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THE GENUS *PLEURIDIUM* (DITRICHACEAE, BRYOPHYTA) IN RUSSIA

РОД *PLEURIDIUM* (DITRICHACEAE, BRYOPHYTA) В РОССИИ

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Abstract

A revision of the collections of *Pleuridium* from Russia revealed that most of them belong to *P. subulatum,* whereas two specimens from Kamchatka represent a species new for science described here as *P. kamchaticum* Czernyadjeva & Ignatova. All herbarium specimens from Russia referred to *P. acuminatum* were found to be *P. subulatum*. Thus *P. acuminatum* is known from the Russian territory only based on literature, including publication of Klinggraff with detailed correct description of this species in addition to locality data. *Pleuridium subulatum* is widespread in European Russia, having scattered findings in Altai, Transbaikalia, Yakutia, and Kamchatka.

Резюме

Ревизия гербарных коллекций *Pleuridium* из России показала, что большинство образцов относится к *P. subulatum,* в то время как два образца с Камчатки принадлежат новому для науки виду, описанному здесь как *P. kamchaticum* Czernyadjeva & Ignatova. Все образцы из России, хранившиеся в гербариях под названием *P. acuminatum,* были переопределены как *P. subulatum*, так что *P. acuminatum* приводится для России только на основании литературных данных, из которых указания Клинггрэфа сопровождаются детальным морфологическим описанием. *Pleuridium subulatum* широко распространен в европейской части России, тогда как в ее азиатской части имеются немногочисленные находки на Алтае, в Забайкальском крае, в Якутии и на Камчатке.

KEYWORDS: new species, Kamchatka, mosses, endemic.

INTRODUCTION

Pleuridium is a small genus of the family Ditrichaceae, with 31 species in the world and 8–9 species in the Northern Hemisphere (https://tropicos.org/name/35000982, accessed 28 May 2023). Recent ckecklists accept two species of the genus in Europe, *P. acuminatum* Lindb. and *P. subulatum* (Hedw.) Rabenh. (Hodgetts *et al.*, 2020). In China the only species of the genus is *P. subulatum* (Tong & He, 1999), while in Japan all earlier records of *P. subulatum* and *P. palustre* (Bruch & Schimp.) Bruch & Schimp. were revised by Deguchi *et al*. (1994) and all specimens of these species were referred to *P. japonicum* Deguchi, Matsui & Z. Iwats., the only species of the genus in Japan.

The treatment of *Pleuridium* in the Flora of North America (Yip, 2007) accepts four species: in addition to those known in Europe there are two American endemics: *P. sullivantii* Austin and *P. ravenelii* Austin. Both latter species have clear morphological distinctions from *P. acuminatum* and *P. subulatum.* At the same time, *P. acuminatum* and *P. subulatum* are superficially similar, which caused a lot of confusions in their distinctions and nomenclature. Many authors even considered *P. acuminatum* as a synonym of *P. subulatum* (Lawton, 1971; Crum & Anderson, 1981). The distinction and typification of these two species were discussed in detail by Yip (2000, 2007).

Savich-Lyubitskaya & Smirnova (1970) reported for the territory of the USSR two species of *Pleuridium* in the current circumscription: *P. subulatum* was considered as a common species in European part of the country and the Caucasus, while *P. acuminatum* was known from few records in Kaliningrad Province, Crimea and the Russian Far East. Subsequent checklists (e.g., Ignatov *et al.*, 2006) largely repeated this opinion, but excluded *P. acuminatum* from the Russian Far East, where its record was apparently based on the misapplication of the name *P. acuminatum* instead of *P. subulatum*.

Pleuridium palustre was often segregated in its own genus *Sporledera* (Savich-Lyubitskaya & Smirnova, 1970), or *Cleistocarpidium* (Hodgetts *et al.*, 2020), although some recent authors continue its inclusion in *Pleuridium* (Halingbäck, 2006). We are inclined to accept its including in *Pleuridium* as well. This species was reported from the Caucasus by Podpera (1954); however, without a precise locality, we are uncertain to which country this locality belongs in the current political boundaries.

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Materials and Methods

In the course of preparation of the Moss Flora of Russia we provided a revision of the Russian collections of the genus *Pleuridium*. All the collections of the genus in LE, MHA and MW were revised, with few samples from SASY and NSK. All species reported from Russia were included, and some specimens from neighbouring countries were used as well.

In addition to standard microscopic observations, peristomes were studied by SEM Jeol 6380, coated by gold without any additional preparation, and SNE-4500M. Light microscope observations were made under a stereomicroscope (Olympus SZX7) equipped with an Infinity 8-8 digital camera, and compound light microscope Olympus CX-43 with an Infinity 1-2 digital camera. Stacked micrographs using several optical sections were composed using the software package HeliconFocus 4.50 (Kozub *et al.*, 2008).

Results

The revision confirmed identification of most specimens of *Pleuridium subulatum*; this species is not rare in European Russia and is known from scattered collections in Asian Russia. We saw no collections of *Pleuridium acuminatum* from the territory of Russia: some samples named so appeared to belong to *P. subulatum*. However, the report by Klinggraef (1893) of both *P. acuminatum* and *P. subulatum* in Königsberg area (now Kaliningrad), with perfect descriptions of both species, convinces us that *P. acuminatum* occurred in this area; furthermore, this locality is rather close to the *locus classicus* of of *P. acuminatum* near Stockholm, which is ca. 500 km to the north from Kaliningrad. Partyka (2005) reported *P. acuminatum* in several areas of Crimea, and this is the only species of the genus she reported from it.

In the course of the revision, two puzzling collections of *Pleuridium* from Kamchatka were revealed. They possessed paroicous sexual condition, but did not perfectly fit either *P. acuminatum*, *P. japonicum* or *P. palustre* (as well as any other known species of the genus). On the basis of them a new species, *Pleuridium kamchaticum*, is described below as a new species.

Taxonomy

Pleuridium Rabenh., Deutschl. Krypt.-Fl. 2(3): 79. 1848.

