GYMNOMITRION SCHUSTERANUM (GYMNOMITRIACEAE), A NEW SPECIES FROM THE SINO-HIMALAYA

NADEZHDA A. KONSTANTINOVA1, DAVID G. LONG2, YURIY S. MAMONTOV1,3 & ANNA A. VILNET1

Abstract

A new species of Gymnomitrion, G. schusteranum is described based on specimens from the Sino-Himalaya (South-west China and North India). It differs well from other species of the genus by the presence of a pronounced vitta not known in any other Gymnomitrion spp., as well as its distinctly elongate leaves with unequal lobes, very deep sinus, and revolute margins of sinus and margins of leaves. So far, the species has been found in China in an area with a concentration of other endemic and subendemic Sino-Himalayan liverworts and in West Bengal (India) located ca. 1000 km apart.

KEYWORDS: Hepaticae, Gymnomitrion, new species, morphology, ITS1-2 nrDNA, trnL-F cpDNA, Himalaya, Yunnan, West Bengal

INTRODUCTION

The genus Gymnomitrion Corda is predominately Northern Hemisphere in distribution with several species occurring in the Southern Hemisphere (Váňa et al., 2010). Almost all species of the genus are restricted to subalpine and alpine environments (i.e., Schuster, 1996, 2002) and occur in “ecologically demanding” sites, often above the tree line. Suitable habitats for species of the genus are found in remote areas in the Arctic or high in the mountains, which are often still poorly studied. The Himalayas, which are the highest and one of the most extensive mountain systems in the world, have long attracted the attention of botanists including bryologists. Many species of both vascular plants and bryophytes have been described from these mountains. The genus Gymnomitrion is no exception. As accepted by Söderström et al. (2015), six species of Gymnomitrion (G. crenatilobum Grolle, G. crystallocaulon (Grolle) Váňa, Crand.-Stotl. et Stotler, G. rubidum (Mitt.) Váňa, Crand.-Stotl. et Stotler, G. sinense Müll.Frib., G. obtusilobum N.Kitag. and G. verrucosum W.E.Nicholson) were recorded by Váňa et al. (2010) as described from the Himalayas. Of particular interest are the specimens of the genus collected by the second author at very high altitudes over 3000 m. One of these specimens is the recently described as Gymnomitrion fissum Mamontov & Potemkin, differing very strikingly in having a leaf surface that is fissured (Potemkin et al., 2017). Here we describe another unique species of Gymnomitrion from Long’s collections.

MATERIALS AND METHODS

Morphological study. The specimens of the new species were studied and photographed using a stereomicroscope Olympus SZX-16 equipped with a digital camera Nikon D70S, and with light microscopes Leitz Wetzelar Orthoplan and Nikon Eclipse 50i equipped with digital cameras Nikon D700 and Nikon DS-Fi1 respectively. In order to better illustrate three-dimensional features, the stacks of photomicrographs obtained from several optical sections were combined using the stacking software HeliconFocus.

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**Taxa sampling**

The estimation of phylogenetic affinity of the specimen of the genus *Gymnomitrium* from China (Yunnan Prov., Long 35728) was implemented based on a modified ITS1-2 nrDNA+trnL-F cpDNA dataset from Mamontov et al. (2019). This dataset contained 23 samples, including the newly sequenced Chinese specimen and two specimens of *Gymnomitrium revolutum* (Nees) H. Philib. from Trans-Baikal Territory (Russia), previously published data for 15 specimens of *Gymnomitrium*, four outgroup species from the family Gymnomitriaceae and *Eremonotus myriocarpus* (Carrington) Lindb. & Kaal. ex Pearson from the Jungermanniaceae. GenBank accession numbers and voucher details are listed in Appendix 1. DNA isolation, PCR amplification and DNA sequencing followed the procedures as described by Mamontov et al. (2019).

