

A NEW FOSSIL MOSS FROM THE LOWER PERMIAN
OF THE RUSSIAN FAR EAST

НОВЫЙ ИСКОПАЕМЫЙ МОХ ИЗ НИЖНЕПЕРМСКИХ ОТЛОЖЕНИЙ
РОССИЙСКОГО ДАЛЬНЕГО ВОСТОКА

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Abstract

A new genus and species *Palaeocampylopus buragoae* is described by imprints in the Lower Permian deposits from the Russky Island in the Sea of Japan, the Russian Far East. The plant size and the overall habit, orthotropic growth, narrow leaves, and especially terminal cup-like structures, resembling rosettes of perigonial leaves, indicate the most probable affinity with Dicranaceae (cf. *Campylopus*) or Polytrichaceae (cf. *Polytrichum* and *Polytrichastrum*). The costa is unseen in leaves and likely was very broad. Although the cell structure is not well seen, striation of abaxial costa surface allows to estimate the width of dorsal epidermal cells.

Резюме

Из отложений нижней перми с острова Русский (Японское море, российский Дальний Восток) описан новый вид и род, *Palaeocampylopus buragoae*. Он похож на современные виды Dicranaceae (например, *Campylopus*) и Polytrichaceae (например, *Polytrichum* и *Polytrichastrum*) по размерам и общему габитусу растений, прямостоячему росту, узким листьям, и, особенно, по чашевидным структурам на верхушках побегов, которые весьма сходны с собраниями перигониальных листьев мужских растений указанных родов. Жилка на отпечатках листа не выделяется, что, очевидно, свидетельствует в пользу того, что она занимала практически всю ширину листа. Хотя клеточная структура в целом не видна, продольная исчерченность жилки позволяет сделать заключение о ширине клеток ее дорсального эпидермиса.

KEYWORDS: *Palaeocampylopus*, Bryophyta, fossils, Permian, Russian Far East, Polytrichaceae, Dicranaceae

INTRODUCTION

Despite the common belief that mosses are an ancient group of plants, the paleobotany does not fully support this statement. There is no one Devonian record, and Carboniferous mosses are extremely few (Renault & Zeiller, 1885, 1888; Lignier, 1914; Thomas, 1972), and none of them allows complete enough restoration of plants. In the Permian, however, mosses became much more common in Angaraland (Neuburg, 1960; Fefilova, 1978), Eurameria (Gomankov & Meyen,

1987; Ignatov, 1990), and two earliest records from Gondwanaland belong to this period as well (Townrow, 1959; Smoot & Taylor, 1986). Angarian material in many collections is preserved well enough for studying cell structure of leaves that is an important character for moss taxonomy. Only gametophytic remains are known up to now and all of them represent sterile plants, with one exception of the genus *Protoochyraea*, where one leaf fragment may represent a perigonial bract (Ignatov, 1990).

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Collecting fossil insects in the Russky Island of the Sea of Japan in 2008, the second author found a slab with interesting imprints resembling modern male plants of *Polytrichum* and *Campylopus*, and they are described here as a new genus *Palaeocampylopus*.

MATERIAL AND LOCALITY

The moss imprints were found on the surface of black coaly shales (containing abundant plant fossils, *Bivalvia* and few *Conchostraca*) of the lower subformation of the Pospelovo Formation, cropping out in the coastal cliff 0.3 km SSW of the Cape Novosilsky, the Russky Island near Vladivostok.

This subformation is dated Middle Kungurian (ca. 273 Ma) according to the International Stratigraphic Scale (Zakharov et al., 2009; corresponds to Late Kungurian of the East European Stratigraphic Scale).

The diverse vascular flora of the lower Pospelovo Formation is of the Siberian type, consists of sphenopsids, ferns, and Angaran cordaites and lacks undoubted pteridosperms and Cathaysian elements (Tashchi & Burago, 1974; Zimina, 1977, 1997; Zakharov et al., 2009). This plant assemblage is similar to those from the Rudnik Subformation (the Lek-Vorkuta Formation, Vorkuta Group, the Kungurian or the Ufimian) of the Pechora Basin and from the Usa and Starokuznetsk Formations (the Kuznetsk Subgroup) of the Kuznetsk Basin (Kotlyar et al., 2006). Abundant mosses (including *Intia* sp.: V.I. Burago in Meyen, 1982, and pers.comm.) and liverworts are recorded.

The Russky Island belongs to the Bureya-Jiamusi-Khanka block at the east of the Amuria microcontinent. In the Permian it was situated at the eastern margin of Asia. According to paleomagnetic data, Amuria had accreted to the North China block by the Late Carboniferous, but had not been sutured to Siberia until the Late Jurassic (see Hankard et al., 2007). Basing on wide occurrence of the Siberian-type flora and the high boreal marine fauna in Amuria, some authors suggested that, in the Permian, the latter block was situated closer to Siberia (Rees et al., 1999; Chumakov & Zharkov, 2002). Other researchers explain these facts by global climatic oscillations rather than significant drift of the terranes, and

consider the lower Pospelovo time belonging to one of the coldest intervals (Markevich & Zakharov, 2008; Zakharov et al., 2009).

CHARACTERISTICS OF COLLECTIONS

The collection consists of three slabs (5–6 × 3–4 cm) with imprints (PIN¹ no.5328/1, 2, 3), one of them with counterpart, and 3 smaller slabs (PIN no.5328/4, 5, 6), one with counterpart. One slab, PIN no. 5328/1 (Fig. 1) has shoots which are more or less spaced and rather well visible, and some of them have cup-like structures on the shoots tops. Two others, 5328/2 & 5328/3, have imprints of sterile leafy shoots many of which strongly overlap each other and are not so clearly seen (Figs. 11–14) and in general are slightly smaller than the shoots in Fig. 1 (cf. also Fig. 16).