Description (based on Russian collections [or with some features of species, which could be found in Russia and therefore included in the key to identification]. *Plants* small, in small loose tufts, green or yellow-green. *Stems* short, simple or weakly branched; central strand present [or, rarer, absent], rhizoids at stem bases, smooth. *Leaves* erect-spreading or erect, in proximal parts of stems distant, small, ovate to deltoid; becoming larger and crowded near stem apex, from oblong or ovate base gradually or abruptly narrowed into subulate acumina filled by costa; margins plane, serrulate distally or subentire, all cells smooth, alar cells not differentiated; costa with one row of guide cells, differentiated dorsal and ventral epidermal cells, dorsal stereid band of 1–2 cell layers, ventral stereid band of 0–1 cell layers; lamina unistratose or partially to completely bistratose at shoulders; cells short rectanular to elongate rectangular. *Gonioautoicous* or *paroicous*. *Sporophytes* usually single in perichaetia. *Setae* short. *Capsules* immersed, ovoid to almost spherical, with short beak, perfectly cleistocarpous [or with 2–3 differentiated rows of annulus cells, and then the capsule dehiscence sometimes follows these rows]; stomata in lower part of urn [or in the middle]. *Spores* large. *Calyptrae* cucullate, smooth.

Key to species identification

1. Plants autoicous, antheridia enclosed in leafy buds in axils of stem leaves ..... 1. *P. subulatum*
— Plants paroicous, antheridia naked in axils of upper leaves close to archegonia ..... 2.
2. Annulus ± differentiated; Japan ..... [*P. japonicum*]
— Annulus not differentiated; various regions 3
3. Stomata in the middle of capsule; calyptrae split in several lobes at base; stems without central strand ..... [*P. palustre*]
— Stomata in the lower part of capsule; calyptrae with one split at base; stems with central strand 4
4. Antheridia 4–15; leaves from ovate or oblong-ovate bases ± abruptly narrowed into subulate acumina; perichaetial leaf lamina in transverse section unistratose at shoulders or with few bistratose patches . ..... 2. *P. kamchaticum*
— Antheridia 1–3; leaves from oblong bases gradually narrowed into subulate acumina; perichaetial leaf lamina in transverse section partially to completely bistratose at shoulders ..... 3. *P. acuminatum*

1. **Pleuridium subulatum** (Hedw.) Rabenh., Deutschl. Krypt.-Fl. 2(3): 79. 1848. — *Phascum subulatum* Hedw., Sp. Musc. Frond. 19. 1801.

Description. *Plants* minute to small, green to greenish-yellowish, gregarious or in loose tufts. *Stems* 0.3–0.8 cm, erect, simple or branched; central strand present. *Leaves* erectopatent, spreading or secund, 1.0–1.7×0.15–0.3 mm, from ovate bases abruptly tapered into long, subulate acumina; lamina 1-stratose at base and shoulders, sporadically 2-stratose at apex; margins plane, entire below, serrulate distally; costa distinctly defined, 40–80 μm wide at base; basal cells rectangular to short rectangular, 10–40×5–10 μm, marginal cells narrower than adjacent cells, 4–8 μm wide, shoulder cells short rectangular, upper cells long rectangular to linear. *Autoicous*. *Antheridia* in persistent axillary leafy buds in distal portion of stem or throughout its length. *Perichaetial leaves* from oblong to ovate-lanceolate base ± abruptly tapered into narrow, subulate acumina 2.0–3.5 mm long; perichaetial leaf lamina in transverse section unistratose at shoulders. *Setae* 0.1–0.3 mm, yellowish. *Capsules* yellowish-brownish, ovoid, elliptic to rounded, 0.6–1.2×0.4–0.6 mm;