**Phylogenetic analyses**

The alignments of ITS1-2 and trnL-F were produced and corrected in BioEdit 7.0.1 (Hall, 1999), all positions were taken for estimation; lacking parts of sequences and unsequenced loci were coded as missing. Preliminary phylogenetic estimation revealed congruent topologies with absence of conflict nodes that tested by eyes, thus both loci were combined in a single ITS1-2 + trnL-F dataset.

The MP analysis was run with New Technology Search with a search for the minimum-length tree by five reiterations and 1000 bootstrap resamplings; indels were coded by a modified complex coding algorithm in SeqState (Müller, 2005).

The best-fit evolutionary model of nucleotide substitutions, GTR+I+Γ, was chosen by the program Model-Generator (Keane et al., 2006). The stopping frequency criterion for bootstrapping procedure (Pattengale et al., 2010) revealed 350 replicates as enough for this dataset for reaching BS convergence with Pearson average p100 = 0.994777 realized in RAxML v. 7.2.6 (Stamatakis, 2006). The ML analysis was done with GTR+I+Γ model, gamma distribution with four rate categories and resampling procedure with 350 replicates.

In the Bayesian analysis ITS1-2 and trnL-F partitions were separately assigned the GTR+I+Γ model. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated, and two starting trees were chosen randomly. Chains were run for one million generations and trees were sampled every 10th generation. The software tool Tracer (Rambaut & Drummond, 2007) revealed the effective sample size as 3029.2772, autocorrelation time as 594.2672 and discarded the first 10000 trees in each run as burn-in. Thereafter 180,000 trees were sampled from both runs. The average standard deviation of split frequencies between two runs was 0.004424. Bayesian posterior probabilities were calculated from trees sampled after burn-in procedure.

The *p*-distances were calculated to test of ITS1-2 and trnL-F sequence variability among *Gymnomitrium* species in Mega 5.1 (Tamura et al., 2011) using the pairwise deletion option for counting gaps.

**RESULTS**

**Molecular study**

The ITS1-2 sequences were newly obtained for 3 specimens and trnL-F for a single specimen. The combined alignment of the two genomic regions comprises 1355 character sites, among them 886 positions belonging to ITS1-2 and 469 to trnL-F. The number of constant positions in ITS1-2 is 648 (73.14%) and in trnL-F is 344 (72.35%), variable – 213 (24.04%) and 123 (26.23%), parsimoniously informative – 101 (11.40%) and 50 (10.66%), respectively.

The MP analysis yielded two equally parsimonious trees with a length of 967 steps, with CI= 0.734403 and RI= 0.666667. The ML calculation resulted in a single tree, the arithmetic mean of Log likelihood was -4954.20668.

In the Bayesian analysis arithmetic means of Log likelihoods for each sampling run were -4786.86 and -4788.23. The tree topologies reconstructed by three approaches are quite similar and agree with previously published tree (Mamontov et al., 2019). Thus, we provide the ML tree with an indication of bootstrap support values obtained in the MP and ML analyses and Bayesian posterior probabilities (PP) (Fig. 1).

The tested specimen of *Gymnomitrium* from China (Long 35728) was found in a clade composed by two specimens of *G. revolutum, G. africanum, G. verrucosum* and two specimens of indeterminate species. The relation of the Chinese specimen has support only in the BA analysis (PP=0.56) like majority internal nodes within this clade (Fig. 1). The *p*-distance estimation suggested divergence among tested specimens and other *Gymnomitrium* species by 2.2-4% in ITS1-2 sequences and 2.1-6.1% in trnL-F that corresponded with the level of infrageneric variability in this genus (Mamontov et al., 2019: Table 2).

**Morphological study**

In spite of its weakly supported phylogenetic position the genetic distances of the newly studied Chinese specimen are high enough and along with morphological peculiarities allows us to confidently regard it as a separate species.

**TAXONOMY**

*Gymnomitrium schusteranum* Konstant., D.G.Long, Mamontov & Vilinet, sp. nov. Figs. 2–5.

