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THE GENUS *JOCHENIA* (BRYOPHYTA) IN RUSSIA

РОД *JOCHENIA* (BRYOPHYTA) В РОССИИ

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Abstract

Jochenia pallescens s.l., commonly known as *Hypnum* (or *Stereodon*) *pallescens* has been treated as a monospecific group. Some authors, however, distinguished a second species, most commonly called *Hypnum reptile*, while other authors accepted it as a variety of *H. pallescens*. Recent molecular phylogenetic studies proved the existence of two genetic entities within *Jochenia*. One species, *J. pallescens*, is widespread in the Holarctic, whereas the distribution and morphological delimitation of another species, *J. protuberans*, were not clear. The present study addresses the elucidation of morphological distinctions and geographical distributions of these two species. *Jochenia protuberans* is likely confined to the areas with humid climate. It occurs in the Russian Far East in Kamchatka, Kuril Islands, Sakhalin Island, and in Baikal Lake area, in the Khamar-Daban Range, in humid sites at high elevations. It also occurs in mountains of Central Europe, Caucasus, and Canada (Quebec). Distinctions between the two species of *Jochenia* are numerous both with the gametophyte and the sporophyte, but occasional intermediates between them are found, being probably hybrids between these two species.

Резюме

Jochenia pallescens s.l. – вид, широко известный как *Hypnum* (или *Stereodon*) *pallescens,* обычно понимается в широком смысле. Некоторые авторы, однако, различают второй вид, который чаще всего приводится под названием *Hypnum reptile*; другие авторы принимают этот таксон в качестве разновидности *H. pallescens*. Недавние молекулярно-филогенетические исследования подтвердили существование двух генетически различающихся видов в роде *Jochenia*. Один из них, *J. pallescens,* широко распространен по всей Голарктике; распространение и морфологические отличия второго вида, *J. protuberans*, до сих пор оставались неясными. Целью данной работы является уточнение морфологического разграничения этих видов и их распространения. *Jochenia protuberans*, по-видимому, приурочена к регионам с океаническим климатом. В России этот вид распространен на Дальнем Востоке: Камчатке, Сахалине и Курильских островах, а также он был один раз собран в окрестностях озера Байкал, во влажном месте в высокогорьях хребта Хамар-Дабан. *Jochenia protuberans* известна также в горах Европы, Кавказа и в Канаде (провинции Квебек). Выявлены многочисленные морфологические отличия между этими видами как в гаметофите, так и в спорофите; однако иногда встречаются промежуточные формы, которые, вероятно, являются гибридами между *J. pallescens* и *J. protuberans*.

KEYWORDS: pleurocarpous mosses, molecular barcoding, ITS

INTRODUCTION

The genus *Hypnum* Hedw. in the 19th century included the majority of pleurocarpous moss species, being one of the largest genera of mosses including 4926 published species and infraspecific taxa (http://tropicos.org/name.search, accessed April 2022).

Early molecular phylogenetic analyses considerably clarified the genus *Hypnum*; *Hypnum pallescens* (Hedw.) P. Beauv. was excluded from *Hypnum* and placed, along with many other former species of *Hypnum* s.l., in the genus *Stereodon* (Brid.) Mitt. (Gardiner *et al*., 2005). Subsequent studies further split *Stereodon*, subdividing it into five genera, including *Jochenia* (Schlesak *et al.*, 2018).

The genus *Jochenia* Hedenäs, Schlesak & D. Quandt was originally established for one widespread species *J. pallescens* (Hedw.) Hedenäs, Schlesak & D. Quandt in the family Stereodontaceae (Schlesak *et al.*, 2018). Shortly after, another generic revision of the genus *Hypnum* s.l. (Kučera *et al.*, 2019) confirmed the segregation of the genus and, moreover, segregated it into a monogeneric family Jocheniaceae. Also, these authors accepted the second species in this genus, *J. protuberans* (Brid.) Jan Kučera & Ignatov. For a long time the second taxon, closely related to *J. pallescens,* was mentioned in some European and North American publications, usually under the name *Hypnum reptile* Michx., being accepted as a

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species (Limpricht, 1895) or as a variety (Mönkemeyer, 1927).

Ando (1976) was the first bryologist who re-studied types of taxa now classified in *Jochenia* and produced an exhaustive overview along with the history of application and misapplication of names, including two concepts of *H. pallescens*. He provided illustrations of the type specimen of *Hypnum reptile* Michx. showing that it is not distinct from *H. pallescens*. At the same time, he found *Hypnum protuberans* to be rather distinct from *H. pallescens*, thus reviving the approach of Lindberg (1872) for these two taxa. However, Ando (1976) did not accept *H. protuberans* as a separate taxon, as it required further study. The main reason for that decision was the presence of transitional phenotypes. Unfortunately, Ando gave neither a complete morphological description of *J. protuberans*, nor a description of its distribution, although he mentioned that *J. pallescens* occurs in more continental areas. Most publications of the last decades of 20th century followed Ando, not accepting *J. protuberans* at any rank.

The resurrection of *Jochenia protuberans* as a distinct species was suggested by Kučera *et al.* (2019) based on DNA sequences from Central Europe and the Baikal area in South Siberia. Fedosov *et al*. (2022) stated that there are no data on the occurrence of *Jochenia protuberans* in other regions.

The present paper is focused on the distribution of *Jochenia protuberans,* mainly in Russia, and includes a discussion on its distinction from *J. pallescens.*

Material and Methods

Specimen selection. We studied the material deposited under *Jochenia pallescens* in MHA, MW and LE, selecting for sequencing most common phenotypes as well as superficially extraordinary ones.

Amplification and sequencing protocols were essentially the same as in our previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005).

