophlebis williamsonii* Brongniart, *Cladophlebis haiburnensis* (Lindley & Hutton) Seward, *Cl. nebbensis* (Brongniart) Nathorst, *Raphaelia* cf. *diamensis* Seward, *Raphaelia tapkensis* (Heer) Prynada emend. Kostina, *Czekanowskia rigida*, *Phoenicopsis angustifolia* Heer, *Ixostrobus* sp., *Pityophyllum* ex gr. *nordenskioldii* (Heer) Nathorst, *Podozamites* sp., *Carpolithes heeri* Prynada. Among them *Coniopteris maakiana, Raphaelia diamensis, R. tapkensis, Cladophlebis nebbensis*, *C. williamsonii* and *Phoenicopsis angustifolia* are the key species for beds with *Coniopteris snigirevskiae.* The age of the Middle Subformation of Prisayan Formation is constrain within the Toarcian (Frolov *et al.*, 2022).

MATERIALS AND METHODS

Fossil mosses material is presented on 16 rocks of fine–grained siltstones and mudstones. Among them, 11 specimens are well preserved and show a leaf cellular structure. The thicker parts of the shoot (stem and sporophytes) are seriously carbonized, so their cellular details cannot be recognized. The impressions were studied in reflected light using a MBS–10 stereomicroscope and a Micromed 3 Led M microscope, which are part of the equipment of the Centre of Geodynamics and Geochronology of the Institute of the Earth's Crust of the Siberian Branch of the Russian Academy of Sciences (Irkutsk). Moss photographs were taken using a Canon EOS 650D digital camera and a ToupCam 8.0 MP digital video eyepiece. The samples are stored at the Institute of the Earth's Crust SB RAS (Irkutsk), coll. No. U–B, 2700, 2008–UB, 2020–SM.

SYSTEMATIC PALAEONTOLOGY

Division—BRYOPHYTA

Class—BRYOPSIDA Rothmaler, 1951

Order—INCERTAE SEDIS

Family—INCERTAE SEDIS

Genus—BRYOKHUTULIINIA Ignatov, 1992

Type Species—*Bryokhutuliinia jurassica* Ignatov, Upper Jurassic, Mongolia

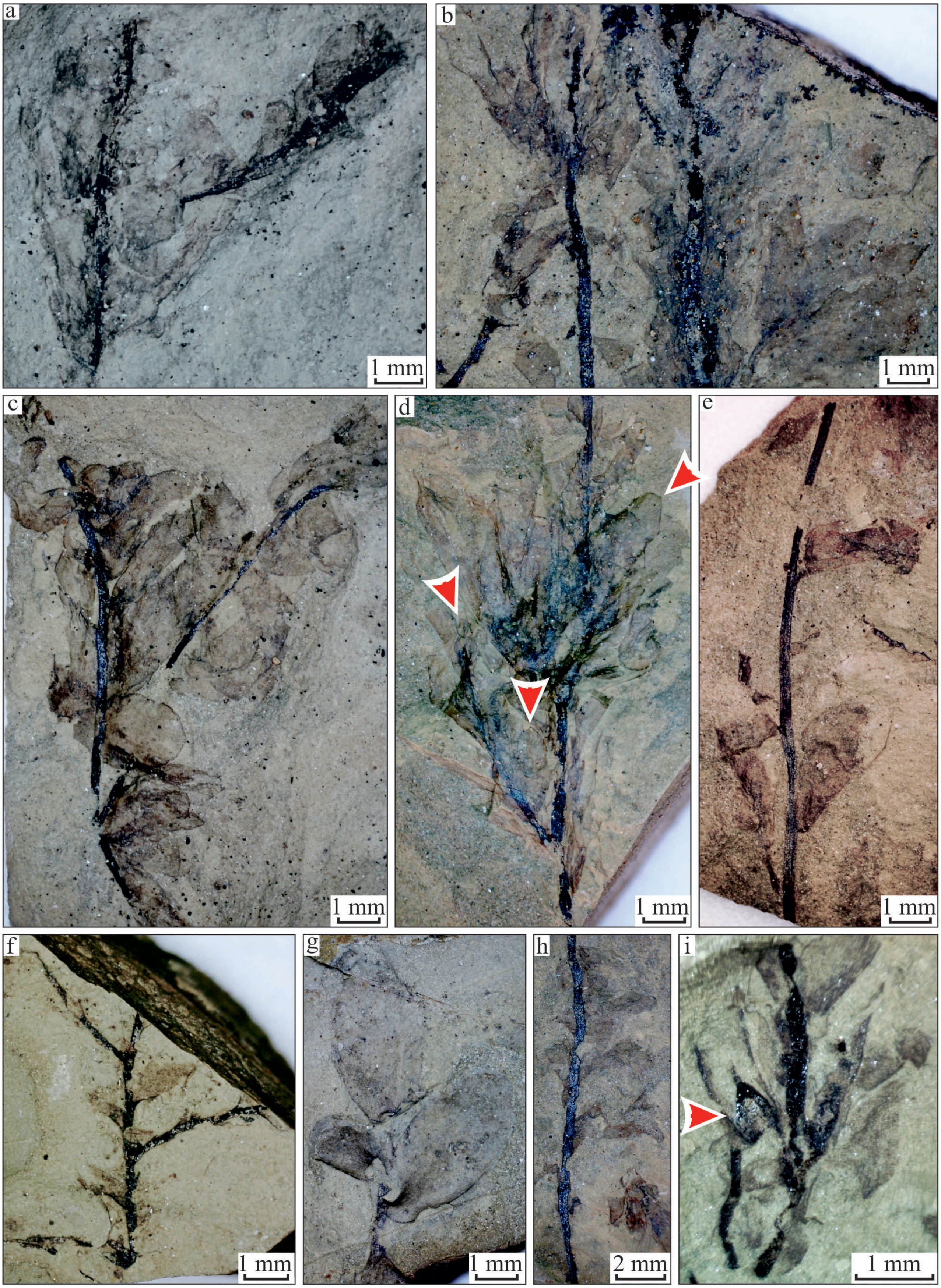
Bryokhutuliinia ignatovii sp. nov.

(Figs 2, 3, 6 b–d)

Diagnosis—Gametophytes simple or monopodially branching. Leaves oblong or tongue–shaped, bordered, entire, spaced to recurved and arranged on stems in spiral order. Leaf bases sharply narrowed, slightly clasping. Leaf apices wide, obtuse, often with weakly cuspidate tip. Cell thin–walled, elongated and short–rectangular and isodiametric forming oblique rows. Sporophytes lateral. Capsules erect, shortly cylindrical, and sessile, on tops of short branches. Operculum conic and shortly rostrate.