**Diagnosis.** Plants blackish brown, middle-sized, with leaves 1.5–2 times as long as wide, deeply divided into two clearly unequal lobes with recurved margins of both lobes and sinuses and characterized by the presence of a clear vitta, 2–3(-4)-layered at the base, bifurcating approximately in the middle of the undivided part of the leaf and reaching the middle of the lobes.
**Gymnomitron schusteranum** (Gymnomitriaceae), a new species from the Sino-Himalaya

*Fig. 1. Phylogram obtained in a maximum likelihood calculation for the genus Gymnomitron based on combined ITS1-2 nrDNA and trnL-F cpDNA dataset. Bootstrap support values of maximum likelihood and maximum parsimony analyses more than 50% and Bayesian posterior probabilities more than 0.50 are indicated. The length of cut branches are marked. The value of P-distances, %, between *G. schusteranum* and other species for ITS1-2 / trnL-F, a given on the right.*

**Type.** China. Yunnan Province, Gongshan County, Cikai Zheng, east slope of Gaoligong Shan, Nu Jiang (Salween) catchment, Yipisaka Lake at head of Pula He valley, 2.2 km SSE of tunnel, 27°45'12.4"N, 98°27'36.4"E, alt. c. 3455 m a.s.l., 12 August 2006, D.G. Long 35728 (KPABG – holotype; E, KUN, CAS, MO, MHA – isotypes).

**Etymology.** The species is named after Rudolf M. Schuster, one of the world’s foremost bryologists over many decades, who made an immense contribution to the study of the diversity, phylogeny and taxonomy of liverworts.

**Description.** Plants when dry blackish, when moist from pale green (uppermost apices) and dark chocolate brown in upper parts of shoots to blackish brown below, with main shoots ca. 0.6 mm wide and branches ca. 0.4 mm, up to 20–25 mm long, branching both dorsal intercalary (*Andrewsianthus*-type) and ventral intercalary, mostly at base of shoots. Cells on dorsal side of stem almost isodiametric, of irregular form, rounded-rectan-
gular or rounded-triangular, thick-walled, small, ca. (12–) 15–17 μm. Stem cross-section (Fig. 3I, 4D) elliptical, on main shoot 200–225 μm high and 260–280 μm wide, with distinct cortex of (3–)4–5 layers of dark brown thick-walled, small, almost isodiametric (or elongate along the margin) cells ca. 7–8(–10) × (10–)14–17(–20) μm and with slightly larger and paler outermost layer of cortical cells. Cells of medulla distinctly larger, thin-walled with distinct trigones, ca. 10–15 × 20–25 μm. Stem surface smooth (Fig. 4D), but in places appearing papilllose through the leaf base cells bearing dome-like projections (Fig. 3I). Rhizoids colorless, 10–11 μm wide, absent on leafy shoots and occurring sparsely only on single small leaved stolon-like shoots arising from rhizome-like leafless structures at base of plants. Leaves (Fig. 2C, E–G, I; 5C, E) when dry slightly falcate, in Long 35728 clearly directed to the ventral side (Fig. 4A), straight with dorsal lobe partly suberect spreading, transversely inserted, imbricate, hiding the stem, slightly decurrent both dorsally and ventrally (Fig. 4C), subovate, variable and smaller on upper parts of shoots, bifid, distinctly longer than wide, 600–700(–900) μm wide near the base, slightly tapering upwards, 1000–1350(–1400) μm long on main axes, the length/ width ratio (1.4–)1.5–1.7(–2), slightly smaller on branches where leaves are 550–650 × 950–1100 μm; leaves deeply divided by narrow sinus rounded at base, up to (0.5)0.6–0.7 leaf length, into two distinctly unequal subulate lobes with more or less distinctly reflexed margins and sinuses. Lobes cuspitate, ending in 1–2 superposed almost isodiametric cells ca. 8–10 × 8–10 μm (Fig. 3C, I). Vitta massive, 2–3(–4) layers thick (Fig. 3F, G, H, J), bifurcate near the base of lamina, just 5–7 cells under the base. Vitta cells (10–)12–15 × (20–)25–50 μm, very variable, thin walled with small to minute trigones. Cells on margins of leaf lobes variously oriented and elongated perpendicular to the margin below, 5–7 × 8–10 μm measured along margins, (6–)7–8 × 8–10 μm in lobes and slightly increasing downwards, 8–10(–12) × 10–15 μm, slightly obliquely elongated towards the vitta, with small to large trigones and a more or less distinct middle lamella in cell walls. Cells at the very base of leaves near the margins thick-walled with lumen 5–8(–10) μm and walls between two leaves 4–5 μm with distinct deeper colored lamella. Above the angular thickening, both inner and outer surfaces of leaves bear at places (especially over vitta) low, dome-like, indistinct to more or less distinct projections (papillae) which can be seen only in leaf cross section (Fig. 3E, F, G, J) due to its high transparency. Plants dioecious. Male shoots have been found only in the Indian specimen (Iwatsuki B9), while the female ones only in the Chinese specimen (Long 35728). Androecia intercalary, composed by 2–4 pairs of bracts, 1–2-andruses; male bracts (Fig. 5A, D, F, G) almost not differing from leaves in length and width, deeply concave, with relatively short sinus (0.28–0.38 of the length) and saccate basal portion; antheridal stalks biseriate, 240–310 μm long. Gymnocia terminal; female bracts erect (Fig. 2A), mostly not differing from leaves in length, but comparatively wider, deeply concave, with relatively short sinus (0.28–0.43 of the length). Perigynium and perianth lacking, shoot calyptra translucent (Fig. 3D), up to 700 μm long. Capsule globose (Fig. 2A), elaters 2-spiral, 7–10 μm in diameter. Spores yellowish brown, 10–12 μm in diameter.