Molecular analysis. The phylogenetic tree for *Jochenia* in Fig. 1A is rooted on *Rhytidium*, which sequence was found to be the closest to *Jochenia* by BLAST search (https://blast.ncbi. nlm.nih.gov/Blast.cgi, on February 2022). Sequences were aligned using Bioedit (Hall, 1999). Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012), with 10 000 000 generations. Maximum parsimony analysis was performed in Nona (Goloboff, 1994) in the Winclada shell (Nixon, 1999), with bootstrap calculations for 1000 replications (N searches 100, starting trees per rep 100, max trees 100, do max).

The program TCS (Clement *et al.*, 1999) was used to evaluate relationships among haplotypes within *Jochenia*. Gaps were coded as separate DNA characters (absent-present), and each was treated as a single character regardless of length.

Illustrations were made under stereomicroscope Olympus SZX-7 (digital camera Infinity 8-8) and Olympus CX43 (digital camera Infinity 1-2), with Z-stacking in Helicon Software (Kozub *et al.*, 2008). In figure captions specimens are marked by TCS code (see Fig. 1 and Appendix).

Results

DNA sequence study

The variation of ITS is low (12 parsimony informative characters, out of 609 in alignment after cutting incomplete ends), thus, expectedly, the tree is poorly resolved. *Jochenia* clade, Fig. 1A, includes a polytomy of: (1-2) two accessions represented the same collection of a putatively hybrid origin, (3) well supported clade of *J. protuberans* (PP=0.99, BS=95), (4) poorly supported clade of *J. pallescens* (PP=0.79, BS=50). Within the latter, one moderately supported clade (PP=0.97, BS=71) combines four specimens from southern Siberia and Russian Far East.

The TCS hapotype network (Fig. 1B) is, in general, consistent with the tree, outlining the most isolated group of *J. protuberans* of seven specimens: three from Asia, three from Europe and one from the North America. All of them belong to the same haplotype. In contrast, *J. pallescens* is more diverse genetically. No apparent geographic segregation was found among the sequenced samples, excepting four samples from southern Siberia and the continental Russian Far East. These four specimens form a moderately supported clade in the Bayesian analysis.

One specimen from the Kuril Islands was morphologically somewhat intermediate between *J. protuberans* and *J. pallescens* (Fig. 2B). Its sequence differed most strongly from the others; thus DNA was re-extracted and re-sequenced (sequences were used in the analysis separately). These two sequences are set apart from the clade of *J. protuberans* and the clade of *J. pallescens* in the phylogenetic analysis (Fig. 1A). In the TCS analysis they form a separate branch in between these species, but closer to *J. pallescens*.

Morphological study

Specimens with the ITS sequences of *J. protuberans* from Europe, Russian Far East, and Canada were found to be morphologically similar and fit well with the illustrations and description of this species by Ando (1976).

An additional search in herbaria revealed more samples of this species in Kamchatka, Sakhalin, and the Kuril Islands.

Specimens with the ITS sequences of *J. pallescens* appeared to be more diverse, as discussed below. The species is widespread in Russia, and confirmed from Central Europe and North America as well.

Taxonomy

Jochenia protuberans (Brid.) Jan Kučera & Ignatov, Taxon 68(4): 647. 2019. — *Hypnum protuberans* Brid., Bryol. Univ. 2: 612. 1827. Type: In saltus Thuringici sylvis, prope Rein-hardsbrunn (Germany), Bridel, B (not seen, illustrations published by Ando (1976)).

Description. *Plants* small to medium-sized, in loose mats, light or stramineous-green, rarely brownish, glossy. *Stems* creeping, 1–3(–6) cm long, regularly or irregular-

