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ON *SYZYGIELLA NIPPONICA* (ADELANTHACEAE, MARCHANTIOPHYTA) AND ITS FIRST RECORD IN RUSSIA

О *SYZYGIELLA NIPPONICA* (ADELANTHACEAE, MARCHANTIOPHYTA) И ПЕРВОЙ НАХОДКЕ ЭТОГО ВИДА В РОССИИ

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Abstract

Syzygiella nipponica was collected in Primorye Territory on rocks. The plants were sterile and recognized due to prostrate shoots, coarsely papillose cell surface and sporadic postical intercalary branches not characteristic of known in Asia morphologically similar species of *Jungermannia, Solenostoma, Plagiochila, Pedinophyllum,* and *Syzygiella*. Collected plants are dissimilar to phylogenetically allied *Syzygiella autumnalis*. Their generic position was identified in the basis of comparison of *rbc*L gene sequence. Joint morphological and molecular study of collected materials and morphological tudy of collections from LE, KPABG, NICH, HIRO, HSNU, E (including types of *Jamesoniella nipponica* and its synonyms *J. verrucosa*, and *J. perverrucosa*) shows separate position of *Syzygiella nipponica* from *S. autumnalis* at the species level.

Резюме

Новый для России вид печёночников *Syzygiella nipponica* собран в Приморском крае на скалах. Растения стерильные и характеризуются стелющейся формой роста, грубопапиллозной поверхностью клеток листьев, развитием ризоидов из брюшных оснований листьев и наличием вентрально-интеркалярного ветвления – сочетанием, которое не свойственно известным из Азии морфологически сходным видам родов *Jungermannia*, *Solenostoma*, *Plagiochila*, *Pedinophyllum* и *Syzygiella.* Собранные растения также не сходны с филогенетически близким видом *S. autumnalis,* и их родовое положение было определено на основании сравнения нуклеотидных последовательностей по гену *rbc*L. Морфологическое и молекулярное исследование собранных материалов, а также изучение морфологии образцов из LE, KPABG, NICH, HIRO, HSNU, E (включая тип вида *Jamesoniella nipponica*, а также типы синонимов этого вида – *J. verrucosa* и *J. perverrucosa*) показали обособленное на видовом уровне положение *Syzygiella nipponica* от *S. autumnalis*.

KEYWORDS: *Jamesoniella, Syzygiella nipponica, Syzygiella autumnalis*, Primorye Territory, Russia, taxonomy, description, distribution, *rbc*L

INTRODUCTION

Sterile Jungermannioid hepatic have been collected by one of us (YM) in the Primorye Territory, Russian Far East. The habit of collected plants recalls with some species of the families Jungermanniaceae sensu Schuster (1969) and Plagiochilaceae. However, such significant distinctions of these plants as prostrate shoots, absence of stem cortex of small thick-walled cells, leaf cells with coarsely papillose cuticle and large nodulose trigones, postical intercalary branches, rhizoids originating near and from postical leaf bases, ovoid to truncate and not opposite leaves never occur all together in any known genera of these families. This led us to molecular investigation of collected materials. Obtained *rbc*L sequences are identical with the sequences of one of the species of the genus *Syzygiella* Spruce, *S. nipponica* (S.Hatt.) K. Feldberg, Váňa, Hentschel & J. Heinrichs.

This species was described as *Jamesoniella nipponica* from Honshu, Japan by Hattori (1943). The author provided only species description without any definition of its differential characters but shortly after started to consider it as a variety, *J. autumnalis* var. *nipponica* (S. Hatt.) S. Hatt. (Hattori, 1951). This status was accepted by Schuster (1969) in his treatment of North American Hepaticae. In this treatment Schuster did not consider papillose cell surface of this taxon described and illustrated by Hattori (1943) and distinguished it on the basis of leaf shape only.

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Horikawa (1934) described *Jamesoniella verrucosa* Horik. from Taiwan. This name, however, appeared to be the later homonym and thus illegetimate. Hattori (1968) in his treatment of Nepal hepatics provides a new name *J. horikawana* S. Hatt. to replace *J. verrucosa* nom. illeg. Amakawa (1969) described *J. perverrucosa* Amakawa from N. Borneo. Grolle (1971) reduced all these species to synonymy of *J. nipponica*.