**Differentiation.** In general appearance, Gymnomitrión schusteraunum resembles G. revolutum in size, color, shape of leaves and sinuses, but in particular, none of the other species of the genus known to us has such a clear leaf vitta (cf. Damsholt, 2002, Plate 103 fig. 5). The elongated leaves with a length exceeding the width by 1.5–2 times and a very deep sinuses up to 0.5–0.7 leaf length are also characteristic. In size, color, and shape of leaves deeply divided into two lobes and having a distinct vitta, the new species resembles representatives of the genus Herbertus Gray at first glance. However, the absence of underleaves serves to immediately distinguish G. schusteraunum from Herbertus species even in the field.

**Additional studied specimen.** INDIA. West Bengal, near Sandakphu, Darjeeling area, 11,600–11,900 ft, 26 April 1965, Z. Iwatsuki et al. B 9 (MO, MHA – paratypes).

**Distribution.** To date this species is known only from China (Yunnan Province) and India (State of West Bengal). However, based on the two known locations that are remote from each other by about 1000 km, we can assume a much wider distribution of the species. Undoubtedly more extensive sampling in the Himalaya will lead to further localities for this species.

**Ecology.** The type specimen of Gymnomitrión schusteraunum was collected on the eastern (Chinese) side of the Gaoligong Shan, the dividing range between Yunnan and Myanmar, within the catchment of the Salween (Nu Jiang) River at a height of 3455 m. The area is dominated by somewhat undisturbed Abies/ Rhododendron forest up to approximately the altitude of the collection where the Abies trees had become relatively few (see image) and the steep rocky slopes were dominated by dense thickets of bamboo (foreground in image) and Rhododendron shrubbery. Around the lake shore were low rock outcrops where the type specimen was collected in a deep shady, moist rock cleft. The species associated with Gymnomitrión schusteranum are the mosses Andreaea rigida Wilson ex Mitt., Atractyloruscarpus alpinus (Schimp. ex Milde) Lindb. and Sanionia uncinita (Hedw.) Loeske, and the liverworts Diplolphyllum taxifolium (Wahlenb.) Dumort., Pseudolepidoceale trollii (Herzog) Grolle & Ando, Scapania contorta Mitt., S. ferruginea (Lehm. & Lindenh.) Lehm. & Lindenh., Schistochilopsis setosa (Mitt.) Konstant., Solenostoma appressiformium (Mitt.) Váňa & D.G.Long, S. oh-