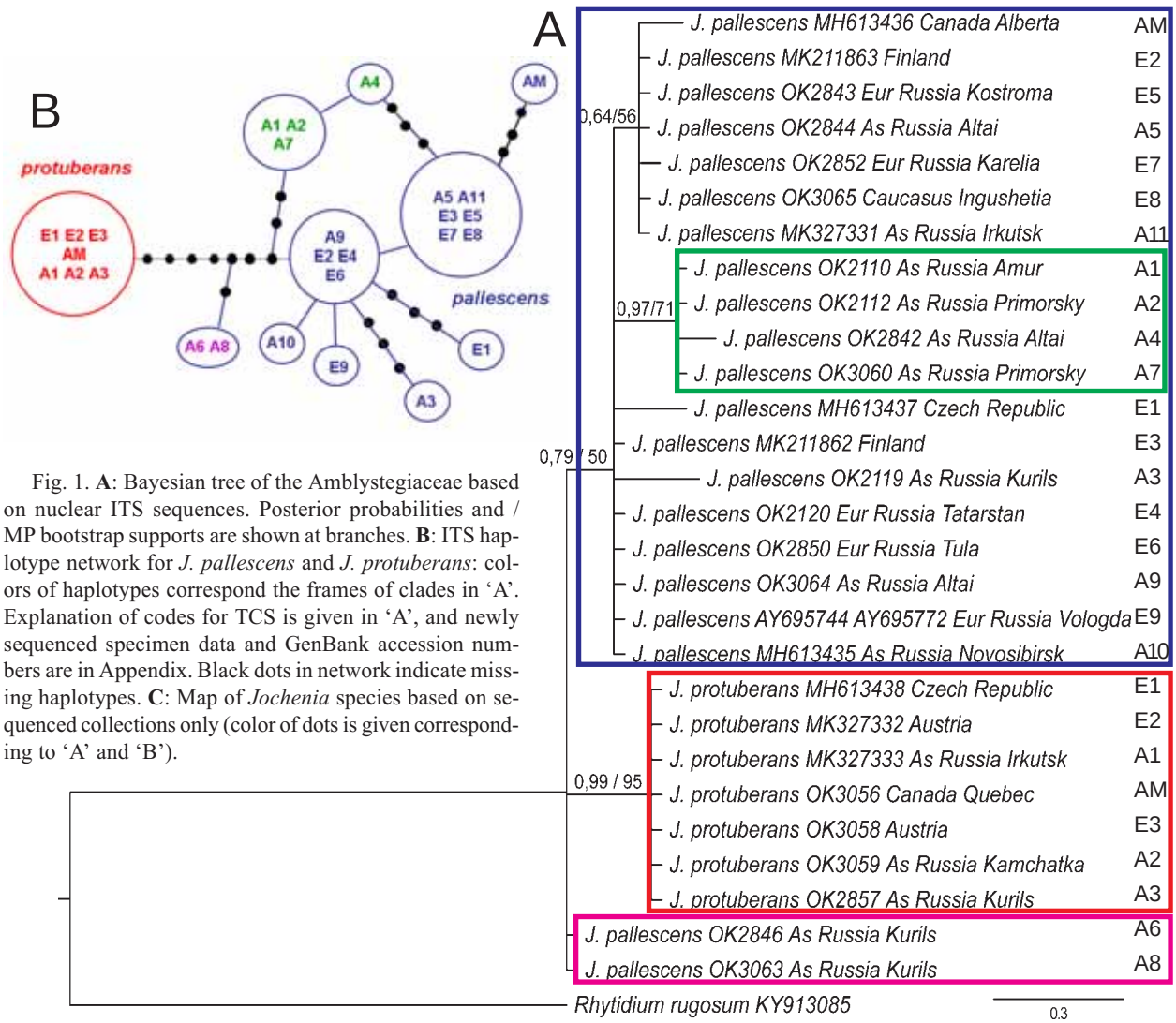

Fig. 1. **A**: Bayesian tree of the Amblystegiaceae based on nuclear ITS sequences. Posterior probabilities and / MP bootstrap supports are shown at branches. **B**: ITS haplotype network for *J. pallescens* and *J. protuberans*: colors of haplotypes correspond the frames of clades in 'A'. Explanation of codes for TCS is given in 'A', and newly sequenced specimen data and GenBank accession numbers are in Appendix. Black dots in network indicate missing haplotypes. **C**: Map of *Jochenia* species based on sequenced collections only (color of dots is given corresponding to 'A' and 'B').

ly pinnate, terete foliate, leaf tips turned to various directions; branches to 2–4(–5) mm long; central strand weak. *Stem leaves* falcate to straight but not secund, 0.8–1.2×0.4–0.5 mm, from ovate base ± abruptly tapered into narrow lanceolate acumina, slightly rounded to the insertions, slightly concave; margins plane or occasionally narrowly recurved below, serrulate throughout or entire below; costa double; *cells* (21–)30–55(–72)×(3–)4–6(–7) µm, elongate to linear, smooth or some cells indistinctly prorate; alar cells quadrate to short rectangular, ± thick-walled, in weakly delimited groups 3–6(–10) cells along leaf margins, (8–)12–17(–19)×(6–)8–12(–13) µm. *Branch leaves* 0.6–1.1×0.2–0.4 mm. *Setae* 0.8–1.2 cm. *Capsules* inclined, straight or slightly curved, urns cylindrical, 1.1–1.5 mm long, smooth; exothecial cells short-rectangular and polygonal, thin-walled. *Spores* 15–17 µm.