Four terminal cup-like structures are clearly visible (Fig. 1) on stems tops (A, B, C, E), and one more (F) is seen without any connection to stems. Cup-like structures are less flattened comparing to the rest of the shoots and rise above the overall surface of imprint (and correspondingly lower in the counterpart). This may indicate that their texture was more rigid or the content inside them was more solid. The specimen shown in Fig. 17 is only tentatively referred to the species described here; it is also ascribed to have a perigonal structure, which is, however, unapparent, as will be discussed below.

Shoots bearing cup-like structures are rather loosely foliate, the leaves having lanceolate proximal portion and subulate acumen. Differences in foliage density obviously indicate that not all leaves are preserved or exposed on the rock surface, and for many of them only the proximal part is seen.

Leaves on different shoots have certain differences in shape, but the present material does not allow to sort them out into several distinct types. We are inclined to consider these differences as an infraspecific (or even intraindividual) variation, assuming: (1) variation within separate shoots (Figs. 6–16); (2) intermixed growth; (3) variation pattern in superficially similar extant mosses, e.g. *Dicranum* and *Campylopus* species. Concerning this variation, an important point would be that the upper leaves in many species have longer and narrower lamina with a subulate distal part. In *Dicranaceae*, *Polytrichaceae* and

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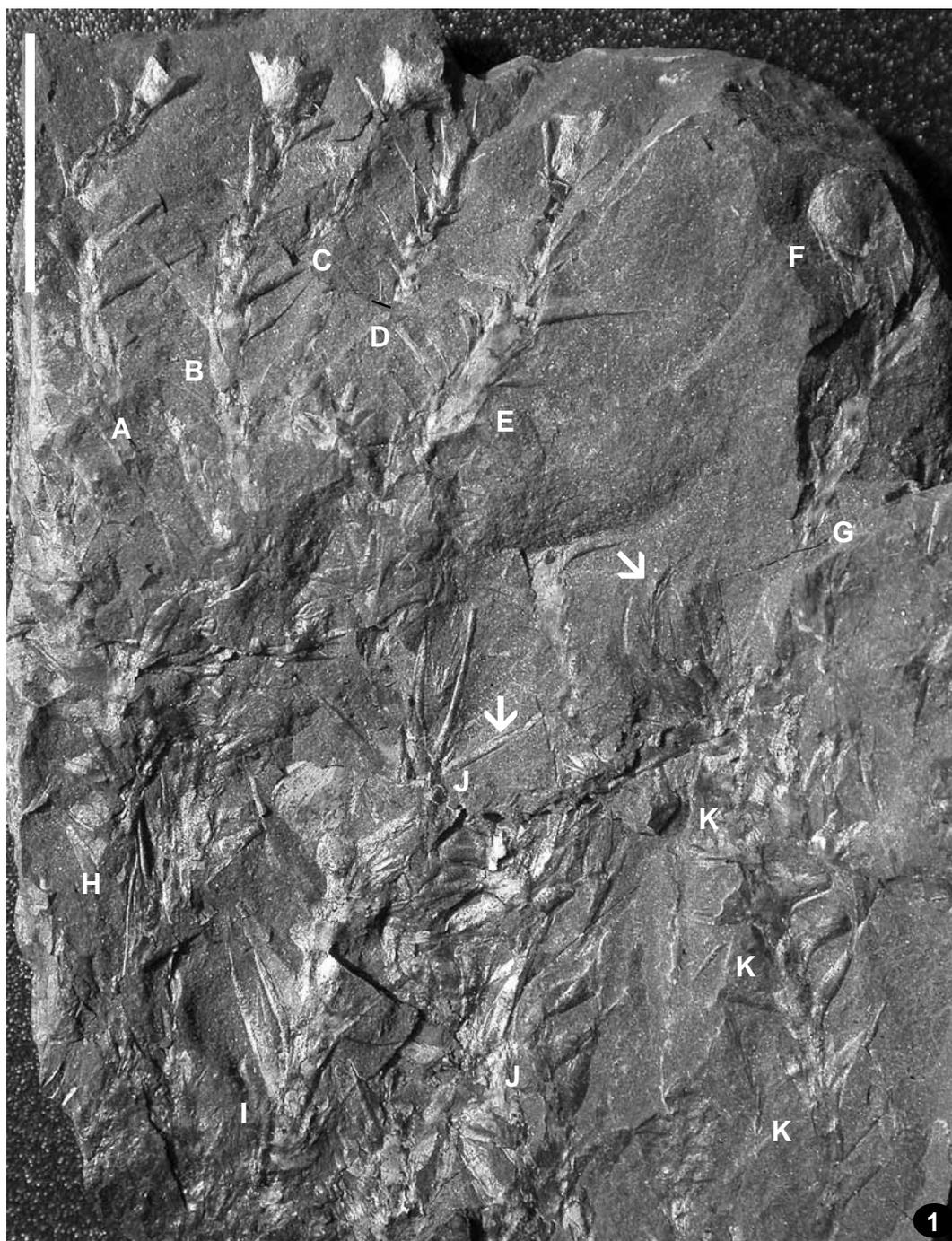
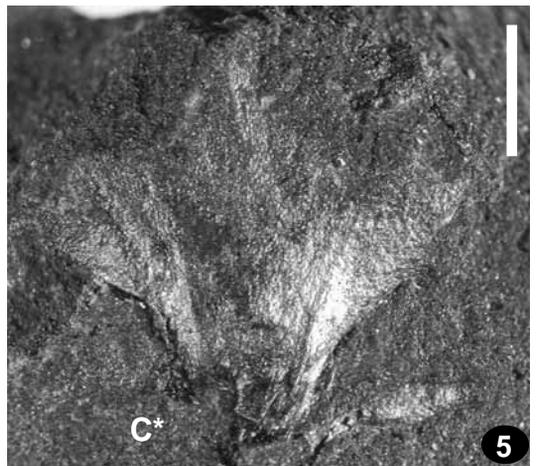
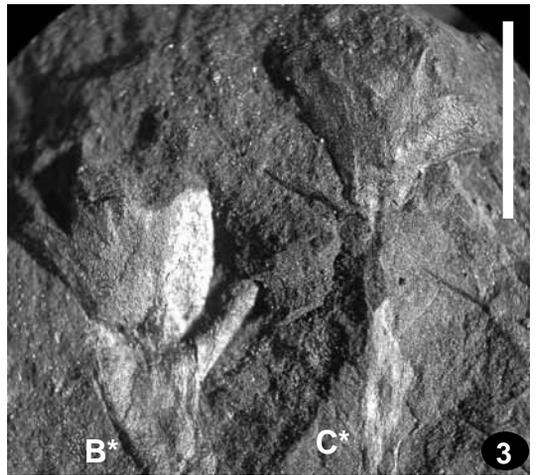
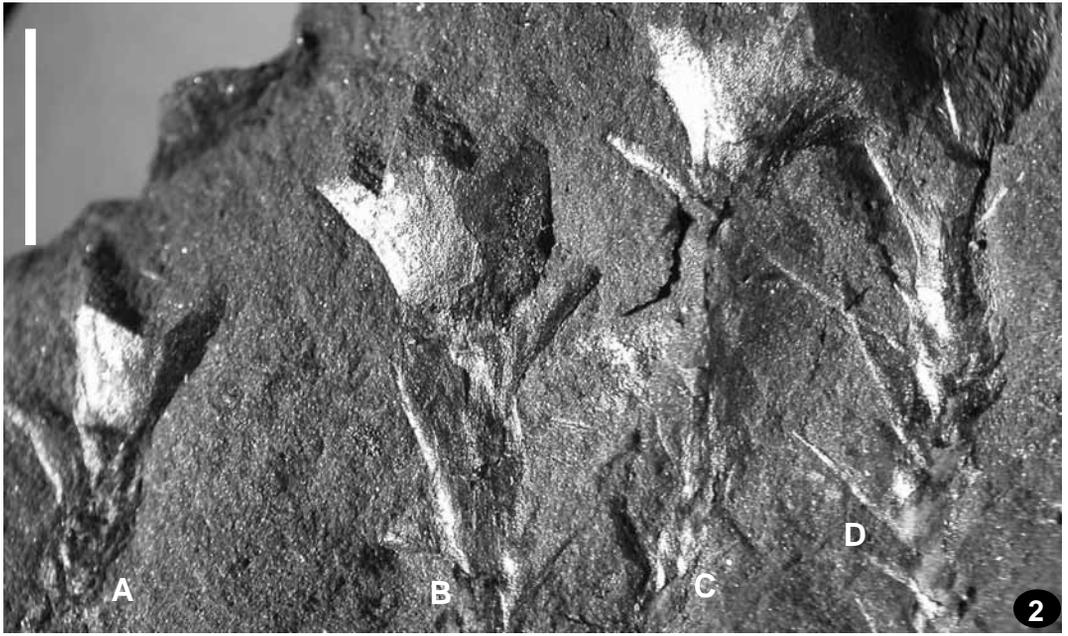
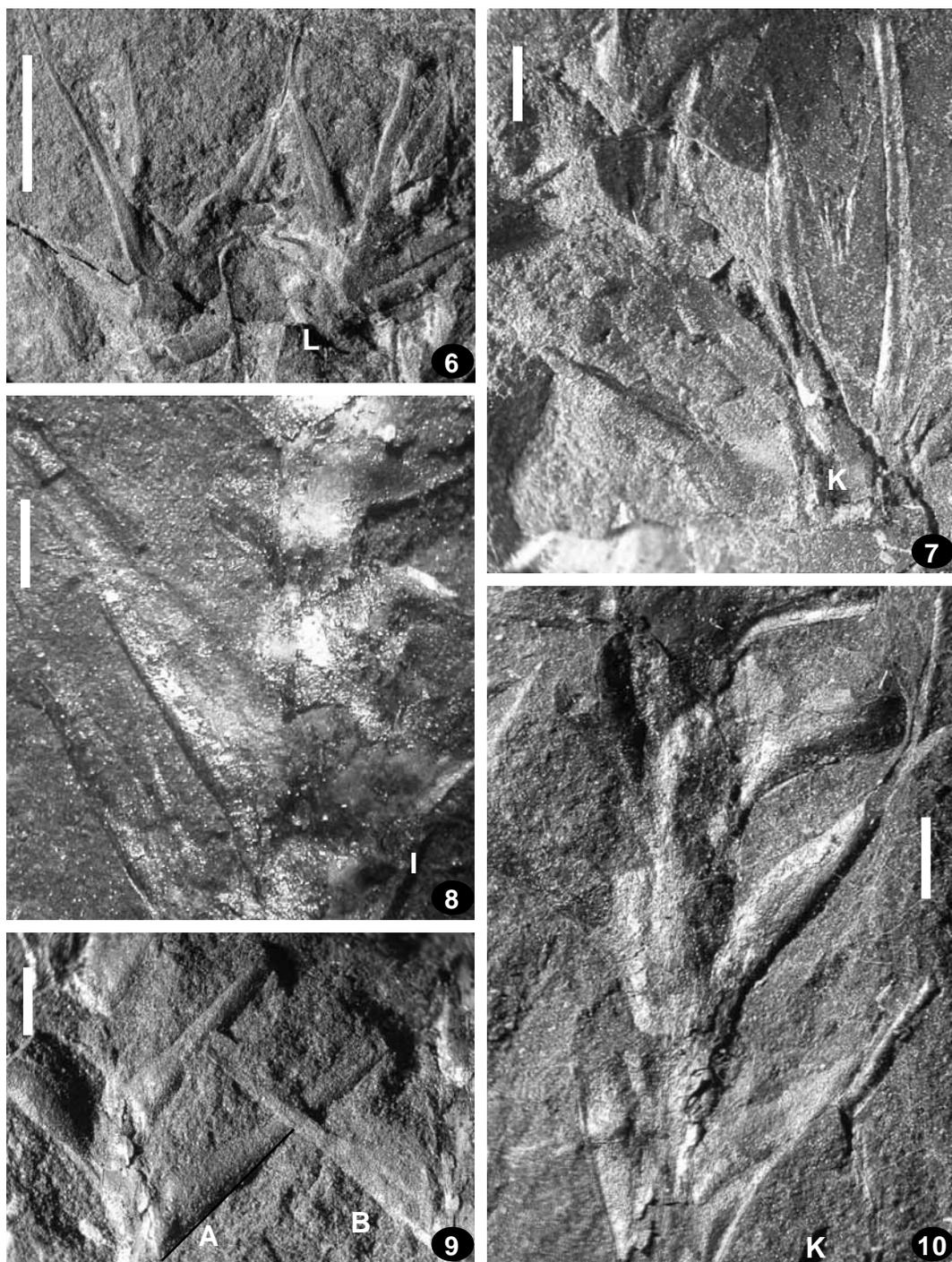