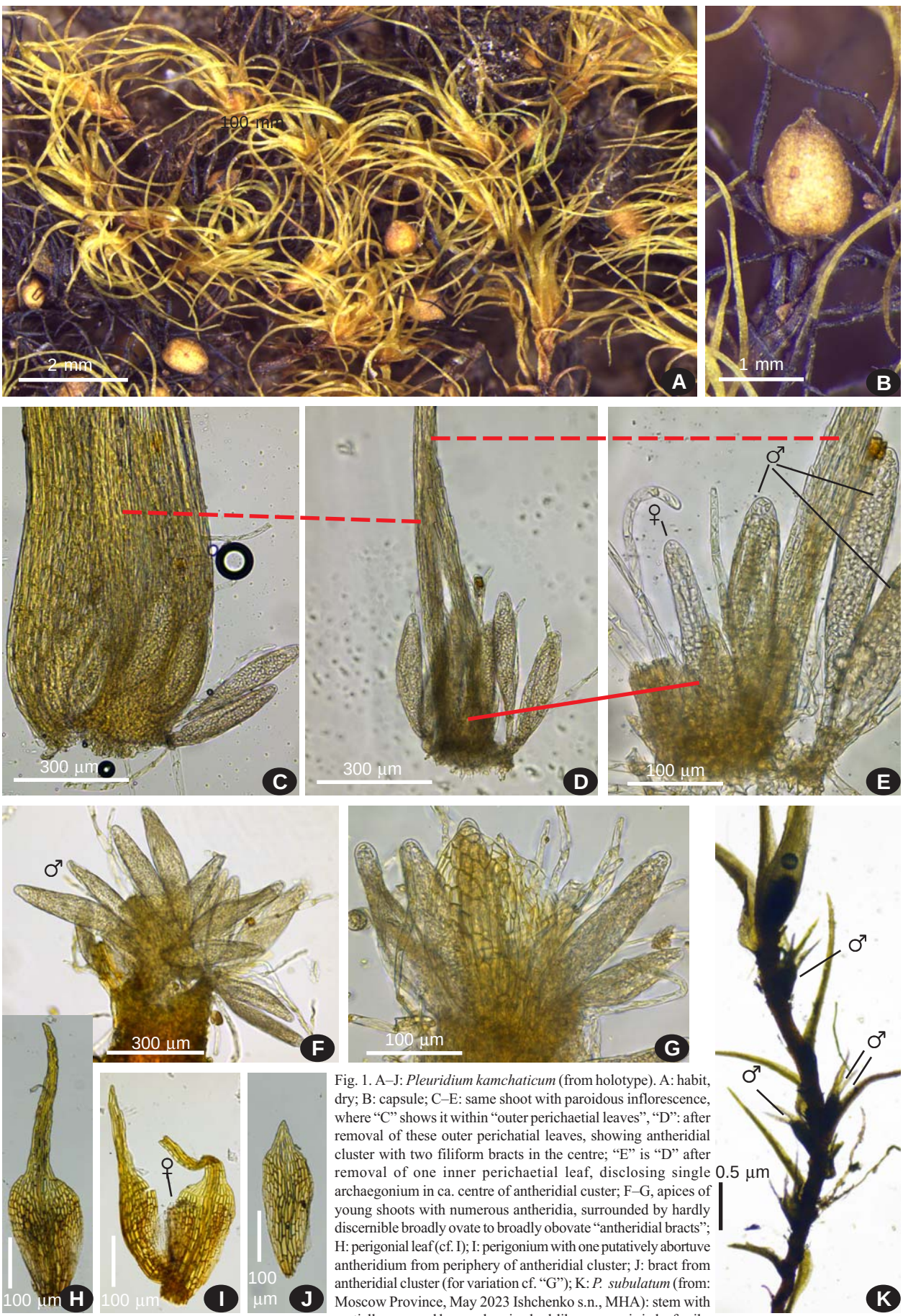

Fig. 1. A–J: *Pleuridium kamchaticum* (from holotype). A: habit, dry; B: capsule; C–E: same shoot with paroidous inflorescence, where "C" shows it within "outer perichaetial leaves", "D": after removal of these outer perichatial leaves, showing antheridial cluster with two filiform bracts in the centre; "E" is "D" after removal of one inner perichaetial leaf, disclosing single archaegonium in ca. centre of antheridial custer; F–G, apices of young shoots with numerous antheridia, surrounded by hardly discernible broadly ovate to broadly obovate "antheridial bracts"; H: perigonial leaf (cf. I); I: perigonium with one putatively abortuve antheridium from periphery of antheridial cluster; J: bract from antheridial cluster (for variation cf. "G"); K: *P. subulatum* (from: Moscow Province, May 2023 Ishchenko s.n., MHA): stem with partially removed leaves showing bud-like perogonia in leaf axils.

Fig. 2. A–B, E: *Pleuridium kamchaticum* (from holotype); C–D, F: P. acuminatum (from Spain, La Pedrisa, Ignatov & Spirina 19-1135, MHA. A, C: distal portion of leaf acumina; B, D: leaf shoulders; E, F: leaf transverse sections.

exothecial cells thin-walled, round-polygonal to shortly rectangular-polygonal, stomata superficial, in proximal part of capsule, annulus cells totally absent. *Spores* 21–33 µm. *Calyptrae* cucullate.

Distribution. *Pleuridium subulatum* is the most widespread species of the genus, occurring in Europe, North Africa, Macaronesia, Asia, North America, West Indies (Puerto Rico), New Zeland, Oceania; in Russia it is common in its European Part, while in Asian Russia it is a rare species in Altai Territory, Transbaikalia, Central Yakutia and Kamchatka. It grows on bare soil.

Specimens examined: EUROPEAN RUSSIA: **Kaliningrad Province**: Bagrationovsk Distr., *Rozhina s.n.* (MHA9042241). **Leningrad Province**: Sablino Settl., 7 June 1951, *Abramov* (LE); Vel'kota village, *Vyunova 464a* (LE); Shchugovitsy village, *Ignatov s.n.* (LE, MHA9042236). **Pskov Province**, Sebezh Sity, 19 Apr 2001 *Andreeva* (LE); Bezhanitsy Distr., *Nosova s.n.* (MHA9042237). **Novgorod Province**: Volkhov River, 24 Apr 2001 *Andreeva* (LE B-0039597); Batutino village, 1 Jul 1999 *Andreeva* (LE B-0039598). **Vologda Province**: Molochnaya station, 20 June 1926 *Korczagin* (LE); Okulovskoe Lake, 30 June 2002 *Andreeva* (LE). **Tver Province**, Nelidovo Distr., Tsentralno-Lesnoy Nature Reserve, *Ignatov s.n.* (MHA9101527). **Moscow Province**: Podolsk District, June 1965, *Tikhomirova* (LE); Odintzovo District, 1 May 1990, *Ignatova & Ignatov* (LE B-0039599); Mozhaisk District, 14 Apr 1900, *Fedchenko* (LE); Moscow, 11 May 1897, *Zickendrath* (LE); Istra Distr., Pavlovskaya Sloboda Settl., *Ignatov s.n.*

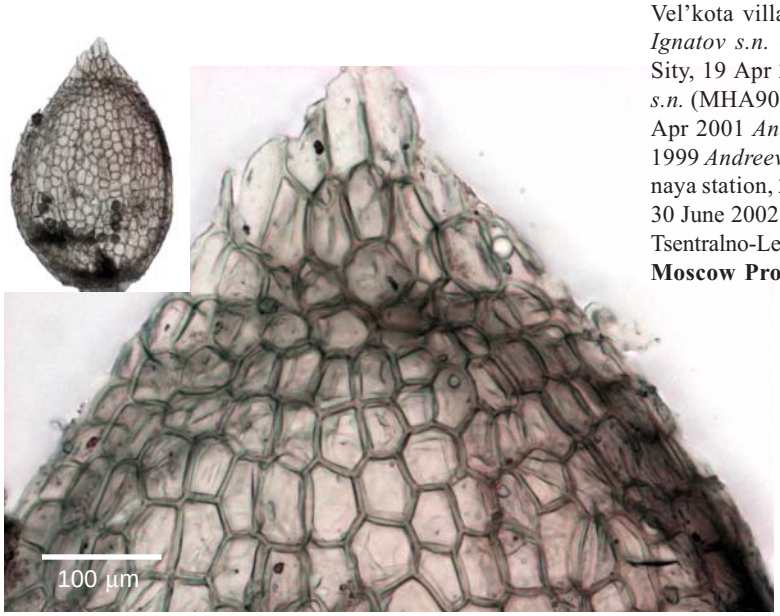

Fig. 3. *Pleuridium kamchaticum* (from holotype): exothecium, showing the absense of any annulus-like cells differentiation in supapical part of capsule; inset: photo of whole capsule longitudinally sectioned into halves.