Discussion

According to modern concepts, the genus Gymnomitrion comprises 35 species and includes some species previously attributed to Marsupella and Apomarsupella (Söderström et al., 2016). Along with the widespread circumpolar, mostly arctic montane species (for example, Gymnomitrion concinnatum (Lightf.) Corda, G. corallioides Nees, G. brevissimum (Dumort.) Warnst.), a significant proportion are species with a very restricted distribution. Typically, these are species described in the mid to late twentieth century from hard-to-reach

Furthermore, the concept of the distribution of many species has changed significantly during the relatively recent study of the mountains of Latin America, the western coast of North America and Southeast Asia (Váňa *et al*., 2010). Moreover, after publication of the World Checklist of Liverworts (Söderström *et al*., 2016), several species of the genus *Gymnomitrion* mainly from Asia were resurrected or described as new (Potemkin *et al*., 2017; Mamontov *et al*., 2018, 2019). Basically, the recent species were described on the basis of one or two adjacent specimens, thus having a very limited distribution e.g. *G. fissum* (Potemkin *et al*., 2017) or *G. kamchaticum* Mamontov, Vilnet & Konstant. (Mamontov

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et al., 2019). In this respect, the new species described by us is somewhat exceptional, since only two extremely distant populations of the species are known to date. This gives us reason to believe that the species may not be uncommon in Sino-Himalaya at altitudes of more than 3000–3500 m. In the type locality of the Gymnomitrion schusteranum in Yunnan Province we found a high concentration of east Asian elements including more or less strict endemics both Himalaya or South-East Asia. Particularly the list of its associates along with species widely distributed in the Holarctic e.g. Sanionia uncinata, Diplophyllum taxifolium, includes endemics to the Himalayan Region Pseudolepicolea trolitii, Scapania contorta, Solenostoma appressifolium, S. subacutum as well as a somewhat more widespread Solenostoma ohbae that occurs north of the Himalaya in Tibet (Váňa & Long, 2009). Scapania ferruginea was found in addition to the Himalayas (India, Nepal, Bhutan) also in China, Taiwan and Indonesia (Singh et al., 2008) and Schistochilopsis setosa occurs in the Sino-Himalaya and mountainous Northern Indochina (Bakalin et al., 2020). Schuster (1983: 540-541) suggested the Gondwanalandic origin of species with a somewhat similar distribution, including those found among associates with a new species e.g. Solenostoma subacutum (Horikawaella subacuta (Herz.) S. Hatt. et al.). The diversity, distribution and phylogenetic relationships of Gymnomitrion species in the Southern hemisphere are still very

poorly studied, so confirmation or refutation of this hypothesis is a matter of the future studies including molecular.

Taking into account the two Gymnomitrion species described after the publication of the World Checklist and the species described here, the number of known species of the genus increases to 38. We think that this is still far from revealing the full diversity of the genus; the study or revision of existing specimens stored in herbaria along with further collections from high altitude in unexplored mountain ranges, especially Himalaya and American Cordilleras, may lead to the description of other new species in future.

ACKNOWLEDGEMENTS

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LITERATURE CITED


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Appendix 1. The list of taxa, specimen vouchers and GenBank accession numbers, accessions obtained in this study are in bold.

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<th>Taxon</th>
<th>Specimen voucher</th>
<th>GenBank accession number</th>
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<td><strong>Gymnomitrion africanum</strong> (Steph.) Horik.</td>
<td>Rwanda, T. Pócs 8210 (F)</td>
<td>ITS1-2 nrDNA: no data, trnL-F cpDNA: KF943101</td>
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<td><strong>G. brevissimum</strong> (Dumort.) Warnst.</td>
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<td><strong>G. fission</strong> Mamontov &amp; Potemkin</td>
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