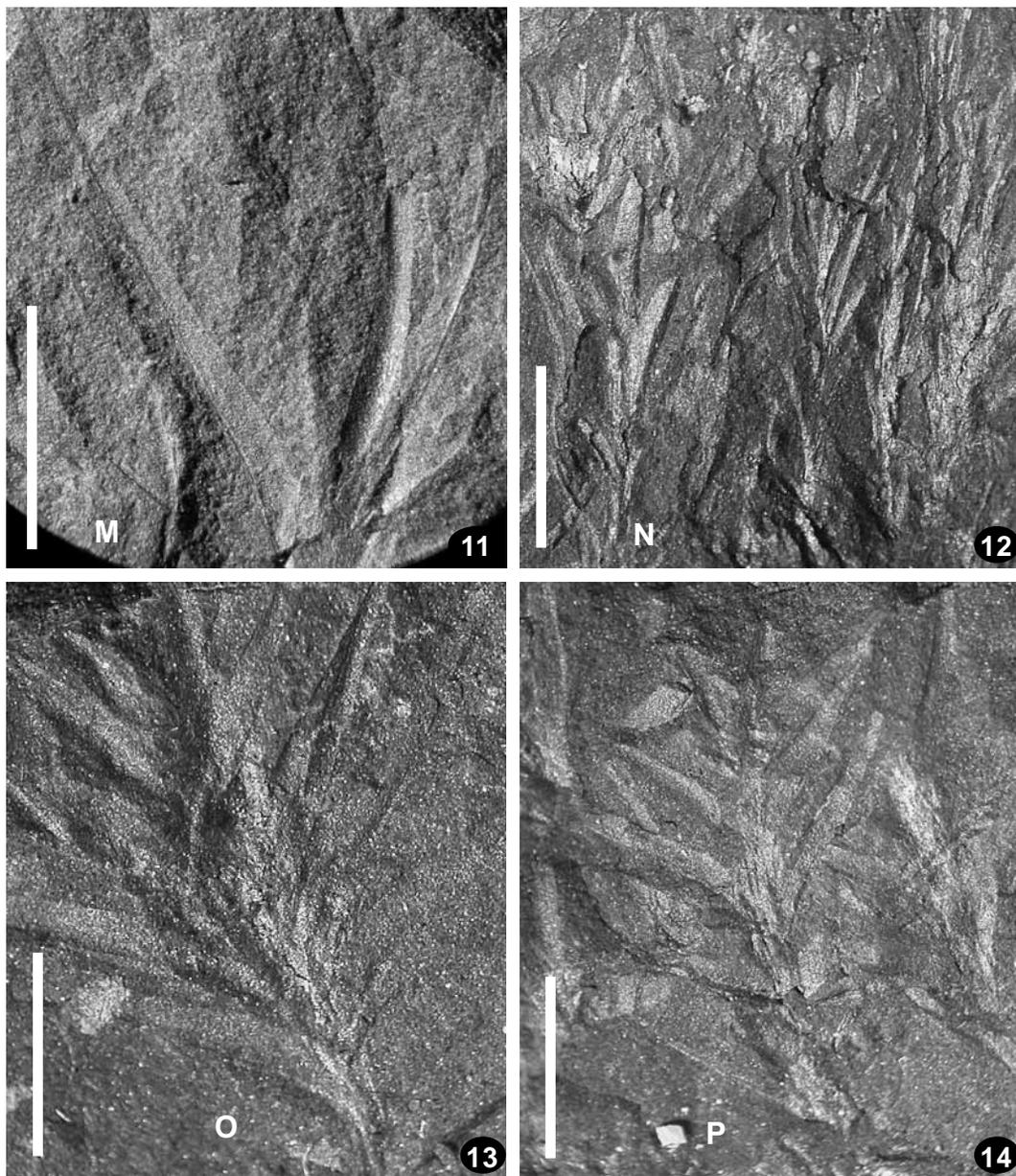
Fig. 1. *Palaeocampylopus buragoae* Ignatov & Shcherbakov (from PIN no. 5328/1; letters upon picture: B – holotype; A and C–K other shoots). Shoots A, B, C, E represent plants terminated with putative perigonia, and F is interpreted as isolated perigonium (by resemblance with those of specimens A–C, E); plants D, I–K have no perigonia-like structures, but their distal leaves are longer and distally subulate. Shoot K has above the terminal cluster of narrow leaves on almost leafless axis (oblique arrow), which immediate connection however not apparent. Shoot G, H and some smaller remnants are poorly preserved, although solitary leaves indicate that they likely belong to the same species. Vertical arrow points the leaf shown at higher magnification in Fig. 15. Scale bar 10 mm.