Amakawa (1959) included *J. nipponica* in synonymy of *J. autumnalis*. No comments on their comparison with *J. nipponica* were provided in that paper. Grolle (1971) in his treatment of *Jamesoniella* (Spruce) Carrington accepted *J. nipponica* as a species. He distinguished *J. nipponica* from the closely related *J. autumnalis* on the basis of coarsely papillose cell surface and larger trigones. This point of view was accepted by Schljakov (1975) that proposed a new combination *Crossogyna nipponica* (S. Hatt.) Schljakov. Inoue (1976) studied all above mentioned taxa and reduced them to synonymy of *J. autumnalis,* mentioning that distinctions of cell surface structure and shape of trigones between *J. autumnalis* and *J. nipponica* are gradual and not tenable. The latter point of view was not followed by Yamada & Iwatsuki (2006) and Choi (2013), who accepted this taxon as a variety, and by Piippo (1990), who included it in the Check-list of Chinese hepatics as a species, *J. nipponica.*

Recent molecular treatment of Adelantaceae Grolle (Feldberg *et al.*, 2010a) has shown integrity of the genera *Jamesoniella* (Spruce) Carrington, *Cryptochila* R.M. Schust., *Roivainenia* Perss., and *Syzygiella* Spruce as one genus *Syzygiella.* Despite complete description of the genus *Syzygiella* sensu Feldberg *et al.* (2010b) is absent at present, the complex of characters, mentioned above for Russian plants of *S. nipponica*, e.g. coarsely papillose cuticle, postical intercalary branches, rhizoids originating near and from postical leaf bases, is developed in different degree in some species presently attributed to this genus.

The study of Adelanthaceae by Feldberg et al. (2010a) shows close phylogenetic relationship of *Syzygiella nipponica* with *S. autumnalis* (DC.) Feldberg, Váňa, Hentschel et Heinrichs also and points at their separate position at species level. Meanwhile morphological distinctions of *Syzygiella nipponica* and status of *Jamesoniella verrucosa* and *J. perverrucosa* described earlier from Nepal and Borneo and treated by Grolle (1971) as synonyms of *Jamesoniella nipponica* (= *Syzygiella nipponica*) were out of scope of Feldberg *et al*. (2010a) study. To clarify morphological variability of *S. nipponica* as well as status of *Jamesoniella verrucosa* and *J. perverrucosa* we have studied types of *Jamesoniella nipponica, J. verrucosa* and *J. perverrucosa*, the specimens of *J. nipponica* that were used by Feldberg *et al*. (2010a) for molecular study and available collections cited below. On the other hand we made molecular analysis of our material and compared it with available from GenBank *rbc*L sequences of *Syzygiella nipponica* from China and Nepal. Due to close phylogenetic relationships of *S. nipponica* and *S. autumnalis* all available *rbc*L sequences of *S. autumnalis* were involved in our analysis.

MATERIAL AND METHODS

Two new cpDNA *rbc*L sequences generated from 2 our specimens of *Syzygiella nipponica* were used. Our attempts to obtain ITS sequences were unsuccessful. DNA extraction has been made with AxyPrep Multisource Genomic DNA Miniprep Kit (from AxyGen). Protocol used is the same as in the study of Fledberg et al. (2010a). The initial alignment for sequences was automatically created by ClustalW implemented by MEGA version 5.2 (Tamura et al., 2011) and then manually corrected.

To test phylogenetic relation of *S. nipponica* and allied *S. autumnalis*, the majority of subgenera of the genus *Syzygiella* sensu Fledberg *et al*. (2010b) and a number of species of subg. *Syzygiella* that included presently *S. nipponica* and *S. autumnalis* were analyzed. The genus *Cuspidatula* Steph. (*C. monodon* Steph.) was chosen as outgroup as most closely related to the genus *Syzygiella* (Feldberg *et al*., 2010). In general, thirty one analyzed sequences were taken from GenBank and analyzed (Appendix 1).

Phylogenetic tree for *rbc*L (Fig. 1) was inferred using maximum parsimony method (MP) with Nona under the Winclada shell (Goloboff, 1994). Jackknife support was calculated in Nona for 1000 replications (number of search reps 10, hold 10, max tree 100, do max). Obtained values for nodes in tree are shown in Fig. 1.

Morphological investigation. General collections and type specimens from several herbaria (LE, KPABG, NICH, HIRO, E, HSNU) were studied using standard microscopical techniques.