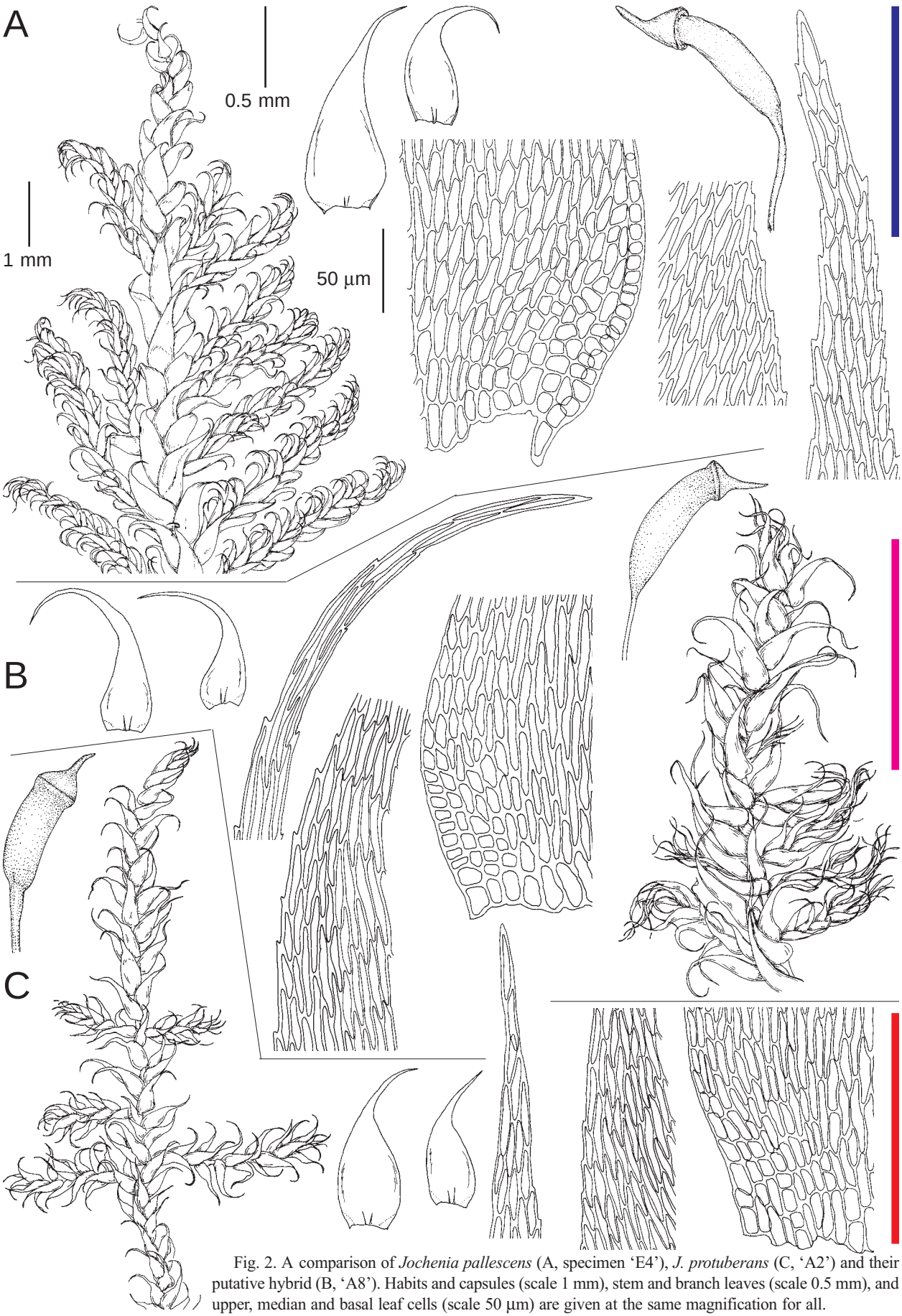

Fig. 2. A comparison of *Jochenia pallescens* (A, specimen 'E4'), *J. protuberans* (C, 'A2') and their putative hybrid (B, 'A8'). Habits and capsules (scale 1 mm), stem and branch leaves (scale 0.5 mm), and upper, median and basal leaf cells (scale 50 µm) are given at the same magnification for all.

Specimens examined: **EUROPE**: Poland, Sudety, 850 m, *Lisowsky* 3 Oct 1956 (Bryotheca Polonica 399) (LE); Germany, Reisengebrige (900 m elev.), *Limpricht* 29 Jul 1867 (Bryotheca Silesiaca 189)(LE); Germany, Saarberg (750 m elev.), [*Rose*?] 2 Sept 1861 (LE); Germany, Reisengebrige, [unclear] Jul 1867 (LE); Germany, Tölz, 900-1200 m [anonym] spring 1861 (LE); Germany, Melzer[…] 1866 (LE); Germany, Thuringia, 840 m [unclear] 5 Sept1872 (LE); [Central Europe] Hercynia [anonym] 1780 (LE); Austria *Schrök* 7 Aug 2010 (MW9078353). **CAUCASUS**: Georgia, Oni ad fl Rioni, 1 Jul 1877 *Brotherus 11259* (LE). **EAST ASIA**: Kamchatka, Levyj Kikhchik, 12 Aug 2001 *Czernyadjeva #87* (LE); Kamchatka, Khodutka Bay, 30 m elev., 26 Jul 2002 *Czernyadjeva #31* (LE); Sakhalin, Chamga Pass, 500 m, *Ignatov & Teleganova 06-839* (MHA9024482; MHA9024483); Sakhalin, Yuzhno-Sakhalinsk, 500 m, *Ardeeva* (MHA); Kamchatka, *Samkova #30* (MW9022178); Kuril Islands, Kunashir, 10 m elev., *Ignatov 06-3038* (MW9061903). **NORTH AMERICA**: Canada, Quebec, *Ignatov 17-1014* (MW9110997).

Differentiation. Plants of *J. protuberans* look distinct from *J. pallescens* especially when they are wet (Fig. 3E–F), because the leaf apices are strongly curved and reflexed in various directions giving the plants a non-*Hypnum* aspect that is very different from that of *J. pallescens* (Fig. 3E). When dry, the irregularly curved leaves with variously turned apices is the key character to imply *J. protuberans* (cf. Figs. 2–5). In the Kuril Islands, there are plants that are genetically intermediate between *J. protuberans* and *J. pallescens* (Figs. 2B, 4D, 5D, 6C,D). Their aspect with somewhat flexuose leaf apices is somewhat similar to *J. protuberans*, but alar cells extend upwards along leaf margins and their leaves are rather gradually tapered to the apices.

Microscopically, leaf shape and, especially, alar cells are important characters for differentiation. In *J. protuberans,* leaves are somewhat abruptly tapered to narrowly lanceolate acumina (Fig. 6B,F); alar groups are composed of 3–6(–10) mostly short-rectangular cells along the leaf margins (Fig. 6A,E,I,J); in *J. pallescens* leaves are gradually narrowed to their apices (Fig. 6C,G); alar groups are composed of 10(15) mostly quadrate cells along the leaf margins (Fig. 6H,K).

With respect to sporophyte characters, capsules and exothecial cells are clearly shorter (Fig. 7) in *J. protuberans* than in *J. pallescens*. The relatively short capsules (Fig. 7c–F), and shorter exothecial cells (Fig. 7G–L) in *J. protuberans* are also suggestive in Russian material, although Ando (1976) reported short capsules in *J. pallescens* s.str. as well, and according to our observation in North America, *J. pallescens* often has shorter capsules.