Figs. 6-10. Shoots of *Palaeocampylopus buragoae* Ignatov & Shcherbakov, showing leaf shape variation (6 – from PIN no. 5328/3; 7-10 from no. 5328/1); 6 and 7 represent foliage near shoot tops; 8-10 – foliage in middle part of shoots. Letters upon pictures are the same as in Fig. 1; Scale bars 3 mm for 6; 1 mm for 7-10.

Figs. 2-5 (opposite page). Putative perigonia of *Palaeocampylopus buragoae* Ignatov & Shcherbakov (from PIN no. 5328/1; letters upon pictures are the same as in Fig. 1, including B – holotype; B* – counterpart of holotype; C* is counterpart of C). Scale bars 3 mm for 2-3; 1 mm for 4-5. [Fig. 3 is horizontally flipped].



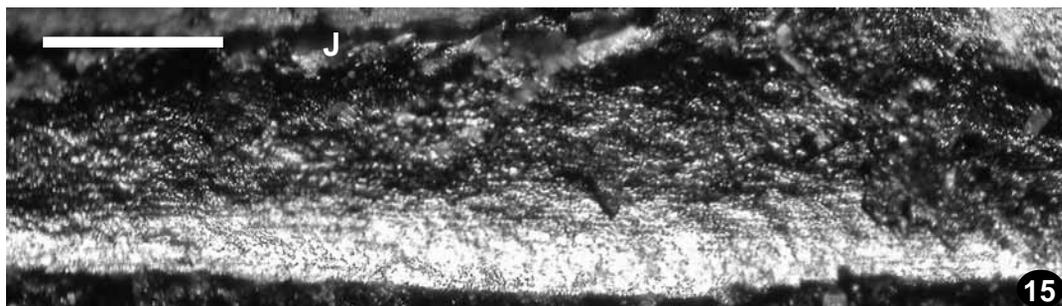
Figs. 11-14. Shoots of *Palaeocampylopus buragoae* Ignatov & Shcherbakov, showing leaf shape variation (from PIN no. 5328/2). Letters M-P upon pictures correspond those in Fig. 16. Scale bars 3 mm.

most of other moss families perichaetial leaves (around female gametangia) are longer and narrower than vegetative leaves, whereas perigonal leaves (around male gametangia) are shorter. Correspondingly there is a tendency for vegetative leaves to elongate near perichaetial, but not near perigonal leaves.

Assuming this albeit indirect evidence, we may speculate that the cup-like terminal structures are

perigonal leaves, and therefore plants with them are male ones. At the same time, stems terminating with longer leaves with a subulate upper portion are likely to be female. Although hypothetical, this assumption may be helpful at least for the circumscription of the present material.

The longest “female” shoot (K in Fig. 1) is 25 mm long, while the longest “male” shoot (B in Fig. 1) is 18 mm. Most of the shoots range



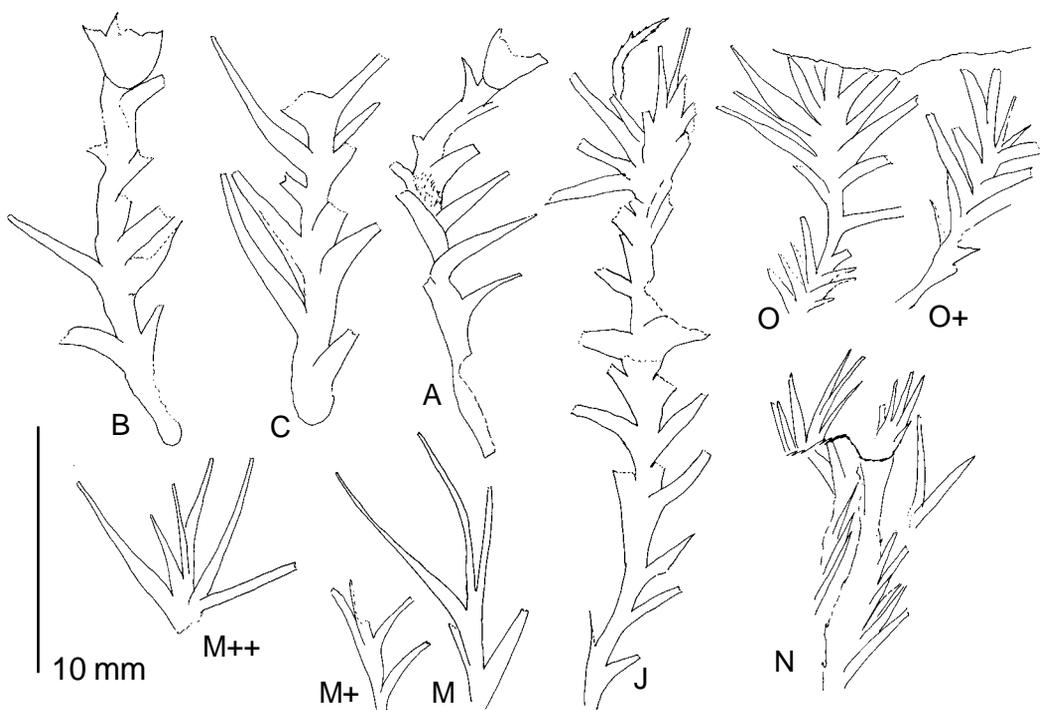
Figs. 15. Leaf of *Palaeocampylopus buragoae* Ignatov & Shcherbakov, showing longitudinal striation, likely indicating the width of cells of dorsal epidermis (from PIN no. 5328/1; leaf in upper part of shoot J in Fig. 1 (marked in Fig. 1 by vertical arrow). Scale bar 300 μ m.