RESULTS

In the phylogenetic tree (Fig. 1) two specimens of *Syzygiella nipponica* from Russia and the specimens of this species from China and Nepal form a high supported subclade within a basal clade; this clade includes also low supported subclade of several specimens of *S. autumnalis.* It corresponds to morphological resemblance of these species in prostrate shoots, absence of stem cortex of small thick-walled cells, ovoid to truncate and not opposite leaves and gametoecia structure. In these features *S. nipponica* and *S. autumnalis* differ from other species of *Syzygiella* subg. *Syzygiella* located nearly at low (70%) supported clade on the basal grade. However, such morphological differences as coarsely papillose cuticle of leaf cells, postical intercalary branches, rhizoids originating near and from postical leaf bases, in combination with differences in *rbc*L sequences confirm the separate position of *S. nipponica* at species level. In these morphological features *S. nipponica* is similar to *S. colorata* (Lehm.) Feldberg, Váňa, Hentschel et Heinrichs known from Southern Hemisphere (Chile, South Africa, Australia, New Zealand), but the latter clearly differs in aspect (in *S. colorata* stem leaves appresed and trans-

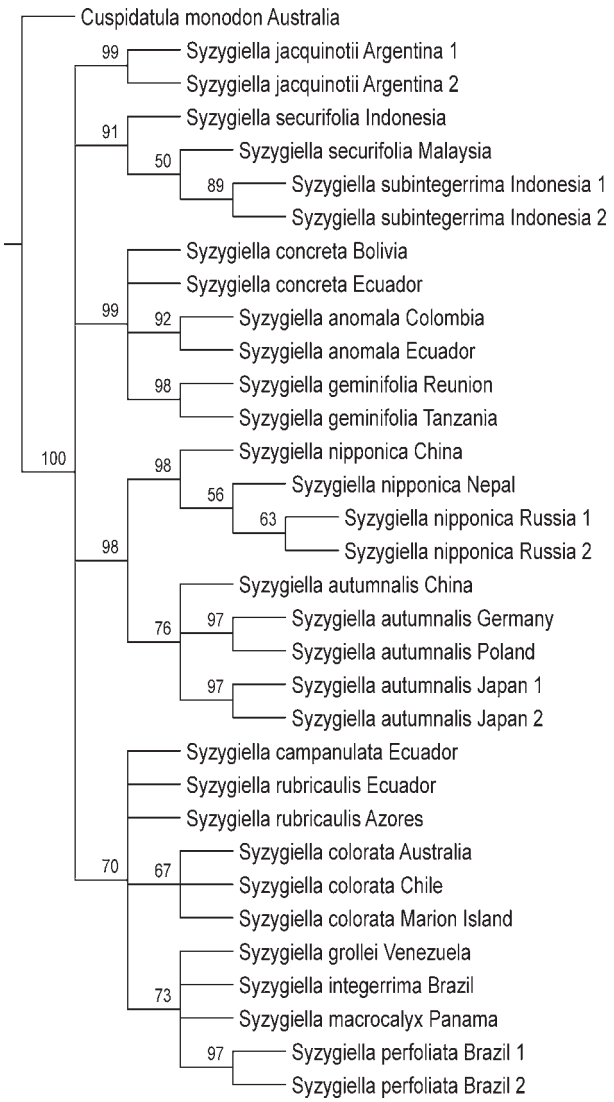

Fig. 1. Strict consensus of 1000 shortest trees found in MP analysis of chloroplast *rbc*L sequences of Adelanthaceae. Jackknife support calculated by 1000 iterations in Nona, are indicated above branches.

versely inserted, thus oriented to shoot apex, much as in *Cryptocolea imbricata*), and in stem anatomy. *Syzygiella colorata* has a stem cortex of smaller (in cross section) equally thick-walled tinted cells gradually dragging into the medullary cells with strongly bulging confluent trigones.