Jochenia pallescens (Hedw.) Hedenäs, Schlesak & D. Quandt, Bryoph. Diversity & Evol. 40(2): 47. 2018. — *Leskea pallescens* Hedw., Sp. Musc. Frond. 219–220, pl. 55, f. 1–6. 1801. — *Hypnum pallescens* (Hedw.) P. Beauv., Prodr. Aethéogam. 67. 1805. — *Stereodon pallescens* (Hedw.) Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1(2): 99. 1859. Type: E Suecia mist D.O. Swartz, G (not seen, illustrations published by Ando (1976)).

Description. *Plants* small to medium-sized, in dense, flat mats, whitish-green or brownish-green, glossy. *Stems* creeping, 2–5 cm long, regularly pinnate, terete foliate or ± complanate, leaf tips turned toward substrate; branches to 5 mm long. *Stem leaves* slightly to strongly falcate-secund, 0.8–1.4×0.3–0.5 mm, ovate-lanceolate, gradually tapered into narrow acumina, slightly rounded to the insertions, concave; margins serrulate throughout, plane or occasionally narrowly recurved below; *cells* (25–) 35–55(–80)×(6–)7–8(–9) μm, alar cells quadrate, short-rectangular and transversely rectangular, ± thick-walled, in weakly delimited groups 10–15 cells along leaf margins. *Branch leaves* 0.6–1.0×0.2–0.35 mm. *Setae* 0.8–1.2 cm. *Capsules* inclined, slightly curved, urns elongate-cylindrical, 1.5–2.0 mm long, smooth; exothecial cells elongate-rectangular or irregularly tetragonal, with thick longitudinal and thin transverse walls. *Spores* 12–17 μm.

Distribution: The species is common in Russia in the southern part of the boreal zone and in the hemiboreal zone. It is rare in the northern boreal zone and in the temperate forests (only in the Caucasus at rather high elevations). Southernmost localities of the species are in the Western Himalayas (Kashmir, India).

Variation: The species is usually easy to recognize by regular branching, regular leaf curvation, common presence of numerous sporophytes, and long rostrate operecula. At the northern limit of its distribution it grows on rocks, not tree trunks, and sometimes has straight leaves (Figs. 4H, 5H). In Altai there are plants with larger leaves that are strongly curved (Figs. 4G, 5G).

KEY TO IDENTIFICATION OF *JOCHENIA* SPECIES

1. Leaves falcate-secund, gradually narrowed to apices; leaf margins with 10(15) mostly quadrate alar cells; capsules 1.5–2 mm long ..... 1. *J. pallescens*
— Leaves ± falcate, not secund, pointed in various directions, somewhat abruptly tapered to narrowly lanceolate acumina; leaf margins with 3–6(–10) mostly short-rectangular alar cells; capsules 1.1–1.5 mm long ..... 2. *J. protuberans*

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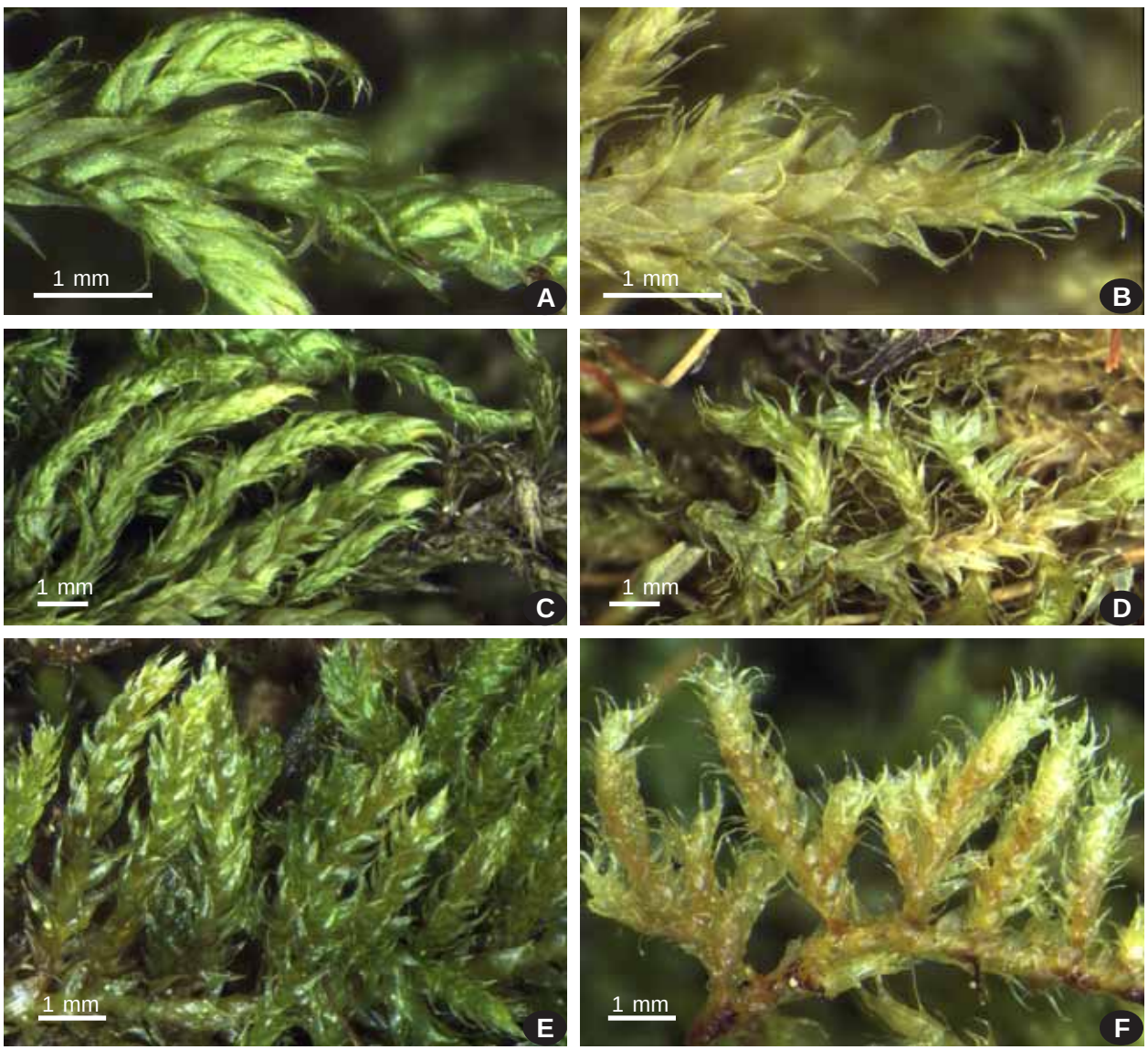