Fig. 4. *Pleuridium kamchaticum* (from holotype): A–D: leaf transverse sections; E, J: habit< wet; F: laminal cells in acumen; G: shoulder laminal cells; H: distal leaf cells; I: habit, dry; K–L: perichaetial leaves; M–P: stem leaves; R: basal leaf cells. Scale bars: 2 mm for E; 1.5 mm for, I–J; 1 mm for K–P; 100 µm for A–D, F–H, R.

(MHA9042232); Krasnogorsk Distr., between Arkhangelskoe and Glukhovo, *Ignatov s.n.* (MHA9042221); Moscow, Krylatskoe, *Ignatov s.n.* (MHA9042216); Moscow, Main Botanical Garden, *Ignatov s.n.* (MHA9042223). **Vladimir Province**: Suzdal distr., *Seregin M-1490* (MHA9042239) **Kaluga Province**: Peremyshl Distr., *Teleganova 07-144* (MHA9042240); Kaluga, *Teleganova 04-1a* (MHA). Borovsk Distr., Satino, *Maksimova s.n.* (MW). **Orel Province**: Mtsensk City, *Vyshegorodskikh* (LE B-0039595, MHA9042243). **Kursk Province**: Tsentralno-Chernozemny Nature Reserve, *Zolotov s.n.* (MHA9042244); same place, *Ignatov s.n.* (MHA9042242); same place, *Ignatov s.n.* (MHA9042245). **Voronezh Province**: Boguchary Distr., *Popova 28* (MHA9042238); Verkhniy Mamon Distr., *Popova s.n.* (MHA). **Ulyanovsk Province**: Ni-

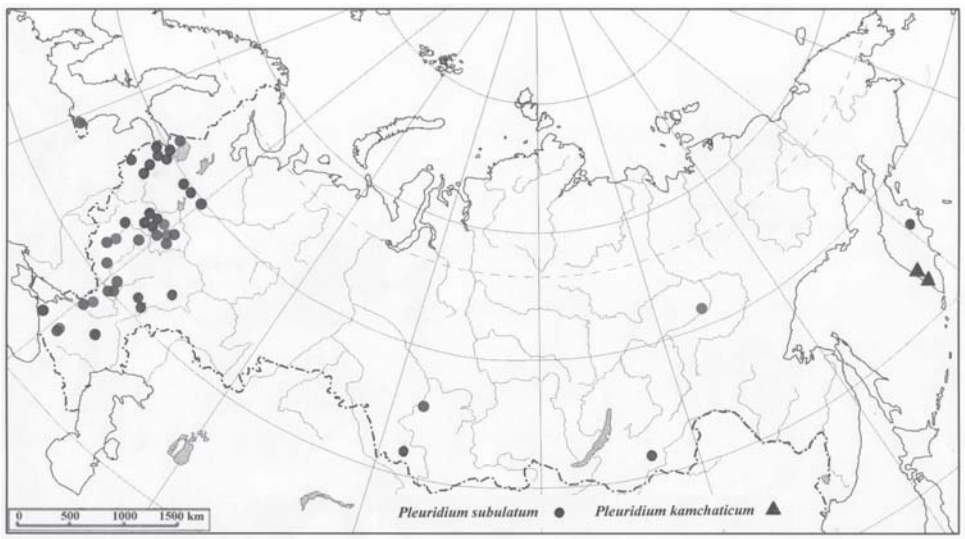

Fig. 5.Distribution of *Pleuridium subulatum* and *P. kamchaticum* in Russia based on the studied collections.

kolaevsk District, Proskovino village, *Mordvinov* (LE B-0039596). **Saratov Province**: Saratov District, Burkino station, 12 May 1970, *Cherepanova s.n.* (LE); Atkarskii District, Nesterovka village, 15 May 1979, *Cherepanova s.n.* (LE). **Republic of Kalmykia**: Gorodovikovsk District, 19 May 2010, *Ulrainskaya s.n.* (LE). **Republic of Adygea**: Maikop Distr., *Akatova 11-04* (MHA9042249); 26.IV.2009 *Akatova s.n.* (MHA9042248). **Krasnodar Territory**: Anapa Distr., Utrish Nature Reserve, *Ignatov & Ignatova 05-709* (MHA9042250).

ASIAN RUSSIA: **Altai Territory**: Krasnoshchekovsky District, 20 June 1995, *Pisarenko s.n.* (LE). **Transbaikal Territory**: Daursky Ridge, Aratsa River, 51°54'50"N, 114°25'06"E, 14 Jul 2012, *Czernyadjeva 4-12* (LE). **Republic Sakha/Yakutia**: Yakutsk, *Ivanova s.n.* (MHA9042246). **Kamchatka Peninsula**: Ushkovsky volcano, 56°11'N, 160°21'E, 21 Jul 2003, *Czernyadjeva 53* (LE).

2. **Pleuridium acuminatum** Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 20: 406 1863.

Description [based on European collections and description of Klingraeff (1893)]. *Plants* small, green or yellowish, gregarious or in loose tufts. *Stems* 0.2–0.6 cm, erect, simple or branched; central strand present. *Leaves* mostly erect, 0.8–1.4×0.1–0.3 mm, from ovate base gradually tapered into long subulate acumina; lamina at shoulders often bistratose at places; margins plane, entire below, entire or minutely serrulate distally; costa indistinctly defined, 40–70 μm wide at base; basal cells rectangular to short rectangular, 15–40×4–8 μm, marginal cells narrower than adjacent cells, 4–8 μm wide, shoulder cells short-rectangular, upper cells long-rectangular to linear. *Paroicous*. *Antheridia* 2–3, around archegonia at stem apex. *Perichaetial leaves* 2.0–3.0 mm long, from oblong to ovate-lanceolate base ± grdually tapered into narrow, subulate acumina; perichaetial leaf lamina in transverse section partly bistratose at shoulders. *Setae* 0.1–0.3 mm, yellowish. *Capsules* yellowish-brownish, elliptic to rounded, 0.6–1.0×0.4–0.8 mm; stomata superficial, in proximal part of capsule. *Spores* 22–30 μm. *Calyptrae* cucullate.