Discussion

Different interpretation of taxonomic status of *Syzygiella nipponica* apparently resulted from its considerable variability in cell surface structure and leaf shape that may resemble *S. autumnalis*. This may result in under recording of *S. nipponica* when its collections are sterile, particularly. Study of type materials of *J. nipponica, J. verrucosa* and *J. perverrucosa* has shown they have much in common and are characterized by coarsely papillose cell surface, leaves 1.03–1.3(-1.55)× as long as wide with often incurved margins, often gradually rounded at apex, mostly coarse trigones, sporadic postical intercalary branches and strong pigmentation (brown and/or intensive red to purplish). Plants from all these type specimens were apparently collected in more xeric habitats and in higher altitude on rotten wood that cause their pigmentation. Our collections were made on rocks near waterfalls in partial shade in low altitude about 500 m that resulted in their different morphology. They are mostly green and have coarsely papillose to smooth cell surface and often small acute trigones. They have much in common with small *Jungermannia* species. We suppose that study of similar plants with variable distinctive characters may lead to interpretation of this species as a variety or synonym of *J. autumnalis*. However, when enough material is in hand it becomes obvious that these two species are different. Therefore we consider important to provide complete description of *S. nipponica*, its variability and the key below forming the basis for its differentiation and definition of its taxonomic status.

KEY TO RUSSIAN SPECIES OF SYZYGIELLA

1. Cell surface at least on some leaves ± coarsely papillose; leaves 1.03–1.3(-1.55 in type of *J. nipponica*, Japan) × as long as wide, when dry nearly vertical, often with concave margins and then concave, ovate to oval elliptical, broadly to rather narrow lingulate or sometimes subquadrate, ± frequently gradually narrowed to rounded apex, rare truncate and retuse; postical *intercalary* branches sporadically present . ..... *S. nipponica*
— Cell surface usually finely striolate or smooth; leaves 0.8–1.15× as long as wide, when dry oblique oriented (rarely vertical), with usually plane, not concave margins, often convex (rarely concave, in strongly pigmented plants from high latitudes) and, largely rotund-quadrate to very shortly oblong-oval, often truncate or retuse at apex; postical *intercalary* branches unknown ..... *S. autumnalis*

Description below is based on materials from the Russian Far East. Data from the other studied specimens from Japan, China and Nepal are provided in square brackets to complete the description.

Syzygiella nipponica (S. Hatt.) Feldberg, Hentschel et Heinrichs, Cryptog. Bryol. 31(2): 145. 2010. – *Jamesoniella nipponica* S. Hatt., J. Jap. Bot. 19: 350. 1943. – *Jamesoniella verrucosa* Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2 (Bot.) 2: 146. pl. 11: 15–24. 1934. nom. illeg. (later homonym) – *Jamesoniella autumnalis* (DC.) Steph. var. *nipponica* S. Hatt., J. Hattori Bot. Lab. 5: 76. 1951. – *J. perverrucosa* Amakawa, J. Hattori Bot. Lab. 32: 121. f. 4. 1969. – *Crossogyna nipponica* (S. Hatt.) Schljakov, Novosti Sist. Nizsh. Rast. 12: 311. 1975. – *Crossogyna autumnalis* (DC.) Schljakov var. *nipponica* S.S. Choi, Bakalin & B.-Y. Sun in Choi, Taxonomy of the Liverworts and Hornworts of Korea: 53, 2013. – Fig. 2.