Fig. 3. Comparison of *Jochenia pallescens* (A, C, E: from Novosibirsk, specimen 'A10') and *J. protuberans* (B, D, F: from Austria, 'E3'). Habit, dry (A–D) and wet (E–F).

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Fig. 4. Shoots (dry) of *Jochenia*. A–C: *J. protuberans*: A: Kamchatka 'A2'; B: Canada, Quebec, 'Am'; C: Sakhalin, Ardeeva 1966, MHA; D: ?*J. pallescens* × *J. protuberans*, Iturup, 'A6'; E–H: *J. pallescens*: E: Novosibirsk 'A10'; F: Tatarstan, 'E4'; G: Altai, 'A4'; H: Karelia, 'E7'. Scale bar 2 mm for all images.

APPENDIX (codes in TCS network, ITS GenBank number, isolate number and the specimen voucher data)

***Jochenia pallescens*: A1** ON650757 OK2110: Russia, Amurskaya Province, Bezgodov 5 July 2010 #204 MHA; **A2** ON650758 OK2112: Russia, Primorsky Territory, Ignatov 07-521 MHA9024463 ; **A3** ON650759 OK2119: Russia, Kuril Islands, Kunashir, Ignatov 06-1144 MW9022160; **A4** ON650761 OK2842: Russia, Altai, Ignatov #3/64 MHA9024453; **A5** ON650763 OK2844 Russia, Altai, Ignatov 35/37 MHA9024445; **A7** ON650767 OK3060: Russia, Primorsky, Berezovy, Ignatov 07-521 MW9022153; **A9** ON650768 OK3064: Russia, Altai Republic, Gorno-Altaisk, Ignatova 6-8-2000 MW9022137; **E4** ON650760 OK2120: Russia, Tatarstan, Ignatov & Ignatova 16 Aug 2003 MHA9016526; **E5** ON650762 OK2843: Russia, Kostroma, Donskov 25 July 2008 MHA9024607; **E6** ON650764 OK2850: Russia, Tula Province, Seregin M-920 MHA9024549; **E7** ON650766 OK2852: Russia, Karelia, Maksimov 22 Jan 2001 MHA9024556; **E8** ON650769 OK3065: Russia, Ingushetia, Bersanova 18-161 MW9090983; ***?Jochenia pallescens* × *J. protuberans*, A6** ON650763 **A8** ON650765 (two extractions) OK2846: Russia, Kurils, Iturup, Bakalin K-26-26-07 MHA9024480; ***Jochenia protuberans* Am** ON650770 OK3056: Canada, Quebec, Ignatov 17-1014 MW9110997; **A2** ON650772 OK3059: Russia, Kamchatka, Samkova #30 MW9022178; **A3** ON650773 OK2857: Russia, Kurils, Kunashir, Ignatov 06-3038 MHA9000859; **E3** ON650771 OK3058: Austria, Schröck 7 July 2010 MHA9065581.