⟶

Fig. 2—*Bryokhutuliinia ignatovii* sp. nov. (a–h) leafy gametophytes. The leaves which have weakly cuspidate tips at the apices are shown by arrows. (a) specimen no. 2020–SM/14–77. (b) specimen no. 2020–SM/14–76. (c) specimen no. 2020–SM/14–74 (holotype). (d) specimen no. 2020–SM/14–81. (e) specimen no. 2020–SM/14–80. (f, g) specimen no. 2020–SM/18–30. (h) specimen no. 2020–SM/14–78. (i) gametophyte with lateral sporophyte, specimen no. 2020–SM/14–76. The capsule is shown by an arrow.


a
1 mm
b
1 mm
c
1 mm
d
1 mm
e
1 mm
f
1 mm
g
1 mm
h
2 mm
i
1 mm

Derivation of Name—In honour of the Russian bryologist M.S. Ignatov.

Holotype—No. 2020–SM/14–74, Fig. 2c; Fig. 3d, h, k.

Other Material—Specimen No. 2020–SM/14–77 (Fig. 2a), 2020–SM/14–76 (Figs 2b; 3i), 2020–SM/14–81 (Fig. 2d), 2020–SM/14–80 (Fig. 2e), 2020–SM/18–30 (Figs 2f, g; 3a, b) 2020–SM/14–78 (Fig. 2h), 2020–SM/14–76 (Fig. 2i), 2020–SM/14–31 (Fig. 3c, f, g), 2020–SM/14–82 (Fig. 3e, j). The specimens are stored in Institute of the Earth's Crust Siberian Branch of the Russian Academy of Sciences.

Type Locality—Russia, Eastern Siberia: Irkutsk Coal Basin, right bank of the Angara River, Sukhov cape locality, (52°30'12.6" N, 103°59'07.4" E).

Horizon—Middle Subformation of Prisayan Formation.

Age—Early Jurassic (Toarcian).

Description—Gametophytes are tender, leafy, simple or monopodially branching. They are up to 17 mm. The width of the main and lateral stems is 0.5 mm. The lateral stems arise at an acute angle (25–60°, usually 45°). The surface of the stems is covered with fine longitudinal striation (Fig. 2e), which is visible in some specimens. The leaves are oblong or tongue–shaped in outline, without costa, thin, borded, with an entire margin and arranged relatively closely on stems in spiral order. They are attached to the stem at an angle of 30–45°, rarely 50–60°, straight (Fig. 2a, d, f, g), and less often recurved (Fig. 2c, e). Leaf apices are wide, obtuse (Figs 2c, g; 3g, h), often with weakly cuspidate tip (Fig. 2d), sharply narrowed bases, slightly clasping the stem (Fig. 3a–e). Leaves are 3–5 × 2 mm in size.

The leaf blade is unistratose, composed of thin–walled, elongated, short–rectangular and isodiametric cells. Short–rectangular and isodiametric cells are mainly constrained at the base and apex (Fig. 3a–j). The margins and middle parts of the blades are composed of elongated rectangular cells (Fig. 3f, k, i). Sometimes short–rectangular and isodiametric cells occur in the middle part of the plate, forming oblique rows (Fig. 3i). The rectangular elongated cells are 80–160 (usually 90–100) µm long and 20–40 (usually 30) µm wide. Isodiametric and short rectangular cells are 40–60 × 20–50 µm in size. The border formed by two rows of prosenchymal cells reaches 20–30 µm in width.

Lateral branches with sporophytes are 0.4–0.5 mm long. Capsule is sessile, erect, shortly cylindrical, 0.8–1.3 mm long and 0.3–0.5 mm wide. Operculum is conic and shortly rostrate (Fig. 2i).

Genus—**PALAEODICHELYMA** Ignatov & Shcherbakov, 2007

Type Species—***Palaeodichelyma sinitzae*** Ignatov & Shcherbakov, Lower Cretaceous, Transbaikalia

Palaeodichelyma kiritchkovae sp. nov.

(Figs 4, 5, 6a, e–g)

Diagnosis—Gametophytes leafy, simple or irregularly branched. Leaves lanceolate, keeled, intermittently bordered, declined and entire, with a slightly clasping base and gradually narrowed, acute apex, arranged relatively closely on the stems in spiral order. Costa does not reach the leaf apex. Leaf blade composed of thin–walled, elongated cells. Sporophytes lateral. Seta quite long, surrounded by perichecial leaves covering the base of the capsule. Capsules erect, shortly cylindrical or oval. Operculum conic and shortly rostrate.

Derivation of Name—In honour of the Russian palaeobotanist A.I. Kiritchkova.

Holotype—No. 2700–2a, Figs 4a–f, h, i, l, m; 5d, f, g, i, j.

Other Material—Specimen No. 2700–3a (Figs 4g; 5a–c, h), UB/54 (Figs 4j, k, n, o; 5e), 2008UB–8/15 (Figs 4p; 5k). The specimens are stored in Institute of the Earth's Crust 172 Siberian Branch of the Russian Academy of Sciences.

Type Locality—Russia, Eastern Siberia: Irkutsk Coal Basin, right bank of the Angara River, 1.3 km below the Ust–Baley Village, 52°37'34" N, 103°58'07" E.