3. **Pleuridium kamchaticum** Czernyadjeva & Ignatova sp. nova Figs. 1A–G; 2A–B, E; 3–4.

Holotype: South-West Kamchatka Peninsula, interfluve of Bolshaya Bystraya and Nachilova Rivers, 53°05'N, 156°53'E 160 m alt., on bare soil along of the roadside among the sedge marsh, 18 August 2002, Czernyadjeva 83 (Holotype: LE B-0040287!, isotypes MHA!, MW!).

Diagnosis: The new species is similar to *P. acuminatum* and *P. japonicum* in having paroicous sexual condition and habit; it differs from *P. acuminatum* in having 4–12 vs. 2–3 antheridia in axils of perichaetial leaves, more abruptly narrowed leaf acumina and mainly unistratose vs. bistratose leaf lamina at leaf sholders; the differences from *P. japonicum* include total absence vs. presence of smaller, thick-walled cells at the level of operculum, at least sometimes causing operculum fall off.

Description: *Plants* small, yellowish-green, becoming blackish with age, in small loose tufts. *Stems* 0.3–0.6 cm, erect, simple or branched; central strand present; rhizoids at base, smooth. *Leaves* erectopatent, often secund, slightly flexuose when dry, becoming larger in upper part of stem, crowded at stem apex, (1.0–)1.5–2.3×0.15–0.3 mm, from oblong-ovate bases ±abruptly tapered to a long, subulate acumina; margins plane, entire below, serrulate to irregularly serrate distally; costa distinctly defined, strong, often filling most of the subula, 64–100 μm wide at base, with guide cells in 1 row, dorsal stereid band 1–2 layered, ventral stereid band 0–2-layered, ventral and dorsal epidermal cells differentiated; lamina unistratose at base, sporadically 2-stratose distally; basal cells rectangular, (15–)30–45(–55)×7–15(–20) μm, marginal cells narrower than adjacent cells, 4–7 μm wide, shoulder cells short-rectangular to quadrate, upper cells long-rectangular to linear, all cells smooth, alar cells not differentiated. *Paroicous*. *Antheridia* 4–12, clustered with archegonium in a groups within "outer perichaetial leaves", which are surrounding inflorescence

and are similar to upper stem leaves; occasinally 1–2 antheridia with small perigonial bracts occur immediately below apical inflorescence. *Outer perichaetial leaves* from oblong-ovate base ±gradually narrowed into subulate acumina, 1.9–3.0 mm long, perichaetial leaf lamina in transverse section often bistratose at shoulders. *Perigonial bracts* broadly ovate, broadly obovate to obovate-lanceolate. *Inner perichaetial leaves* are thiny filiform bracts near archaegonium. *Setae* 0.1–0.4 mm, yellowish. *Capsules* cleistocarpous, erect, immersed, yellowish-brownish, ovoid, elliptical to spherical, 0.6–1.1×0.4–0.6 mm; exothecial cells thin-walled, round-polygonal to shortly rectangular-polygonal, stomata superficial, in proximal part of capsule. *Calyptrae* cucullate. *Spores* 24–29 μm.

Specimens examined: RUSSIA, **Kamchatka Peninsula**, Left Kihchik River basin, 53°25'N, 156°40'E, on bare soil along of the roadside, 9 August 2001, *Czernyadjeva 75* (LE B-0040288).

Distinction. *Pleuridium kamchaticum* is similar to *P. acuminatum*, *P. subulatum* and *P. japonicum* in habit, leaves with narrow, subulate acumina, and spore size. Paroicous sexual condition immediately separates it from *P. subulatum*. In the latter species perigonia are speading along the stem in leaf axils, and even if the time of the year is that when antheridia are wanished, 2–3 small perigonial leaves with subulate acumina are usually well seen in leaf axils far below the stem apex. Leaves of *P. kamchaticum* are similar to *P. subulatum* and *P. japonicum* and quite different from *P. acuminatum*. In the latter species, they are more gradually tapered to acumina, and in the transitional part there are many narrow cells (Fig. 2) which form bands, so the transverse sections of leaves in this portion look uneven: there are bistratose patches outside the costa, whereas in three other species there are no such bistratose parts separated from costa by unistratose areas. The presence of this pattern is apparent from the frontal view, because cells in bistratose places are narrower, making the costa looking "branched" towards the base (Fig. 2).

Pleuridium japonicum is similar to *P. kamchaticum* in paroicous sexual condition and leaves with clearly defined costa, but it has 2–4 antheridia near stem apex, and its capsules have clearly differentiated annulus of 2–3 rows of smaller and more thick-walled cells. This annulus seems not always causes separation of the operculum, although Deguchi *et al.* (1994) illustrated that at least sometimes operculum falls off. Capsules of *Pleuridium kamchaticum* lack any differentiation of cells in their distal parts (Fig. 3), i.e. this species is similar to *P. acuminatum* and *P. subulatum* in having perfectly cleisocarpous condition.

There is a problem with the exhausive comparison of Kamchatkan plants with *Pleuridium japonicum*. Deguchi *et al.* (1994) referred to it all Japanese specimens, previously identifies as *P. subulatum* or *P. palustre*. We were able to study spores of one such specimen (Musci Japonici Exs. # XXX) and found them quite different from those of the holotype of this species (Deguchi *et al.*, 1994). Therefore it seems possible that in Japan there are more than one species of the genus *Pleuridium.*

Spore ornamentation in the genus Pleuridium

In order to compare a new species with other similar *Pleuridium* species from Eurasia we undertook SEM study of spore ornamentation (Figs. 6–8). Surprizingly, bacula in the premature, the fully and optimally developed, and the fully but suboptimally developed spores appeared to be sometimes different.