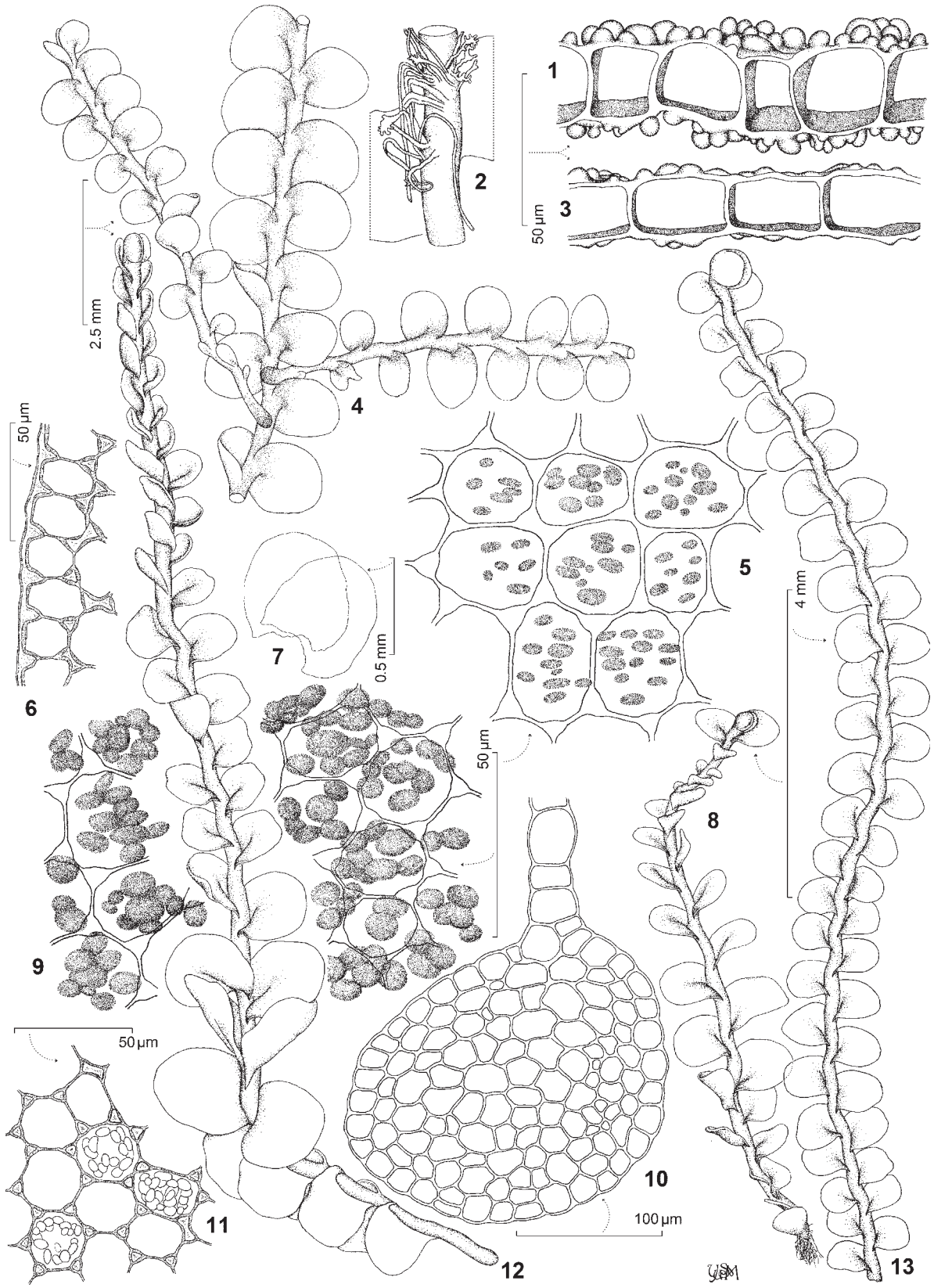

Fig. 2. *Syzygiella nipponica:* 1, 3 – part of cross section of leaf n the middle; 2 – stem sector, postical aspect; 4 – shoot with postical intercalary branches, postical aspect; 5, 9 – cells of leaf middle, with papillae indicated; 6 – cells of leaf margin; 7 – two leaves; 8, 12, 13 – shoots, antical aspect; 10 – stem cross section; 11 – cells of leaf middle, with chloroplasts indicated. 2, 6, 7, 9, 11, 13 from *Mamontov Prim-119-1-10*; 1, 3-5, 8, 10, 12 from *Mamontov # Prim-125-1.*

Plants small to medium size, prostrate (4-)10-20 [-30] mm long and (0.5-)0.7-2[-3] mm wide, dark green [to brown and purplish-brown and purple in sun-lighted habitats]. **Branching** sporadic postical intercalary (Fig. 1: 4), lateral intercalary, and terminal *Frullania*-type. **Stem** ca. 125–250[-270] μm wide, rounded-elliptical in cross section, ca. 8-12 cells high and 9-15 cells wide; cortical cells not differentiated from cells of medulla (Fig. 1: 10) to moderately evenly thick-walled, ca. 17-22 × 12-20(-22) μm. **Rhizoids** scarce, near and from the postical leaf bases (Fig. 1: 2) in upper shoot sectors and through all postical side of stem in lower shoot sectors. Rhizoids sporadically with swollen ends that bear finger-like outgrowths. **Antical leaf-free zone** absent. **Leaves** oblique inserted, nearly vertical (especially in dry condition) to ± horizontal, remote [to subimbricate in mod. colorata], with plane to ± incurved margins [sometimes strongly so in mod. *pachyderma-colorata*] thus concave, largerly ovate to oval-elliptical, broadly to rather narrow lingulate or sometimes subquadrate (Fig. 1: 7) with usually narrowly and broadly rounded, sometimes truncate or retuse apex, 1.04-1.2(-1.3)[-1.55] × as long as wide. Antical base narrowly and often indistinctly decurrent. Decurrent strips of opposite leaves sometimes tend to be nearly contiguous in shoot sectors with ± dense leaves. Postical leaf base occasionally long decurrent (Fig. 1: 12 – lower leaves). **Marginal cells** indistinctly smaller than median, ca. [12-]17-25[-35]×[7-]12-25 μm, with similarly or stronger thickened walls of marginal cells. **Median cells** of leaves [17-]20–35×(12-)20-27 μm, with small acute to moderately and strongly bulging trigones (Fig. 1: 6, 11). **Basal cells** somewhat longer than median cells, ca. 25–40[-50]×[14-]20-32[-37.5] μm. **Cell surface** varies from usually coarsely papillose (Fig. 1: 1, 9) to sometimes smooth. It may be variable even on one shoot. Median and marginal cells have large to rather small spherical papillae, 7-12.5×3.75-7.5 μm near the base [5–12 mm in diam.; up to 25×5-12 mm near leaf base], basal cells develop some elongated papillae (Fig. 1: 1, 9). **Underleaves** originated at base of branches, where they broadly elliptical and obliquely oriented (to almost perpendicular with the stem midline). Underleaves become smaller subulate and vanish aside base of branches. **Specialized asexual reproduction** usually absent. Leaf cladia once seen.