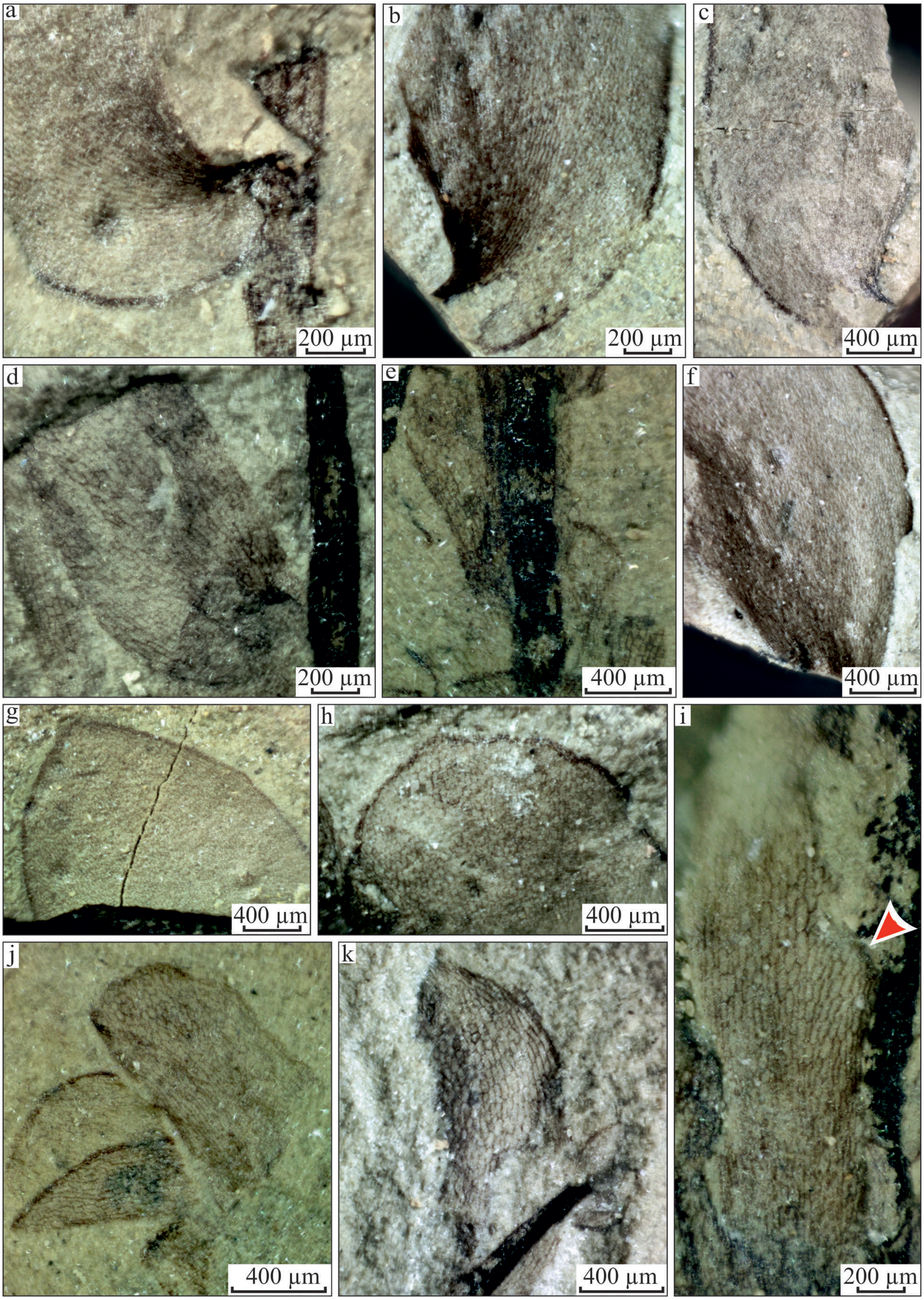
Horizon—Lower Subformation of Prisayan Formation.

Age—Early Jurassic (upper part of Upper Plinsbachian).

Description—Gametophytes are tender, leafy, and simple and rarely irregularly branching (Figs 4a; 5a). The branches are up to 40–45 mm in length. Lateral stems arise at an acute angle (20°) and have the same width (0.3–0.4 mm) with the main stem. The leaves are lanceolate, keeled, thin and declined, with an entire margin and arranged relatively closely on the stems in a spiral order (Figs 4d–g; 5b, c). Their bases slightly clasp the stem (Figs 4f, g; 5e, g) and the apices are gradually narrowed and sharp (Fig. 5c, d). In the lower part of the leaf, there is an obscure mid–costa, which is absent in its upper part (Figs 4c, f; 5b, f–j). Costa width is 50–100 µm. There is an intermittent thin (50 µm) border on some leaves (Figs 4d; 5e, g). Leaf sizes vary from 3.5 × 0.7 to 4.5

⟶

Fig. 3—*Bryokhutuliinia ignatovii* sp. nov. (a–e) leaf bases, slightly clasping the stem. The cellular structure and border are observed. (a, b) specimen no. 2020–SM/18–30. (c) specimen no. 2020–SM/18–31. (d) specimen no. 2020–SM/14–74 (holotype). (e) specimen no. 2020–SM/14–82. (g, h, j) cellular structure of leaf apices. (g) specimen no. 2020–SM/18–31. (h) specimen no. 2020–SM/14–74 (holotype). (j) specimen no. 2020–SM/14–82. (f, i, k) cellular structure of the leaf middle parts. The oblique rows of cells are shown by arrows. (f) specimen no. 2020–SM/18–31. (i) specimen no. 2020–SM/14–76. (k) specimen no. 2020–SM/14–74 (holotype).


a
200 μm
b
200 μm
c
400 μm
d
200 μm
e
400 μm
f
400 μm
g
400 μm
h
400 μm
i
200 μm
j
400 μm
k
400 μm

× 1.2 mm. Lamina is unistratose, composed of thin–walled, elongated cells that are 50–140 × 10–30 µm in size (Fig. 4p).

Lateral sporophytes are 2.8 mm long (Fig. 4b, c, h–o). The setae are long (2–2.5 mm), surrounded by tightly pressed perichecial leaves (Fig. 4h, i, k–o) with acute apices. Due to the fact that the perichecial leaves are tightly attached the seta, their shape and size cannot be estimated. Capsules are sessile, shortly cylindrical or oval, 1.1–1.4 × 0.8 mm (Fig. 4h–o). Operculum is conic and shortly rostrate (Fig. 4h, j, l, n).

COMPARISONS AND DISCUSSION

In the Early and Middle Jurassic of Siberia, the bryophytes were represented exclusively by thalloid bryophyte remains of the genera *Marchantites* Brongniart, *Ricciopsis* Lundblad, *Hepaticites* J. Walton, and *Thallites* Kidston ex J. Walton (Prinada, 1962; Teslenko, 1970; Kiritchkova *et al.*, 1992, 2005; Frolov & Mashchuk, 2018). The presence of bryophytes in the flora was evidenced by numerous and taxonomically diverse spores of *Stereisporites* Pflug (Ankudimova *et al.*, 1982; Ilyina, 1985; Shurygin *et al.*, 2000; Frolov *et al.*, 2022). *Bryokhutuliinia ignatovii* and *Palaeodichelyma kiritchkovae* are the first known megafossils of bryophytes from the Lower Jurassic of Siberia. These species expand our knowledge of the pre–Cenozoic bryoflora that is still insufficiently studied.

The studied samples are assigned to the genus *Bryokhutuliinia* based on the structural features of the leaves. *Bryokhutuliinia* has a distinct border along the entire length of the leaf blade, elongated rectangular cells and no costa (Ignatov, 1992). The same features are observed in our specimens.

B. ignatovii, found in the Lower Jurassic (Toarcian) of the Irkutsk Basin, is the most ancient representative of this genus that inhabited in Siberia. Probably, during the Jurassic, the genus *Bryokhutuliinia* was widespread within the Siberian palaeofloristic region and covered the Siberia, Transbaikalia, and Mongolia areas. The presence of a number of morphological features characteristic of pleurocarp mosses in *Bryokhutuliinia* species, such as the general appearance and branching of the gametophyte and presence of elongated leaf cells, suggests that they belonged to this group. However, the absence of diagnostic feature of sporophyte in *Bryokhutuliinia crassimarginata* (Ignatov *et al.*, 2012) makes it impossible to ensure the phylogenetic position of these mosses. The lateral arrangement of sporophyte–bearing branches is also found in acrocarp mosses (Fissidentaceae, Grimmiales, and some others). In addition, the absence of a costa implies that *Bryokhutuliinia* possibly belongs to acrocarp mosses of the order Hookeriales (Ignatov & Shcherbakov, 2007). Recent studies have shown that most of the features of *Bryokhutuliinia* indicate that it belongs to the Dicranidae, but assignment to the Bryidae may also be possible (Mamontov & Ignatov, 2019). The characteristics of *Bryokhutuliinia* also do not allow us to assign it to any of these subclasses. Based on such features as regular pinnate branching, the shape of the leaves, and the pattern of the cellular network of the leaf, we consider it more likely belongs to Bryidae. However, assignment of *Bryokhutuliinia* to Dicranidae is also not excluded. Fig. 6b–d shows a restoration of the natural habit of *B. ignatovii*.