Pleuridium subulatum spores were especially polymorphous in different populations (Fig. 6), although the spores from any single well-developed capsule were rather homogeneous in their ornamentation. The shape of bacula are somewhat dependent on the gold coating mode. Not coated spores have bacula of the equal width to sligtly broadened above and thus somewhat clavate (Fig. 6C, D). However, after 5 nm coating with gold (Fig. 6E), their caputs appeared to be more abruptly delimited. A similarly ornamented spores from the nearby locality (Fig. 6A–B), coated with ca. 30 nm of gold were found to be still narrower. The bacula are anastomosing at bases by low ridges (Fig. 6A, E), and small granules are scattered among these ridges. Bacula bases are sometimes split and some bacula look raised on short roots (Fig. 6A). Bacula tips are either solid and smooth (Fig. 6C–E) or forked and covered by sparse granules (Fig. 6A–B). Having a relatively limited observation, we refrain from more detailed explanation of effects of a sample preparation. However, drastic variation between various collections shown in Fig. 6 requires at least a preliminary hypothesis if the observed difference discloses a genetic variation or not. SEM and light microscopy studies may be interpreted that the main reason for this variation is a moisture condition during the sporophyte development. Plants collected in hemiboreal forest zone, where sporophytes of *P. subulatum* are developing in cold and wet conditions, have spores with high and thin bacula or clavae (Fig. 6A–E). Some bacula from these areas form arches (arrowed in Figs. 6B, E), which are not seen in other samples. In more southern population, in oak forests vegetational zone, where plants experience periodocal drought during spore maturation, the bacula are shorter and thicker (Fig. 6F–H), and ultimately, in steppe environments, the spore ornamentation is compised of scattered verrucae (Fig. 6I–J). Similarly to the latter, spores taken from Polish plants of *P. subulatum,* illustrated by Deguchi *et al*. (1994) with SEM images, also have scattered granulae or verrucae. Small round granulae in between bacula or verrucae occur more or less regularly on the surface of spores from all studied collections. Currently we are inclined to explain the difference in spore ornamentation by the developmental conditions, but this might have different causes, and this intriguing question certainly requires further study.

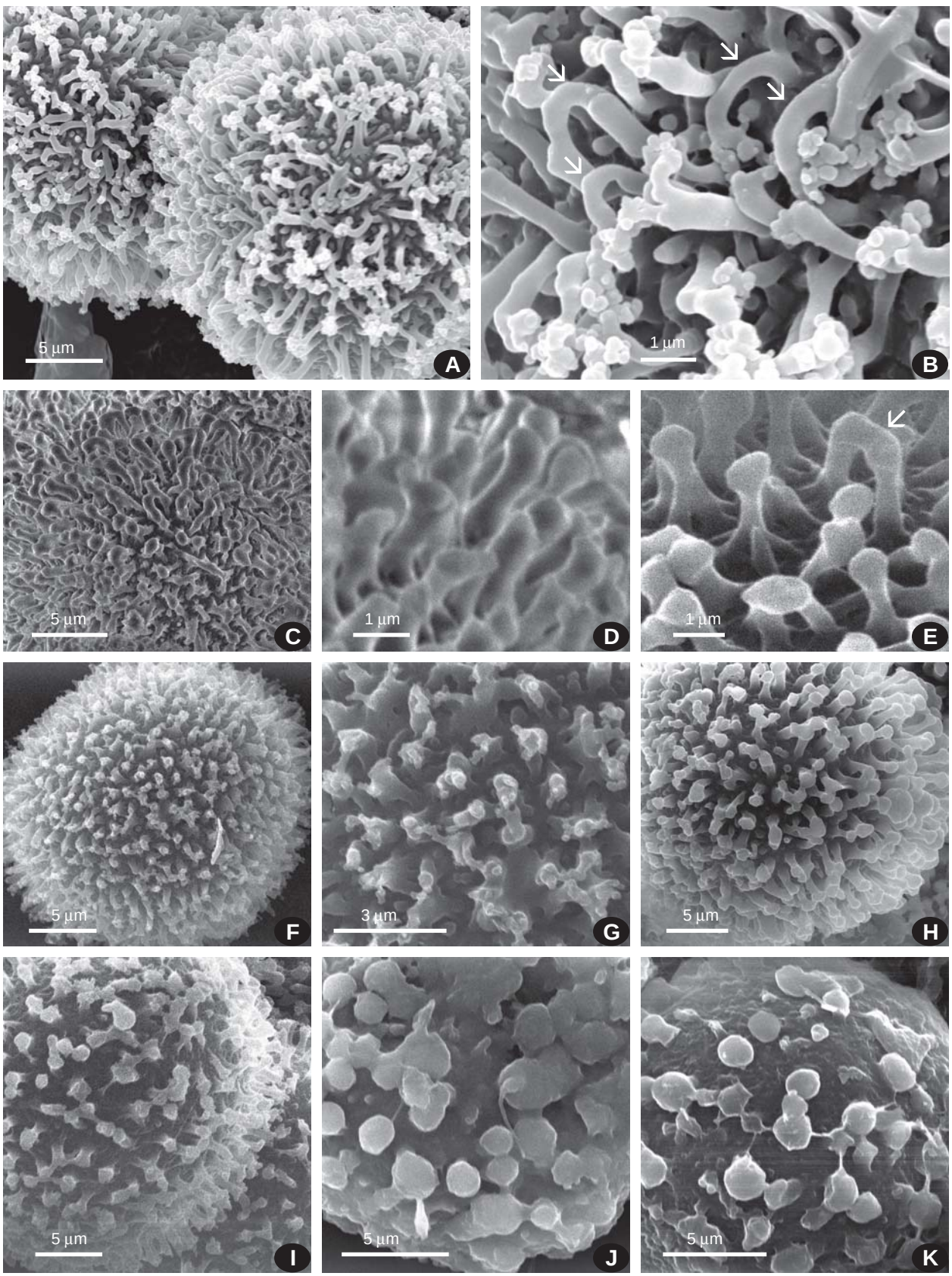

Fig. 6. Spores of *Pleuridium sibulatum* from Russia: A–B: from Moscow Province, Ignatov & Ignatova 10 June 2018 (MW 9110630); C–E: from Vladimir Province, coll. Seregin M1490 (MHA 9042239); F–G: Moscow, Ignatov 21 June 1996 (MHA90422290); H: Adygeia, Akatova 26 April 2009 (MHA 9042248); I: Altai Territory, Pisarenko, 2 June 1995 (MHA9042247); J–K: Kursk Province, Ignatov, 20 May 1989 (MHA 9042243).