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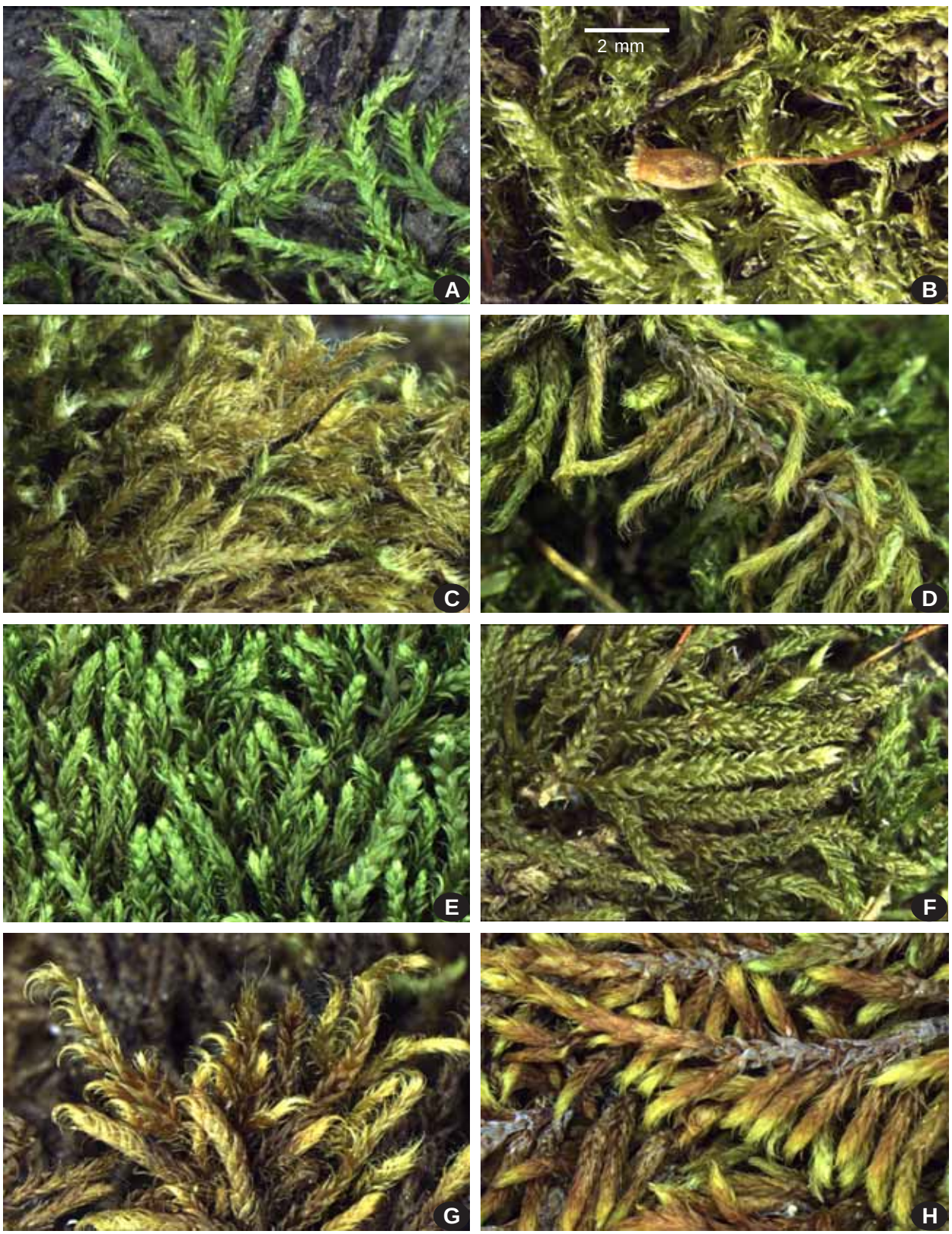

Fig. 5. Habit of *Jochenia* species. A–C: *J. protuberans*: A: Kamchatka 'A2'; B: Kunashir 'A3'; C: Austria 'E3'; D: ?*J. pallescens* × *J. protuberans*, Iturup, 'A6'; E–H: *J. pallescens*: E: Kostroma 'E5'; F: Tatarstan, 'E4';G: Altai, 'A4'; H: Karelia, 'E7'. Scale bar 2 mm for all images.