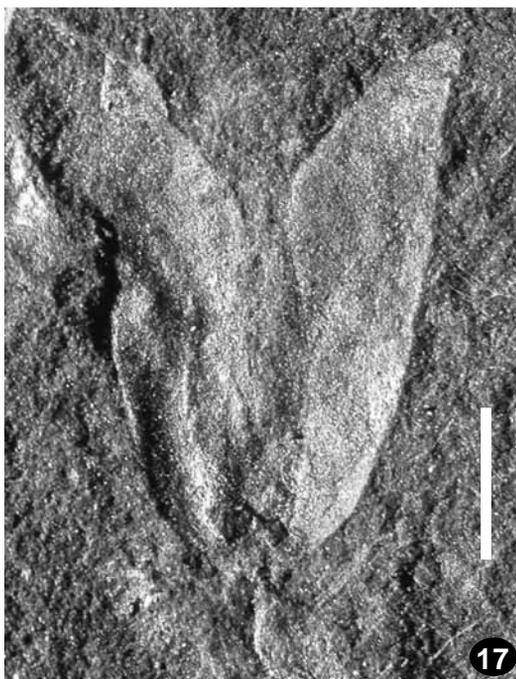
from 10 to 15 mm long. Stem width in compressions together with leaf bases is 0.9–1.2 mm.

Leaves are arranged in a dense spiral typical for mosses. They are erect (Fig. 12) to patent (Figs. 8–10), the former being restricted to smaller plants in dense growth that may be interpreted as younger plants (although the alternative suggestion that they belong to another taxon would be difficult to contest). The angle with the stem in many cases is about 70° ; individual leaves in the cluster of upper leaves deviate to ca. 110° ,

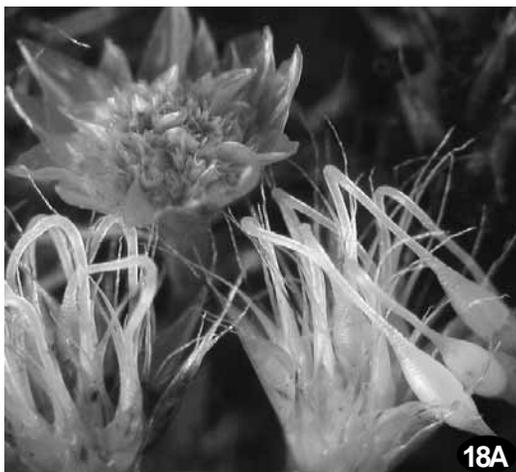
but their position may be considered as an artifact of fossilization. Maximal leaf length is 9 mm (found in 2 leaves) and this is not the total length, as the leaf tips look incompletely preserved. In few cases rock surface above a putatively broken leaf apex has some thin filiform traces 1–2 mm long, but they are never clear enough to make certain that they belong to a given leaf. Most of well-developed leaves reach 5–7 mm long, while smaller shoots may have leaves up to 4 mm only. Leaf width in compression reaches 0.7 mm, but

Figs. 16. Shoots of *Palaeocampylopus buragoae* Ignatov & Shcherbakov: A, B, C, J – from PIN no. 5328/1; M, N, O – from 5328/2. + indicate that specimen is not shown in photographs. Scale bar 10 mm for all.





Figs. 17. Perigonal leaves (?) of *Palaeocampylopus buragoae* Ignatov & Shcherbakov (?) (from PIN no. 5328/4). Scale bar 1 mm.



Figs. 18. Extant *Campylopus*: A-B – *Campylopus umbellatus* (Arn.) Paris. A (photo taken by Ms C. King and provided by B.C. Tan at Singapore Botanic Gardens): male (behind) and female (in front) inflorescences [i.e. gametangia surrounded by perigonal and perichaetial leaves]; B (New Guinea, Streimann, 24782, MHA¹): male inflorescence; C-E – *C. introflexus* (Hedw.) Brid. (Kaliningrad Prov., Razgulyaeva, 2.IV.2000, MHA): C: leaf; D: habit, dry; E: leaf cross section. Scales: 2 mm for B-D; 100 μ m for E.