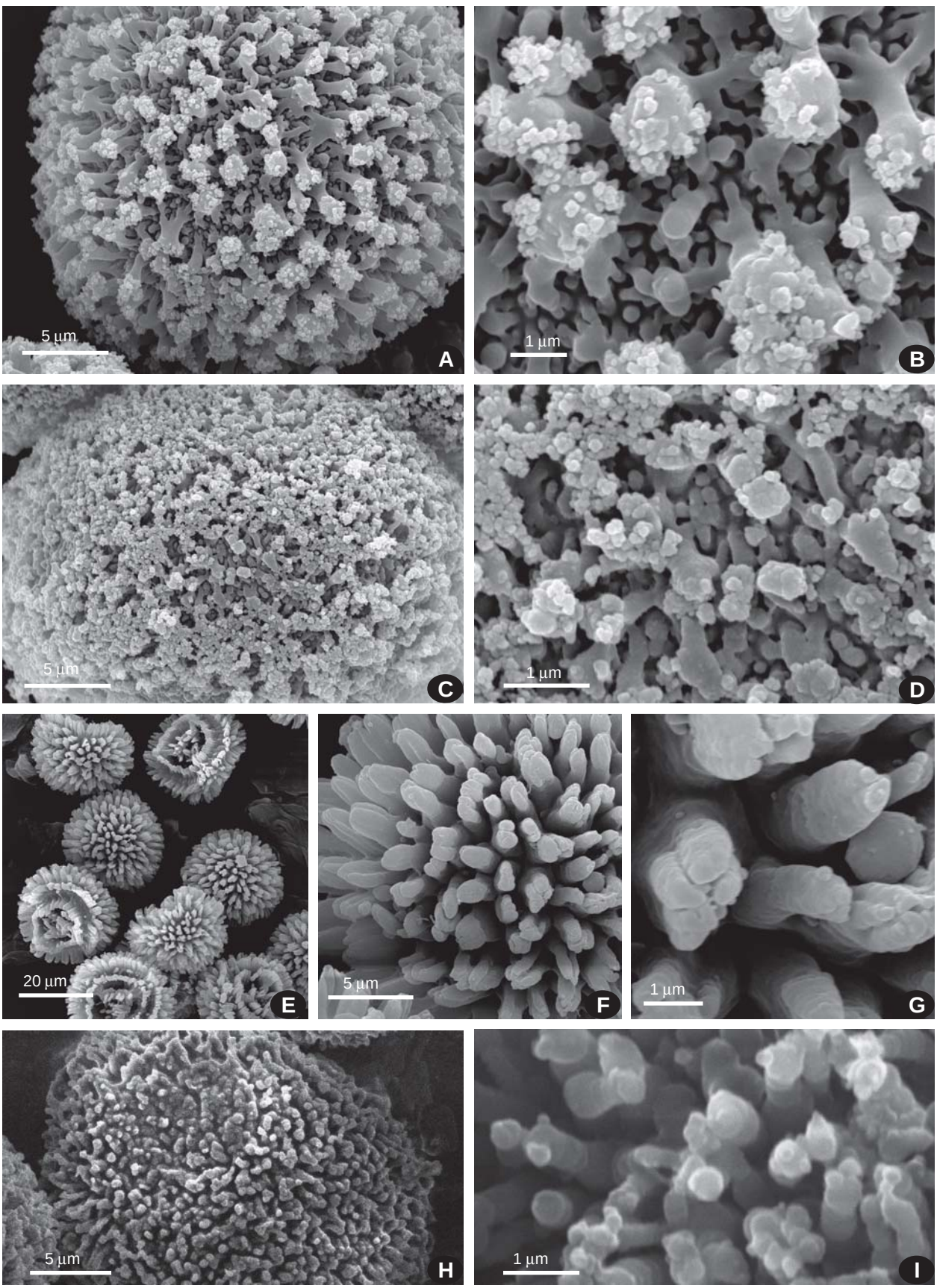

Fig. 7. Spores of *Pleuridium*: A–B: *P. acuminatum* (from Czechia, Bryophyta Czechoslovaca (Prague) Exs 121, coll. Deyl, 5.1933 (LE); C–D: *P. acuminatum* (from USA, North Carolina, Mosses of North America 972 (ed. Crum & Anderson), coll. Schofield & Robinson 11259, 3 May 1960 (LE); E–I: *P. japonicus* (sub *P. subulatum*), from two capsules (E–G premature; H–I mature), from Japan, Musci Japonici Exs. 485 (ed. Noguchi), coll. Mayebara 9 Apr 1952 (LE).