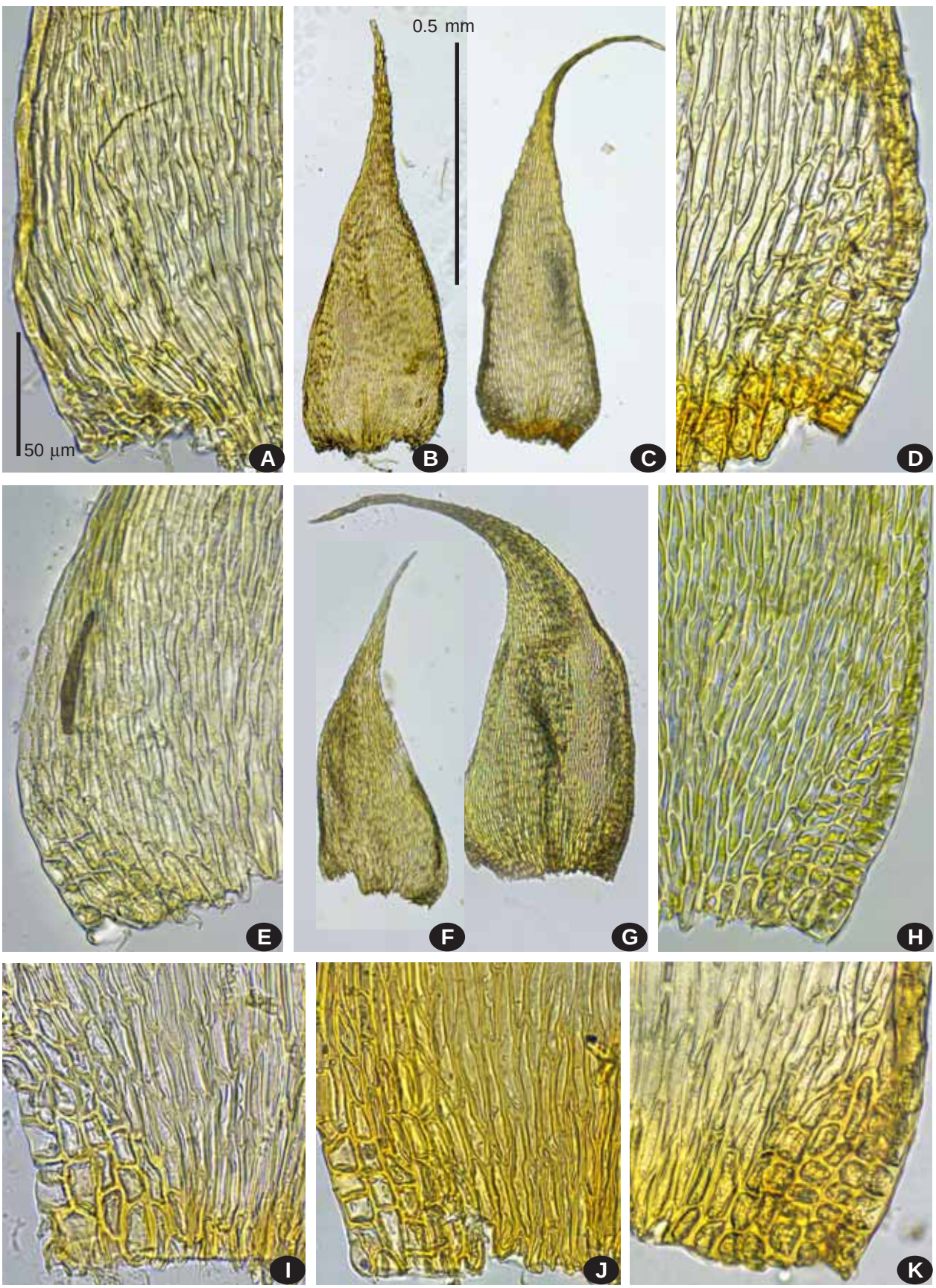

Fig. 6. A comparison of *Jochenia protuberans* (A–B: Austria 'E3'; E–F: Quebec 'Am'; I–J: Sakhalin, Ardeeva); ?*J. pallescens* × *J. protuberans* (C–D: Iturup, 'A6') and *J. pallescens* (G: Mongolia MHA9062173; H: Tatarstan 'near E4'; K: Altai 'A4'). A, D, E, H, I–K: basal leaf cells; B–C, F–G: stem leaves. Scales 0.5 mm and 50 µm for all leaves and cells.

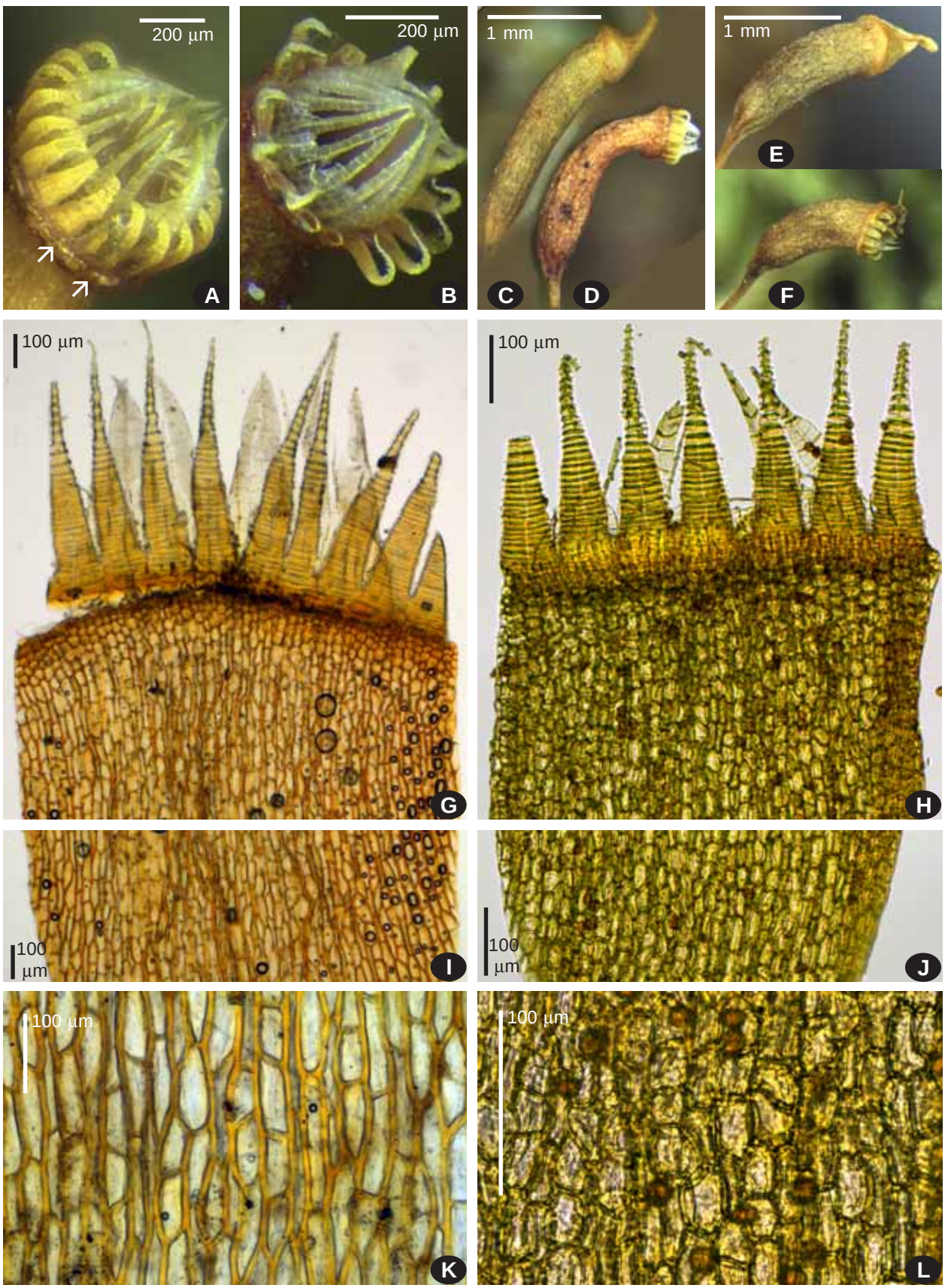

Fig. 7. A comparison of *Jochenia pallescens* (A, C–D, G, I, K: from Novosibirsk, specimen 'A10') and *J. protuberans* (B, E–F, H, J, L: from Kunashir 'A3', E–F: from Austria 'E3', H, J, L: from Sakhalin, Ardeeva 1966 MHA). A, B: perisomes, fragmentary deciduous annulus is arrowed in A; C–F: capsules, operculate (C, E) and open (D, F); G–H: peristomes; I–L: exothecial cells.