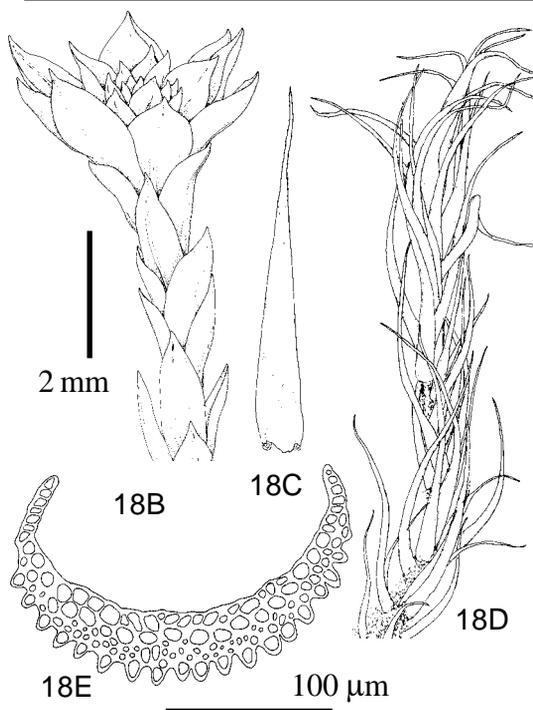
¹ – Herbarium of the Main Botanical Garden of Russian Academy of Sciences

this dimension should be assumed as a compression of an essentially tubulose or concave-tubulose structure. The costa is unseen in leaves as it was most likely very broad (similar to modern *Campylopus* or *Polytrichum*). In few cases a line along the leaf length is visible (e.g. Fig. 11) which possibly indicates one of leaf margins overlapping the rest of the flattened tubulose leaf. If this explanation is correct, then the margin is entire.

Being ca. 0.5 mm in diameter in the proximal leaf portion, the upper part is much narrower and linear-subulate, not exceeding 100(–200) μ m wide. In upper leaves of plants that are interpreted here as female, their subulate part may constitute no less than 3/4 of total length.

The longitudinal striation is seen in some places in the better preserved counterparts. It is quite likely that the width between the striae, 9–10 μ m, may be interpreted as the cell width of dorsal epidermis or width between ridges similar to that occurring on abaxial costa surface in many *Campylopus* species (cf. Fig. 18).

Terminal cup-like structures (Figs. 1–5) are up to 3 mm high and 3.5 mm wide. Their preservation does not allow to define with certainty the shape of bracts, but outlines indicate that 2 or 3 triangular bract ends occur from one side. These



putative perigonal leaves probably were very closely appressed to each other, with no visible traces of borders between them (this is a common case in perigonal leaves of *Polytrichum*).

One imprint (Fig. 17) is considered as a possible perigonal structure because of similar texture, shape and approximately the same size (4.8 mm long, 3 mm wide), although it was found separately with no connection to another part that may be attributable to moss. This specimen is rather cylindrical than cup-like which is characteristic of other terminal 'perigonia'. This difference however may be explained by just premature state of the male gametangia and correspondingly of the leaves surrounding them.

PLANT DESCRIPTION

Palaeocampylopus buragoae Ignatov & Shcherbakov, genus et species nov. Figs. 1-16.

Generic diagnosis: Upper leaves aggregated in cup-like structures; leaves lanceolate to subulate, tubulose; costa indistinctly delimited from lamina in most of leaf length.

Specific diagnosis: Stems to 25 mm long, leaves, (4)–5–9 mm long, 0.4–0.7 mm wide below, gradually tapered to apex to acuminate, in subulate upper portion 0.1–0.2 mm wide. Terminal cup-like rosettes of presumably perigonal leaves to 5 mm long and 4 mm wide.

Description: Stem up to 25 mm long, with leaf bases up to 1.2 mm wide. Branching none. Shoots moderately densely foliate. Leaves polystichous, erect to patent (deviating from stem at 20–70°(–100°), (4)–5–9 mm long, 0.4–0.7 mm wide below, gradually tapered to apex to acuminate, in subulate upper portion 0.1–0.2 mm wide at the distance of upper 1/3–1/2 of leaf length, concave proximally and tubulose distally or plus-minus tubulose throughout. Perigonal leaves tightly crowded at stem apex, shortly triangular, 3–5 mm long and with broad base, forming cup-like structures 3–4 mm in diameter.

Holotype: Russian Far East, Sea of Japan, Russky Island, ca. 43°00'N 131°50'E; Lower Permian (Kungurian, lower Pospelovo Formation), collected in 2008 by Shcherbakov et al.; PIN no. 5328/1-B. Figs. 1, 2, 3, 4 (counterpart), 9, 16 (in all cases marked as B).

Other specimens: same age, locality and collectors as for holotype, PIN no. 5328/1-6.

Distribution: Russky Island (see characteristics of locality).

Etymology: The generic epithet denotes our belief that cup-like structures are formed by perigonal leaves. The species is named in honour of Valentina I. Burago, a paleobotanist (Primorye Prospecting and Mapping Geological Expedition, Vladivostok) who first reported mosses from the Pospelovo Formation of Russky Island.

Differentiation. Permian mosses described before from Angaraland and Subangaraland (Neuburg, 1960; Fefilova, 1978; Meyen & Gomanov, 1987; Ignatov, 1990), had mostly rather broad leaves, except for *Arvidia* and *Viledia*, but these plants were much smaller (leaves shorter than 1 mm) and characterized by specific laminar areolation. For the latter genus the only one incomplete leaf was found (Ignatov, 1990).

Also, the conspicuous perigonal or similar structures were never observed in Palaeozoic and Mesozoic moss collections, though some possess sporophytes (Konopka et al., 1997, 1998).