Plants in studied collecions from Russia sterile. [**Dioicous**. **Androecia** spicate of many pairs of bracts. **Gynoecia** with innermost female bracts often a little smaller than leaves, with several to many elongated lanceolate-subulate marginal cilia. Outer bracts considerably larger than leaves with rounded apex, entire, subentire or remotely short dentate margins, and solitary basal lacinae and/or cilia. Bracteoles large narrow free or, from 2–3-fid to lanceolate with 1–2 lateral teeth. **Perianths** obovoid to oval, in upper part with several (5–7) deep plicae and gradually narrowed to the ciliate mouth. The cilia 2-3 cells at base with uniseriate ends of 3-10[-15] slightly elongated cells, ca. 23-31×13-18 μm. Cilia often purplish and partly bleached, terminated by slime papillae].

Specimens examined: RUSSIA: Primorsky Territory, Lazovsky District, Elomovskie Waterfalls (43°14' N – 133°42' E), 6.IX.2010 *Mamontov # Prim-119-1-10* (KPABG), *Prim-119-1-11* (LE); idem, 6.IX.2010 *Mamontov # Prim-125-1* (LE), *Prim-125-2* (KPABG), *Prim-125-3* (KPABG), *Prim-125-5* (LE), *Prim-125-6* (LE), *Prim-125-7* (KPABG, E). JAPAN: [Honshu] Prov. Uzen, Nishi-murayama, Asahi-kosen, 24.VII.1941 *Hattori # 875* (TNS, type of *Jamesoniella nipponica*); Kumamoto: Mt. Ichifusa, VII.1950 *Mayebara No. 167, Hep. Jap. Ser. 4 (1951)* (LE). CHINA: Zhejiang, Longquan City, Fengyangshan Nature Reserve, 28.VII.2006 *Zhu # 20060728-14* (HSNU, GenBank GQ900311); Hunan Prov., Yizhang Co., Mt. Mangchan, Huoshaoao (24°58' N – 112°56' E), 4.X.1997 *Koponen, Huttunen & Rao # 51356* (LE, as *Jamesoniella autumnalis*). TAIWAN: Prov. Tainan, Mt. Morrison, 19.VIII.1932 *Horikawa # 9166a* (HIRO, type of *Jamesoniella verrucosa*). NEPAL: Upper Simbia Khola (27°32' N – 87°57' E), 17.IX.1989 *Long # 17022* (LE, E, GenBank GQ900312). BORNEO: Mt. Kinabalu, Paca Cave, 21.V.1963 *Mizutani # 3519* (NICH, type of *Jamesoniella perverrucosa*).

Distribution: Japan (Honshui), South Korea (Choi, 2013), SE China (Zhejiang), Taiwan, Himalaya (NW, Nepal, Sikkim, Bhutan), Borneo (Long, Grolle, 2000).

Illustrations: Horikawa, 1934: Pl. 11, *Figs. 15-24*; Hattori, 1943: Fig. 26; Amakawa, 1969: Fig. 4; Schuster, 1969; Fig. 255: *1–8*; Grolle, 1971: Abb. 18h-o, 23g-h.