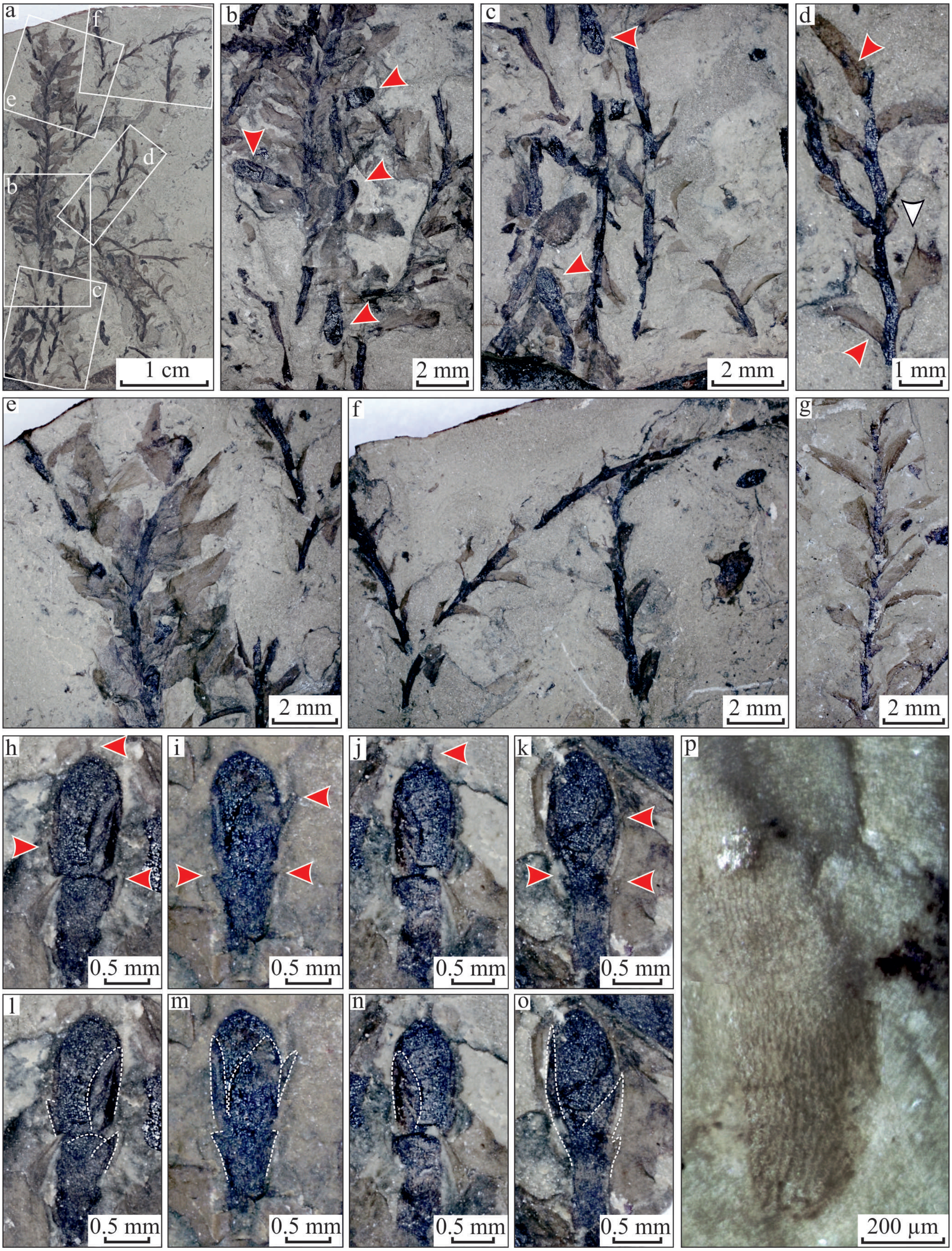
Baigulia complanata Ignatov *et al.* from the Upper Jurassic of Transbaikalia (Ignatov *et al.*, 2011) differ from *Bryokhutuliinia ignatovii* in the absence of a leaf border. Leaves of *Baiguliella minuta* Ignatov *et al.* from the Upper Jurassic of Transbaikalia (Ignatov *et al.*, 2011) have a weak and indistinct costa and do not have a border. On the contrary, the *B. ignatovii* leaves are bordered and do not have a costa.

The most similar to *Bryokhutuliinia ignatovii* is *Bryokhutuliinia obtusifolia* Ignatov & Shcherbakov, known from the Lower Cretaceous of Transbaikalia (Ignatov & Shcherbakov, 2011). The similarities include the presence in both species of tongue–shaped leaves with slightly clasping bases and rectangular cells of the leaf blade. The size of the leaves in these species is also almost the same (Table 2). *B. obtusifolia* differs from the new species in a smaller stem width (0.3–0.4 mm), far–spaced leaves, a broadly rounded apex, and smaller rectangular leaf cells (60–90 × 13–20 µm) (Table 2). *B. ignatovii* is characterized by a large width (0.5 mm) of the stems, a wide and blunt apex, sometimes with weakly cuspidate tip and the presence of isodiametric cells. In addition, the stem of *B. obtusifolia* may terminate with leaf rosettes, which is not seen in *B. ignatovii*.

The capsules of *Bryokhutuliinia crassimarginata* Ignatov *et al.* from the Middle or Upper Jurassic of Transbaikalia (Ignatov *et al.*, 2012), have the same structure as those of *B. ignatovii*, that is shortly cylindrical with conic operculum and shortly rostrate. *B. crassimarginata* is characterized by a two–row leaf arrangement, ovate–oblong or ovate–lanceolate leaves with a gradually narrowed obtuse apex, and thin stems (0.15–0.7 mm). These features clearly distinguish it from *B. ignatovii*, which has oblong or tongue–shaped leaves with

⟶

Fig. 4—*Palaeodichelyma kiritchkovae* sp. nov. (a) leafy gametophytes. (b, c) areas of the gametophyte with lateral sporophytes (shown by arrow). (d, f, g) young stems with underdeveloped leaves. The leaf with a partial border is shown by white arrow and leaves with mid–costa are shown by red arrows in (d). (e) stems with fully developed leaves. (h–o) lateral sporophytes. The apices of perichecial leaves (h, i, k) and shorlty rostrate operculum (h, j) are shown by arrows. The perichecial leaves contour are shown with a dotted line (l–o). (p) leaf cellular structure. (a–f, h, i, l, m) specimen no. 2700–2a (holotype). (g) specimen no. 2700–3a. (j, k, n, o) specimen no. UB/54. (p) specimen no. 2008UB–8/15.


a
f
e
d
b
c
1 cm
b
2 mm
c
2 mm
d
1 mm
e
2 mm
f
2 mm
g
2 mm
h
0.5 mm
i
0.5 mm
j
0.5 mm
k
0.5 mm
p
l
0.5 mm
m
0.5 mm
n
0.5 mm
o
0.5 mm
200 µm

a wide and blunt apex and arranged spirally on wider (0.5 mm) stems. In addition, the width of rectangular cells of *B. crassimarginata* is 11–20 µm, while those of *B. ignatovii* are wider (30–40 µm) (Table 2).