DISCUSSION

Permian mosses of Angaraland described by Neuburg (1960) and Fefilova (1978) have mostly broad leaves with a distinct costa and border, resembling modern species of *Mnium* or *Plagiomnium*. The habit of the latter especially agrees with *Intia*, the fossil genus previously reported from the Lower Pospelovo Formation of the Russky Island (Burago in Meyen, 1982). Two other fossil genera, *Uskatia* Neub. and *Polyssaevia* Neub., recorded from synchronous or younger (Middle to Upper Permian) deposits in other parts of Primorye (Eliseeva & Radchenko, 1964; Burago in Meyen, 1982), are somewhat similar to *Palaeocampylopus*, especially to shoots with a relatively short leaves gradually tapering from broadened bases (e.g. Figs. 8–10, 13–14). However, the leaves of these two genera have an acute rather than subulate upper part, and are shorter and wider (2.6–4 × 0.5–1.3 mm in *Uskatia conferta* Neub., 3.3–5.0 × 2–3.4 mm in *Polyssaevia spinulifolia* (Zasessky) Neub.). In addition, they have a multistratose costa ca. 100 µm wide that could unlikely be indiscernible in material with the present kind of preservation.

Merceria augustica Smoot & T.N. Taylor from the Permian of Gondwanaland (Antarctic)

was a rather large plant known mostly by a series of cross sections with excellent preservation of cell structure, but without any evidence of plant habit and leaf length, the leaves being 0.5–2.5 mm wide and 1/6 to 1/2 of their width was occupied by the costa (Smoot & Taylor, 1986).

As modern *Polytrichum* is quite similar to *Palaeocampylopus*, it would be worthy to discuss fossil taxa compared with the former. The best fossil material of both sporophytes and gametophytes of unequivocal Polytrichaceae, *Eopolytrichum antiquum* Konopka et al., is known from the Late Cretaceous (Konopka et al., 1997). This material represents capsules and anatomically preserved leaves with typical for the family structure of lamellae. The form-genus *Polytrichites* E. Britton was established from the Upper Miocene (Latah Formation, Washington State, U.S.A.) to accommodate one fossil plant similar to *Polytrichum*, *Polytrichites spokaneensis* E. Britton in Knowlton. It was described by just one shoot 2 cm long with leaves 3–4 mm long (Knowlton, 1926). The stem has one branch appearing from its middle, which is an unusual case in *Polytrichum* (and most genera of the family), although in some other genera the branching occurs regularly, e. g. in *Dendrologotrichum*, and also in *Pogonatum urnigerum*. Another dissimilarity with *Polytrichum* is the size, which is too small for this genus. Steere (1946) suggested to extend the concept of the genus and include all the Polytrichales that can't be attributed to the extant genera. In practice this would be a difficult task, because the higher taxonomic units in mosses are usually more difficult to key out than the lower ones. In this light, the circumscription 'Polytrichales that do not fit modern genera' is not practical at all: it seems that there are no grounds to reject the attribution of the type species of *Polytrichites* to a number of Polytrichaceae genera, as well as to some members of Pottiaceae, Dicranaceae, Ptychomitriaceae and Grimmiaceae. Not surprising that the genus was almost unused, and only one more species was placed in it, *Polytrichites aichiensis* Yasui, from the Upper Tertiary of Central Japan (Yasui, 1928). The material of the latter was represented by stem transverse section, showing complex anatomy that is known for mosses only in Polytrichaceae.

Muscites polytrichaceus Renault et Zeiller, despite the species epithet, has very little in common with Polytrichaceae: plants have remote leaves 1.0–1.5 mm long, ovate, with a distinct narrow costa. A resemblance to *Rhizogonium* (Jovet-Ast, 1967) would be more appropriate.

Among modern groups, the superficial similarity can be traced to many acrocarpous moss families, but the most conspicuous cup-like perigonal leaves are known in Polytrichaceae, e.g. *Polytrichum* and *Polytrichastrum*, and some Dicranaceae, e.g. *Campylopus* (Fig. 18). Both these families are appropriate for comparison due to overall size (leaves up to 6–9 mm long are not common in modern mosses, usually they are shorter than 5 mm), as well as to the broad costa filling more than half leaf width, which makes it indistinct in imprints. The abaxial costa in *Campylopus* commonly has some ridge-like structures (Fig. 18) that make its surface striate, with the distance between striae almost equal to those observed in *Palaeocampylopus* (Fig. 15). The abaxial costa in Polytrichaceae also may exhibit sometimes certain striation.

At the same time, Polytrichaceae have a few characters that make their affinity with *Palaeocampylopus* somewhat less probable comparatively to *Campylopus*. The leaf shape, and especially its narrowly subulate upper parts agree with *Campylopus* much better than with Polytrichaceae species where leaves are stiff, more broad almost up to its apex, and usually have more strong differentiation into limb and sheathing base, while the leaf of *Palaeocampylopus* is rather gradually tapered upwards. In return, the perigonal leaves in *Polytrichum*, are more strongly specialized, tightly appressed to each other, making their rosettes thin and seamless, whereas in *Campylopus* they are usually not so conspicuously differentiated, although some of them admit compression up to the shape of *Palaeocampylopus* (Fig. 18).

Finally, it is worthy to note that 'perigonia' may be interpreted in a totally different way. They can be compared, for example, with terminal cup-like structures bearing gemmae in *Tetraphis*. The further comparison is not necessary, as the modern representatives of this ancient genus have small ovate leaves with a conspicuous narrow

costa. However, a possibility that 'perigonia' in *Palaecampylopus* may be a structure of a different function should also be kept in mind.

ACKNOWLEDGEMENTS

We are much indebted to our colleagues V.I. Burago, E.B. Volynets, S.A. Shorokhova and E.V. Bugdaeva, paleobotanists from Vladivostok, who kindly facilitated the 2008 field work of the PIN team in South Primorye and provided valuable information on localities and plants. We thank Photo of *Campylopus umbellatus* (Fig. 18A) taken by Ms C. King and provided by Dr. B.C. Tan at Singapore Botanic Gardens. The work was partly supported by RFBR 07-04-00013, 10-04-01713.

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