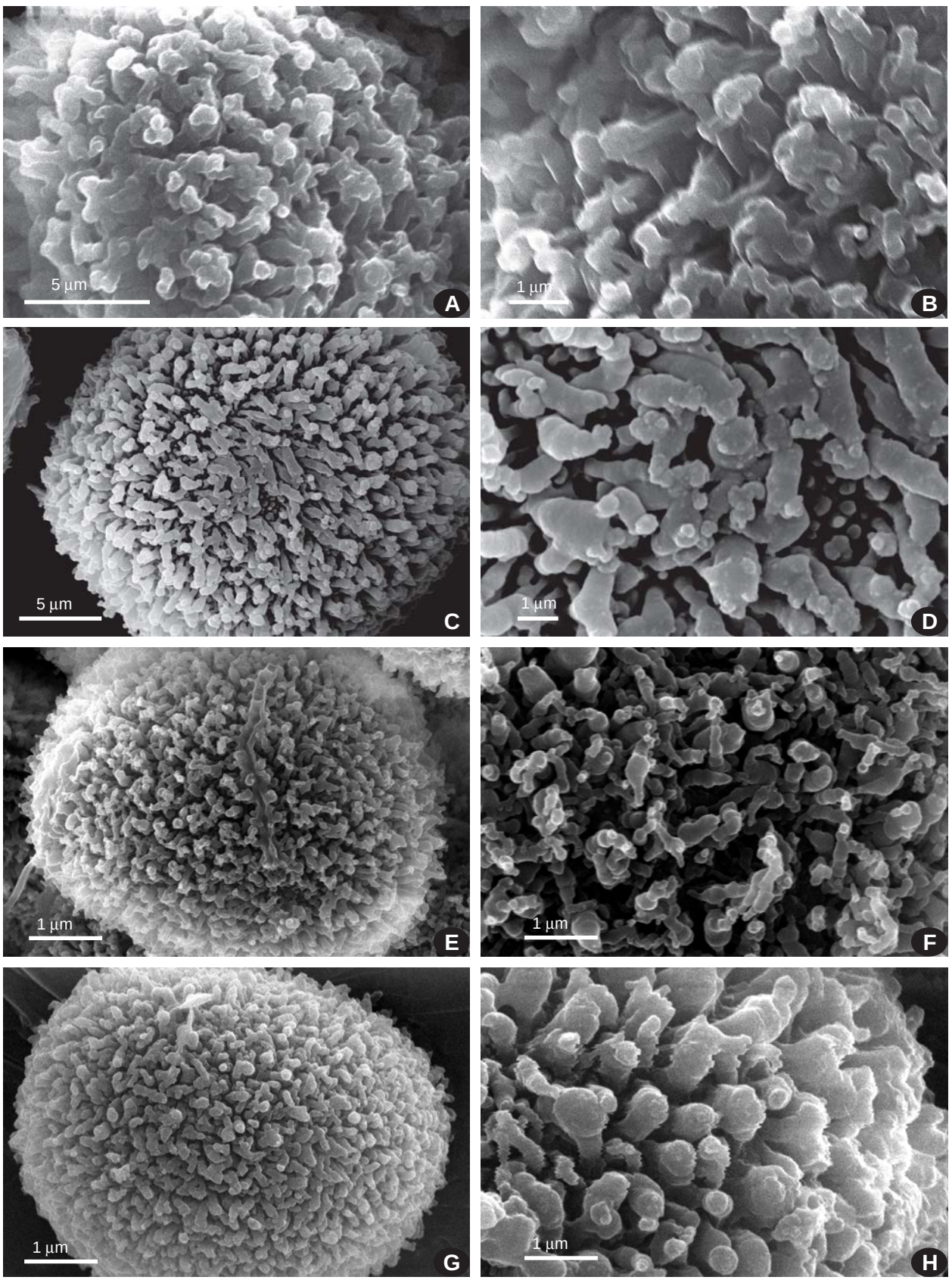

Fig. 8. Spores of *Pleuridium kamchaticum* (A–D), from holotype (Kamchatka, Czernyadjeva 18 August 2002, #83, LE B-0040287), and *P. palustre* (E–I). E–F: from Czechia (Flora Bohemiae et Moraviae Exs. 132 (F. Petral), as *P. alterrnifolium*), coll. A. Schmidt, Sept. 1911 (LE), H–I: from Poland, Bryotheca Silesiaca 311 (as *Sporledera palustris*), coll. Limpricht, May 1869 (LE).

Such wide variation in ornamentation of spore*s* of *P. subulatum* might look unique, however Carrión *et al*. (1990) described another example of quite strong variation, also with TEM study, observed in *Tortula acaulon* Hedw. (as *Phascum cuspidatum*), the species that often grows with *Pleuridium subulatum* in a similar habitats and also occurs in various climatic regions.

Spores of *P. aciminatum* (Fig. 7A–D) are covered with more dense and stout bacula, raised on much higher roots, which are more strongly anastomosed as it is seen in European specimen (Fig. 7A–B), while obscured in the North American one because of dense bacula arrangement. Small granulae on the spore surface are seen between anastomoses, in a way similar to *P. subulatum*. Granulae on bacula tips are larger and more numerous, often forming conspicuous clusters, which are principally similar in two studied samples, from Europe (Fig. 7A–B) and North America (Fig. 7C–D).

Spores of *Pleuridium japonicum* were studied from two capsules of one specimen, but they are very different from other spores (Fig. 7E–I). Spores from one capsule are clearly heteropolar (Fig. 7E–G), possessing collar-like bacula arrangement at the proximal pole, and also the branches of their high bacula are fused by two or four, thus looking as a columns slightly cut at their ends. These spores were taken from a premature capsule, still greenish and somewhat pellucide. Another spore from the same collection has ornamentation much more similar to other species of *Pleuridium*, mainly because of small globules covering distal parts of bacula (Fig. 7I). The mentioned aspect of premature spores, where bacula look slightly cut at their ends is not well seen in mature spores, probably because of bacula branching in the course of maturation.

Baculi on spore surfaces of *P. kamchaticum* (Fig. 8A–D) are massive, regular, but with slight constrictions along their length, and terminate with a cluster of granulae, somewhat similar to those in *P. acuminatum* and *P. subulatum*. However, the bacula of *P. kamchaticum* are never unbracheded. Granulae on the spore surface are seen between bacula.

Most similar to *P. kamchaticum* pattern of spore ornamentation was observed by us in *P. palustre* (Fig. 8E–H); two different samples from Europe were used for that. Their baculi lack constrictions, observed in *P. kamchaticum*, but otherwise are very similar. In addition to similarity in spore ornamentation, *P. kamchaticum* is similar to *P. palustre* in capsule shape, which is broadest markedly below the middle (cf. Fig. 1A), although unlike the latter, its calyptra is cucullate and stem possesses a central strand.

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