Bryokhutuliinia jurassica Ignatov from the Upper Jurassic or Lower Cretaceous of Mongolia (Ignatov, 1992), is characterized by narrowly lanceolate leaves with decurrent bases and gradually narrowed, blunt apexes. For *B. ignatovii*, the leaves are oblong and tongue–shaped, with slightly clasping bases, and broad and blunt apices, and sometimes with weakly cuspidate tip (Table 2). These features distinguish *B. ignatovii* from *B. jurassica.*

The ovate–elongated leaves of *Bryokhutuliinia ingodensis* (Srebrodolskaya) Ignatov, which is common in the Upper Jurassic or Lower Cretaceous of Transbaikalia (Ignatov *et al.*, 2011), are densely arranged (4–7 leaves per 5 mm). On the contrary, the leaves of *B. ignatovii* are sparse (up to 4 per 5 mm) and oblong or tongue–shaped. In addition, the leaf apexes of *B. ingodensis* are blunt without weakly cuspidate tip, and the hexagonal–rectangular cells are smaller than those of *B. ignatovii* (Table 2).

The samples of *Palaeodichelyma kiritchkovae* shown in Fig. 4a and Fig. 5a–c were previously attributed to lycopsids *Lycopodites tenerrimus* Heer (Frolov & Mashchuk, 2018, 2019). Additional study of these samples revealed the presence of capsules and a mid–costa on the leaves. This indicates that these fossils belong to true bryophytes. Other samples given in the Frolov and Mashchuk (2018, 2019) belong to *L. tenerrimus*, because their leaves have no median vein and border, and their reproductive organs are unknown. The lanceolate leaves with acute apex, an interrupted border and a long (almost reaching the apex) mid–costa allow us to assign the specimens to the genus *Palaeodichelyma*, which is characterized by such a combination of characters (Ignatov & Shcherbakov, 2007). The single representative of the genus *Palaeodichelyma* from the Upper Jurassic and Lower Cretaceous of Transbaikalia (Ignatov & Shcherbakov, 2007, 2011) differs from *Palaeodichelyma kiritchkovae* for having ovoid leaves and lack of capsules. In addition, the leaf cells of *P. kiritchkovae* are elongated, while those of *P. sinitzae* Ignatov & Shcherbakov are rectangular.

None of the numerous capsules of *P. kiritchkovae* clearly shows the place where the operculums attach to the capsules. Therefore, it can be assumed that the apical rostrum (Fig. 4h, j, l, n) refers to the caliptra and not to the operculum. Additional samples are needed to confirm this assumption.

For now, *Palaeodichelyma kiritchkovae* is the oldest (Pliensbach) record of the Jurassic moss in Siberia. It is the second member of the genus *Palaeodichelyma* known to date. Taking into account the time interval of *P. kiritchkovae* and *P. sinitzae* (Ignatov & Shcherbakov, 2007, 2011), it can be assumed that this genus existed in Siberia and Transbaikalia during the Jurassic to the Early Cretaceous. *P. sinitzae* has features suggestive of pleurocarp mosses, such as lateral nodular structures. This species has trifoliate phyllotaxis, long mid–costa, keeled leaves, and elongated lamellar cells, which are characteristics of pleurocarp mosses of the family Fontinalaceae (Ignatov & Shcherbakov, 2007). However, the assignment of this genus to pleurocarp mosses is speculative, since the true nature of the lateral nodular structures of *P. sinitzae* is unknown. The laterally arranged sporophytes of *P. kiritchkovae*, which consist of a capsule and a seta surrounded by perichecial leaves, resemble those of modern *Fontinalis*. It allows us to confidently assign *Palaeodichelyma* to pleurocarp mosses. Fig. 6a, e–g shows a restoration of the natural habit of *P. kiritchkovae*.

Muscites ostracodiferus Krassilov from the Cretaceous of Mongolia (Krassilov, 1982) is similar to *P. kiritchkovae*. Both species have lanceolate leaves with a gradually narrowed apex and a long mid–costa. The leaves of *M. ostracodiferus* are long and narrow (5–6 × 0.5–0.6 mm) with an amplexicaul base, while the leaves of *P. kiritchkovae* are short and wide (3.5–4.5 × 0.7–1.2), with a base slightly clasping the stem and a border. In addition, the cell structure of the leaf blade and sporophytes of *P. kiritchkovae* is known.

CONCLUSION

The discovery of the first two species of mosses *B. ignatovii* and *P. kiritchkovae* in the Lower Jurassic of the Irkutsk Basin is a significant step forward in understanding the history and diversity of this group in the Jurassic of Siberia. New species have sporophytes in addition to gametophytes. These findings indicate that the genera *Palaeodichelyma* and *Bryokhutuliinia* are possibly appearing in the Early Jurassic and more widespread in Siberia than previously thought.

⟶

Fig. 5—*Palaeodichelyma kiritchkovae* sp. nov. (a–c) leafy gametophytes. The mid–costa (b) and acute leaf apex (c) are shown by arrows. (d) leaf with acute apex shown by an arrow. (e) leaf base with a thin border shown by an arrow. (f–j) leafy shoots close up. The leaf with a partial border is shown by white arrow in (g) and leaves with mid–costa are shown by red arrows in (f–g). (k) young stems with underdeveloped leaves. (a–c, h) specimen no. 2700–3a. (d, f, g, i, j) specimen no. 2700–2a (holotype). (e) specimen no. UB/54. k–2008UB–8/15.