Ecology. In Russia it grows on both dry and moist rocks and soil-filled rock ledges of the cliffs near waterfalls, in pure mats and together with *Cheilolejeunea obtusifolia, Lejeunea japonica, Liochlaena* cf. *subulata, Pellia neesiana, Plagiochila porelloides, Porella fauriei, Radula japonica, Trichocoleopsis sacculata* [on rocks, grassy banks, rotten wood, soil and forest floor].

Variability and differentiation. *Syzygiella nipponica* has broad variability in its basic diagnostic character – pattern of ornamentation of cell surface – from usually coarsely papillose to sometimes smooth. Degree of papillae development may be different in different parts of the same shoot: coarse cell surface may be developed in younger not pigmented shoot sectors and smooth in older pigmented shoot sector like in *Mamontov Prim-125-6*, or smooth cell surface may be developed in mod. *pachyderma-colorata* like in some leaves in the holotype of *J. nipponica*. Leaves of *Syzygiella nipponica* often gradually narrowed to rounded apex like in *Jungermannia* species. Leaves with truncate and retuse apexes are rare.

All studied specimens of *S. nipponica* from Primorye Territory were gathered on rocks near waterfalls in shaded moist niches and represent mod. *viridis* of this species. In such conditions they were invariably sterile. Specimens from Japan, Himalaya and N Borneo were collected with perianths on rotten wood and rocks and represent mod. *colorata*. Plants from Japan, China (Zhejiang) and Himalaya are ± brown, from N Borneo – purple and brownish-purple. Despite Inoue (1976) considered struc-

ture of cell surface and shape of leaves as untenable characters to differentiate *Syzygiella nipponica*, our observations support point of view of Grolle (1971) to differentiate this species on the basis of leaf shape and cell surface pattern. For correct identification of sterile plants it is important to have enough material for proper evaluation of both characters.

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Appendix 1. GenBank data on specimens used in molecular phylogenetic analysis.

Original data: *Syzygiella nipponica* Russia1, Mamontov Prim-119 (KPABG) KF887996; *S. nipponica Russia2,* Mamontov Prim-125 (KPABG) KF887997

GenBank data used: *Cuspidatula monodon* Steph., Australia, GQ900299; *Syzygiella anomala* (Lindenb. & Gottsche) Steph., Colombia, GQ900322; *S. anomala*, Ecuador, GQ900324; *S. autumnalis* (DC.) Feldberg, Váňa, Hentschel et Heinrichs, Germany, GQ900303; *S. autumnalis*, Poland, GQ900304; *S. autumnalis*, Japan 1, GU593093; *S. autumnalis*, Japan 2, GU593094; *S. autumnalis*, China, AY462303; *S. campanulata* Herzog, Ecuador, GQ900330; *S. colorata* (Lehm.) Feldberg, Váňa, Hentschel et Heinrichs, Australia, GQ900305; *S. colorata*, Chile, GQ900306; *S. colorata*, Marion Island, GQ900307; *S. concreta* (Gottsche) Spruce, Bolivia, GQ900332; *S. concreta*, Ecuador, GQ900339; *S. geminifolia* (Mitt.) Steph., Reunion, GQ900342; *S. geminifolia*, Tanzania, GQ900343; *S. grollei* Inoue, Venezuela, GQ900344; *S. integerrima* Steph., Brazil, GQ900345; *S. jacquinotii* (Mont.) Feldberg, Váňa, Hentschel et Heinrichs, Argentina 1, GQ900320; *S. jacquinotii*, Argentina 2, GQ900321; *S. macrocalyx* (Mont.) Spruce, Panama, GQ900348; *S. nipponica* (S. Hatt.) Feldberg, Váňa, Hentschel Heinrichs, China, GQ900311; *S. nipponica*, Nepal, GQ900312; *S. perfoliata* (Sw.) Spruce, Brazil 1, GQ900352; *S. perfoliata*, Brazil 2, AY700002; *S. rubricaulis* (Nees) Steph., Ecuador, GQ120508; *S. rubricaulis*, Azores, GQ900355; *S. securifolia* (Nees ex Lindenb.) Inoue, Indonesia, GQ900359; *S. securifolia*, Malaysia, GQ900361; *S. subintegerrima* (Nees) Spruce, Indonesia 1, GQ900363; *S. subintegerrima*, Indonesia 2, GQ900364.