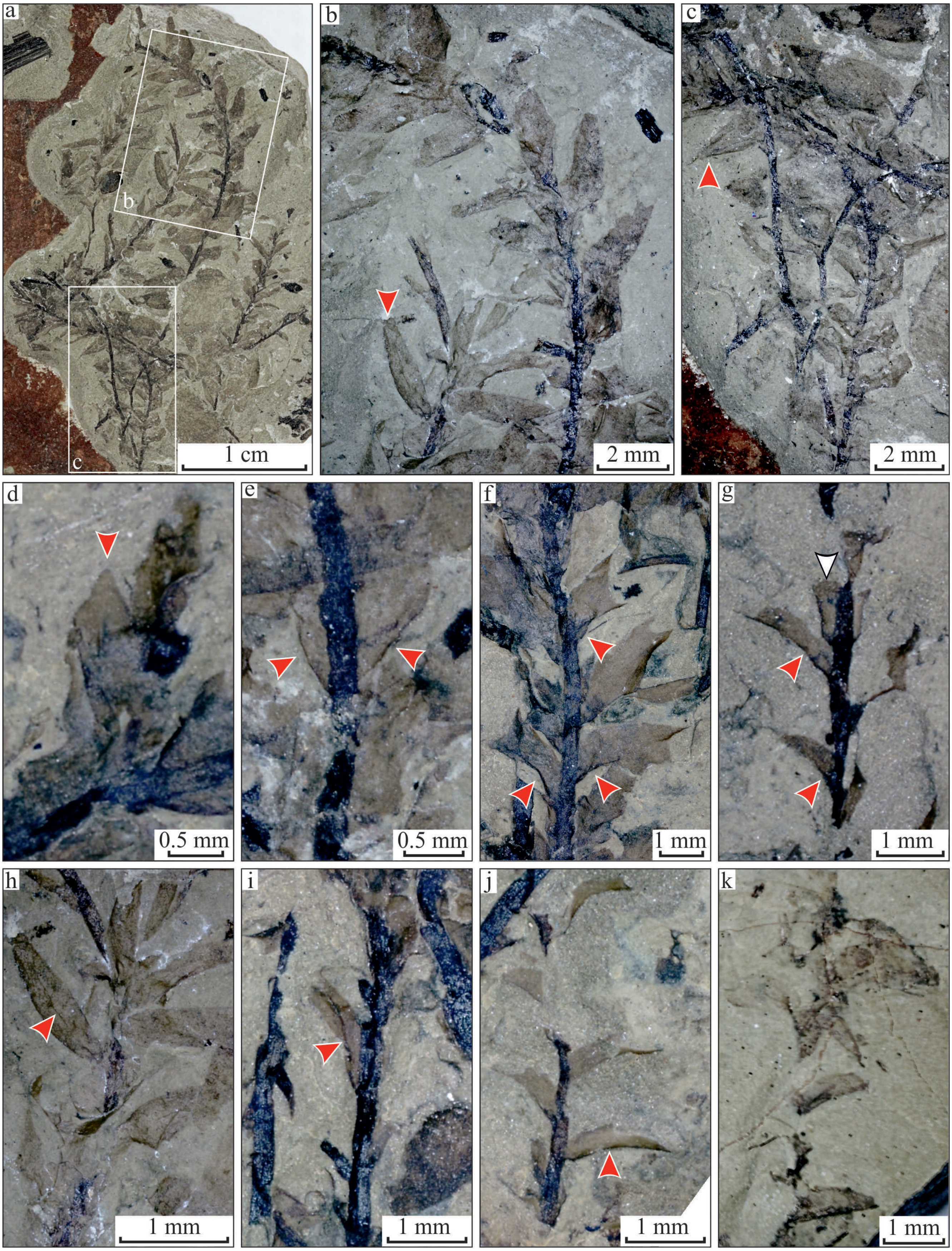

a
b
c
1 cm
2 mm
2 mm
d
e
f
g
0.5 mm
0.5 mm
1 mm
1 mm
h
i
j
k
1 mm
1 mm
1 mm
1 mm

Table 2—Comparison of stem morphology and cellular structure of *Bryokhutuliinia ignatovii* sp. nov. with other *Bryokhutuliinia* species.

Features \ Species	***B. ignatovii* sp. nov.**	***B. obtusifolia* Ignatov & Shcherbakov**	***B. ingodensis* (Srebrodolskaya) Ignatov**	***B. jurassica* Ignatov**	***B. crassimarginata* Ignatov *et al.***
Stem					
Branching	Monopodial	Monopodial	Monopodial	Monopodial	Monopodial
Distance between lateral branches, mm	2	–	2	–	–
Width, mm	0.5	0.3–0.4	0.32–0.40	0.4–0.5	0.15–0.7
Number of leaves in middle part of stem per 5 mm	4	–	4–7	–	–
Leaves					
Arrangement	Spiral	Spiral	Spiral	Distichous	Clearly distichous
Shape	Oblong, lingulate	Ovate–elongate to lingulate	Ovate–elongate	Narrow–lanceolate	Ovate–oblong to ovate–lanceolate
Leaves deviating angle	30–45°, rare 50–60°	55–80°, in abruptly reflexed leaves 150°	55–80°	20–35°	55–80°
Base	Sharply narrowed, somewhat clasping	Somewhat clasping, plane or only weakly concave	Slightly tapered, somewhat concave	Obovate, triangular	Rounded towards cordate or clasping
Apex	Wide, obtuse, with weakly cuspidate tip	Broadly rounded or occasionally apiculate	Blunt	Somewhat rounded	Obtuse
Size, mm	3–5 × 2	3–4 × 1.5–2.1	4.0–4.7 × 1.0–1.3	5 × 1.2	3.0–4.0 (6.0) × × 1.0–1.3 (2.1)
Margin	Entire	Entire	Entire	Entire	Entire
Border width, µm	20–30	50	50	30–50	150–200 at base, 60–100 at apex
Shape of lamina cells	Rectangular, isodiametric	Rectangular	Hexagonal–rectangular	Rectangular	Rectangular
Cell sizes, µm	Rectangular cells: 80–160 × 20–40 (30), isodiametric cells: 40–60 × 20–50	60–90 × 13–20, wider at base (30–42)	60–105 × 18–23	100–150 × 20–30	60–100 × 11–20
Sporophytes					
Capsules	Shortly cylindric with conic and shortly rostrate operculum	Unknown	Unknown	Unknown	Cup–like to shortly cylindric with conic and shortly rostrate operculum
Age and locality	Lower Jurassic (Toarcian), Eastern Siberia, Russia	Lower Cretaceous, Transbaikalia, Russia	Upper Jurassic or Lower Cretaceous, Transbaikalia, Russia	Upper Jurassic or Lower Cretaceous, Mongolia	Middle or Upper Jurassic, Transbaikalia, Russia
Reference	Present article	Ignatov & Shcherbakov, 2011	Ignatov *et al.*, 2011	Ignatov, 1992	Ignatov *et al.*, 2012

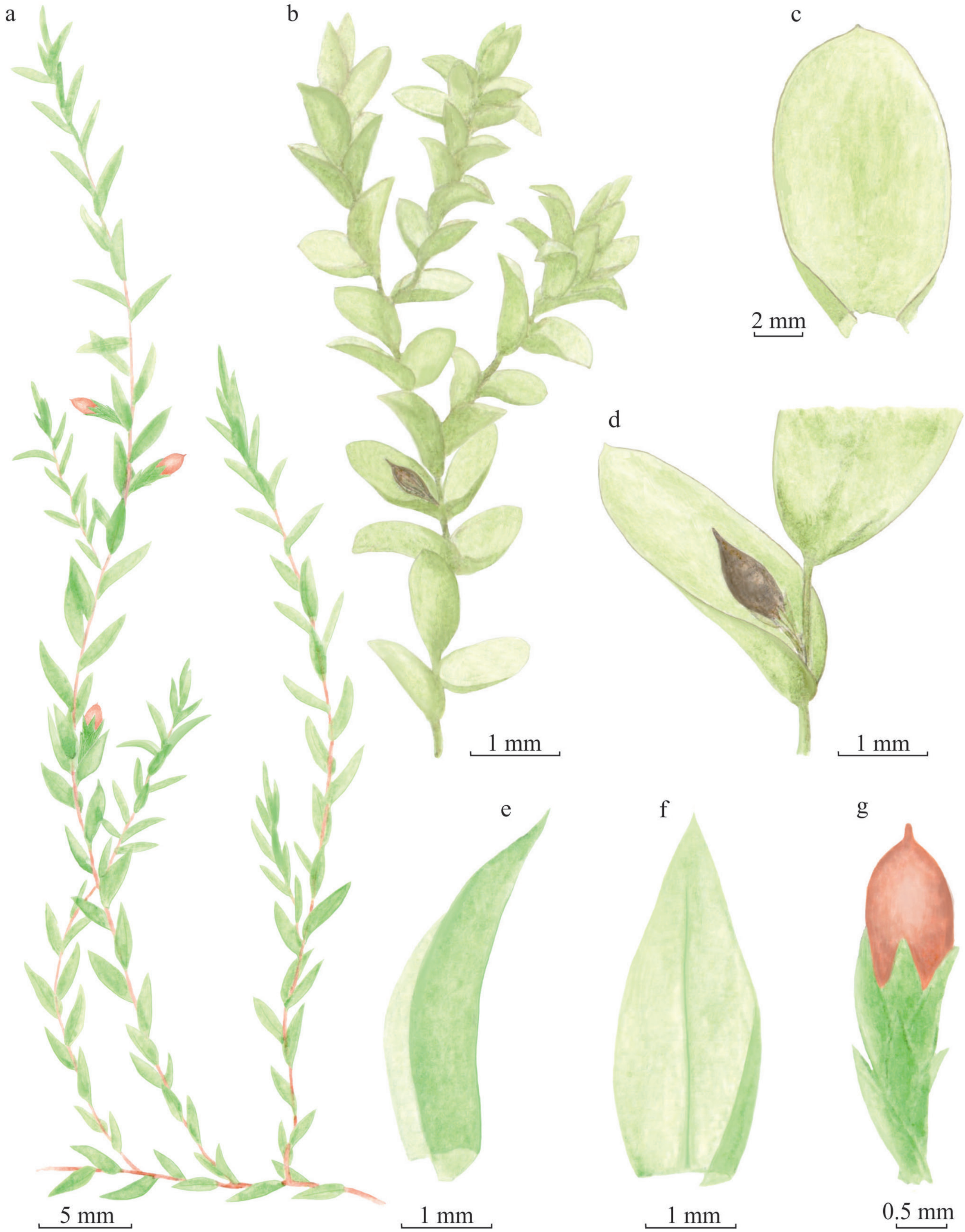


Fig. 6—Restoration of the natural habit of Jurassic mosses from Irkutsk Coal Basin. (a, e–g) *Palaeodichelyma kiritchkovae* sp. nov. (a) natural habit. (e, f) leaves: side (e) and top (a) views. (g) sporophyte. (b–d) *Bryokhutuliinia ignatovii* sp. nov. (b) natural habit. (c) leaf (top view). (d) lateral branch with sporophytes.

Acknowledgements—*We are grateful to two anonymous reviewers for fruitful discussions and helpful recommendations and Dr. Stepan V. Ivantsov (Tomsk State University, Russia) for active participation in field research. We are very grateful to Dr. Josh Jenkins Shaw (University of Copenhagen, Denmark) and Dr. Alfred F. Newton (Field Museum of Natural History, Chicago, USA) for the correction of the English text of the manuscript. This work was carried out in the framework of the State Task of the Institute of the Earth's Crust, Siberian Branch of the Russian Academy of Sciences (Project No. 0346–2018–0004). This work involved the Centre of Geodynamics and Geochronology equipment at the Institute of the Earth's Crust, Siberian Branch of the Russian Academy of Sciences (Grant No. 075–15–2021–682).*

REFERENCES

Ankudimova LA, Kabanova GM, Odintsova MM & Shurygin BL 1982. Stratigraphic scheme of the Jurassic of the Irkutsk coal–bearing basin. *In*: Odintsova MM (Editor)–Organic world of eastern Siberia in the Phanerozoic. Novosibirsk, Nauka: 30–43 p (in Russian).

Bell NE & York PV 2007. *Vetiplanaxis pyrrhobryoides*, a new fossil moss genus and species from Middle Cretaceous Burmese amber. The Bryologist 110(3): 514–520.

Bippus AC, Savoretti A, Escapa IH, García Massini JL & Guido D 2019. *Heinrichsiella patagonica* gen. et sp. nov.: a permineralized acrocarpous moss from the Jurassic of Patagonia. International Journal of Plant Sciences 180(8): 882–891. https://doi.org/10.1086/704832

Frolov AO, Ivantsov SV, Afonin IV, Mashchuk IM & Lyalyuk KP 2022. Prisayan Formation (Lower and Middle Jurassic) of the Irkutsk Coal Basin: new data on lytho–and phytostratigraphy. Russian Geology and Geophysics 63(10): 1133–1161. doi: 10.2113/RGG20214334

Frolov AO & Mashchuk IM 2018. Jurassic flora and vegetation of the Irkutsk Coal Basin. Irkutsk: VB Sochava Institute of Geography SB RAS Publishers, 541 p (in Russian with English summary).

Frolov AO & Mashchuk IM 2019. Taxonomy of the Genus *Lycopodites* (Lycopodiales) from the Jurassic sediments of the Irkutsk Basin (East Siberia). The Bulletin of Irkutsk State University. Series Biology. Ecology. 28: 3–16 (in Russian). https://doi.org/10.26516/2073–3372.2019.28.3

Goffinet B & Buck WR 2004. Systematics of the Bryophyta (mosses): from molecules to a revised classification. *In*: Goffinet B, Hollowell V & Magill R (Editors)–Molecular systematics of Bryophytes. St.–Louis, Missouri Botanical Garden Press: 205–239 p.

Goffinet B, Buck WR & Shaw AJ 2009. Morphology, anatomy and classification of the Bryophyta. *In*: Goffinet B & Shaw AJ (Editors)–Bryophyte biology, 2nd Edition Cambridge University Press, Cambridge: 55–138 p.

Hedenäs L, Heinrichs J & Schmidt AR 2014. Bryophytes of the Burmese amber forest: amending and expanding the circumscription of the Cretaceous moss genus *Vetiplanaxis*. Review of Palaeobotany and Palynology 209: 1–10. https://doi.org/10.1016/j.revpalbo.2014.05.008

Heinrichs J, Wang X, Ignatov MS & Krings M 2014. A Jurassic moss from northeast China with preserved sporophytes. Review of Palaeobotany and Palynology 204: 50–55. https://doi.org/10.1016/j.revpalbo.2014.02.005

Hübers M & Kerp H 2012. Oldest known mosses discovered in Mississippian (late Visean) strata of Germany. Geology 40: 755–758.

Hübers M, Kerp H, Schneider JW & Gaitzsch B 2013. Dispersed plant mesofossils from the Middle Mississippian of eastern Germany: bryophytes, pteridophytes and gymnosperms. Review of Palaeobotany and Palynology 193: 38–56. https://doi.org/10.1016/j.revpalbo.2013.01.006

Ignatov MS 1992. *Bryokhutuliinia jurassica*, gen. et sp. nov, a remarkable fossil moss from Mongolia. Journal of the Hattori Botanical Laboratory 71: 377–388.

Ignatov MS 2013. Mosses of Paleozoic and Mesozoic. Lethaea rossica, Suppl. 1: 29–40 (in Russian).

Ignatov MS, Karasev EV & Sinitsa SM 2011. Upper Jurassic mosses from Baigul (Transbaikalia, South Siberia). Arctoa 20: 43–64.

Ignatov MS, Karasev EV, Sinitsa SM & Maslova EV 2012. New *Bryokhutuliinia* species (Bryophyta) with sporophytes from the Upper Jurassic of Transbaikalia. Arctoa 22: 69–78.

Ignatov MS & Maslova EV 2021. Fossil mosses: What do they tell us about moss evolution? Bry. Div. Evo. 43(1): 072–097. https://doi.org/10.11646/bde.43.1.7

Ignatov MS & Shcherbakov DE 2007. Did Pleurocarpous mosses originate before the Cretaceous? *In*: Newton AE & Tangney R (Editors)–Pleurocarpous mosses: systematics and evolution. CRC Press, Boca Raton–London–New York (Systematic Association Special Volume 71) 321–336 p. https://doi.org/10.1201/9781420005592.ch16

Ignatov MS & Shcherbakov DE 2011. Lower Cretaceous mosses from Khasurty (Baikal area of South Siberia). Arctoa 20: 19–42. https://doi.org/10.15298/arctoa.20.02

Ilyina VI 1985. Jurassic Palynology of Siberia. Moskow, Nauka, 237 p (in Russian).

Kiritchkova AI, Batyaeva SK & Bystritskaya LI 1992. Phytostratigraphy of Jurassic deposits from the south of western Siberia. Moscow, Nedra, 216 p (in Russian).

Kiritchkova AI, Kostina EI & Bystritskaya LI 2005. Phytostratigraphy and flora of Jurassic deposits of the western Siberia. St. Petersburg, Nedra, 378 p (in Russian).

Krassilov VA 1973. Mesozoic bryophytes from the Bureja Basin, Far East of the USSR. Palaeontographica, Abteilung B 143: 95–105.

Krassilov V 1982. Early Cretaceous flora of Mongolia. Palaeontographica, Abteilung B 181: 1–43.

Mamontov YuS & Ignatov MS 2019. How to rely on the unreliable: examples from Mesozoic bryophytes of Transbaikalia. Journal of Systematics and Evolution 57(4): 339–360. https://doi.org/10.1111/jse.12483

Miller NG 1984. Tertiary and Quaternary fossils. *In*: Schuster RM (Editor)–New Manual of Bryology. Hattori Botanical Laboratory, Nichinan, 1194–1232 p.

Newton AE, Wikstrom N, Bell N, Forrest LL & Ignatov MS 2007. Dating the diversification of the pleurocarpous mosses. *In*: Newton AE & Tangney R (Editors)–Pleurocarpous mosses: systematics and evolution (Systematic Association. Spec. Vol. 71). Boca Raton, London, N.Y.: CRC Press, 337–366 p.

Prinada VD 1962. Mesozoic flora of eastern Siberia and Transbaikalia. Moscow, Gosgeoltekhizdat, 368 p (in Russian).

Reissinger A 1950. Die "Pollenanalyse" ausgedehnt auf alle Sedimentgesteine der geologische Vergangenheit. Zweiter teil. Palaeontographica, Abteilung B 90 (4–6): 99–126.

Rothmaler W 1951. Die Abteilungen und Klassen der Pflanzen. — Feddes Repert. Spec. Nov. Regni Veg. 54: 256–266.

Shaw AJ, Cox CJ, Goffinet B, Buck WR & Boles SB 2003. Phylogenetic evidence of a rapid radiation of pleurocarpous mosses (Bryophyta). Evolution 57: 2226–2241.

Shurygin BN, Nikitenko BL, Devyatov VP, Ilyina VI, Meledina SV, Gaideburova EA, Dzyuba OS, Kazakov AM & Mogucheva NK 2000. Stratigraphy of Petroleum basins in Siberia in 9 Books. The Jurassic. Novosibirsk, Publishing House of SB RAS, Filial "Geo", 480 p (in Russian).

Skoblo VM, Lyamina NA, Rudnev AF & Luzina IV 2001. Continental Upper Mesozoic of Cisbaikalia and Transbaikalia (stratigraphy, sedimentation conditions, correlation). Novosibirsk, Publishing House of the SB RAS, 332 p (in Russian).

Taylor TN, Taylor EL & Krings M 2009. Paleobotany. The Biology and Evolution of Fossil Plants. Second Edition. Academic Press is an imprint of Elsevier, 1230 p.

Teslenko YuV 1970. Stratigraphy and flora of Jurassic srdiments of west and south Siberia and Tuva. Moscow, Nedra, 270 p (in Russian).

Tomescu AMF, Bomfleur B, Bippus AC & Savoretti A 2018. Why are bryophytes so rare in the fossil record? A spotlight on taphonomy and fossil preservation. *In*: Krings M, Harper C, Cuneo N & Rothwell G (Editors)–Transformative Paleobotany. Papers to commemorate the life and legacy of Thomas N. Taylor. Academic Press. 375–416 p. https://doi.org/10.1016/B978–0–12–813012–4.00016–4.

Wu SQ 1999. A preliminary study of the Jehol flora from western Liaoning. Palaeoworld 11: 7–57 (In Chinese with English summary).

Wu X–W, Wu X–Y & Wang Y–D 2000. Two new forms of Bryiidae (Musci) from the Jurassic of Junggar Basin in Xinjiang, China. Acta Palaeontologica Sinica 39 (Suppl.): 167–175.