**Plagiochila xerophila** (Plagiochilaceae, Marchantiophyta) – a highly xerophilous new species from the Tibetan Spur (China)

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**Background and aims** – The xeric landscapes of the Tibetan floristic province are adverse habitats for leafy liverworts. Here we report on the occurrence of a population of a species of the genus *Plagiochila* from exposed high-elevation cliffs in the Sichuan Province, China. We assessed its taxonomic distinctiveness and affinities within a morphological and phylogenetic framework.

**Results and discussion** – The population is accommodated in a new species, *Plagiochila xerophila* Bakalin & Vilnet – probably the most xerophilous taxon within the genus in Asia – and a new section (sect. *Xerophilae* Bakalin & Vilnet) based on integrative analyses of molecular and morphological traits. The species is characterized by a greenish colour, unexpected given the highly exposed habitat, rigid texture and stem paraphyllia. The closest morphological relatives from sect. *Poeltiae* are phylogenetically only distantly related, whereas members of its sister groups, namely of sect. *Trabeculatae* and sect. *Fruticosae* are morphologically conspicuously different.

**Keywords** – China; East Asia; liverworts; integrative research; *Plagiochila*; taxonomy.

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**INTRODUCTION**

With an estimated 400 species (Frey & Stech 2009), of which many remain poorly studied, *Plagiochila* (Dumort.) Dumort. is currently the most speciose genus of liverworts. It is widely distributed in suboceanic areas, and most diverse in tropical montane forests. Söderström et al. (2016) listed 744 accepted names, about half of them (366) ‘incertae sedis’, and potentially belonging to other genera. The remaining taxa are distributed among 28 sections (Söderström et al. 2015). In total, 196 species are widely accepted, 379 are relatively poorly known (Söderström et al. 2016) and 167 are suspected to be doubtful, suggesting that even an estimate of the diversity of *Plagiochila* remains ambiguous. Renner et al. (2017), for example, suggest that the species diversity of Australasian *Plagiochila* is 29% higher than currently recognized, whereas, Gradstein (2015) only retained 34 species of the 135 reported from Brazil.

The diversity of *Plagiochila* is noticeable high in East Asia not only in the areas adjacent to the Pacific Ocean and its insular part (e.g. in Japanese archipelago, cf. Inoue 1958a, 1958b), but also in mountainous highlands inland, relatively far from the Pacific Ocean coasts, but still moistened with wet air masses coming from the Pacific. A robust framework for the study of Asian species of *Plagiochila* is provided by the taxonomic revision of Chinese species by So (2001), who recognized 80 species, including the majority of taxa known from East Asia. The latter work was exclusively based on morphological features. Recently, Bakalin & Vilnet (2017) described a peculiar new species of *Plagiochila* from the...
Russian Far East based on integrative approach. Here, we describe a further highly unusual new species from xeric high-elevation cliffs in eastern Asia based on morphological and molecular evidence.

Exploring the liverwort flora of high elevations areas in the Sichuan Province of China, we unexpectedly uncovered an unidentified, green and vermicular plant resembling *Plagiochila*. The specimen was collected in an area where *Plagiochila* species are indeed hardly expected: a desert habitat at 4474 m a.s.l., of gentle slopes from the ridge with many well exposed and virtually most of the year dry rocky outcrops. These outcrops lack vascular plant vegetation, except for a few low *Rhododendron* and *Dasiphora* shrubs on fine gravel between rocks. The specimen of *Plagiochila* occurred in micro-crevices in the rocky outcrops in patches of two highly xerophilous liverworts, *Gymnomitron sinense* Müll. Frib. and *G. crenatiolobum* Grolle. It stands out from among other species of the *Plagiochila* by the transversely inserted and orbicular leaves. To assess whether its morphological distinctiveness is not merely reflecting a phenotypic response of a more widespread species in this extreme habitat, we reconstructed its phylogenetic relationship based on variation in three genetic loci, and demonstrate that the sample is best accommodated in a new species and even new section of *Plagiochila*.

MATERIAL AND METHODS

Studied area

The specimen was collected in Sichuan Province (China) near the Kangding airport (30°07′01.1″N, 101°46′41.7″E), at 4474 m a.s.l., in dry rock crevices in an open SW-facing gentle slope in an alpine environment. The climate in the area can only be characterized by data for the Xinduqiao Settlement (30°01′54″N, 101°30′48″E) located at 3400 m a.s.l., which is the nearest settlement, but while far lower than 4400 m a.s.l., reflects a similar environment. Based on Climate-data.org (https://en.climate-data.org/asia/china/sichuan/xinduqiao-483085/) the mean annual temperature at the Xinduqiao Settlement is 5.4°C and the annual precipitation is slightly above 800 mm with distinct summer maximum. The total precipitation from June to September is 595 mm, corresponding well to that of forestless landscapes in the plateau reported by Miehe et al. (2001). Local inhabitants, however, mention a considerably colder climate near the Kangding airport, with negative mean monthly temperatures from November to March and a mean annual temperature near 0°C.

Overall, the studied area bears an ‘alpine meadow’ formation on permafrost soil (Wang et al. 2017). However, the vegetation of the landscape is more complex, composed of a mosaic of different communities ranging from very sparse plant cushions in gravelly barrens to dry alpine steppes and *Kobresia* meadows. In general, the mesophytic *Kobresia* communities are more abundant in the southeastern part of the Tibetan Plateau and reflect general trends in the climate variations across the plateau (Miehe et al. 2011a). Besides, the edges of the plateau are the ecotone between forested areas and alpine steppe, each with their distinct climatic characteristics, as recently discussed for the southern Tibetan Plateau (He et al. 2012). The series of xerophilous elements in the area where the specimen was collected is in high contrast with rather mesophytic *Picea-Abies* forest flora occurring as near as ca. 15 km eastward from the collecting locality near the city of Kangding in the Sichuan Province. These two nearby localities are divided by the Haizi Shan Range with elevations above 5000 m a.s.l. that may intercept wet air masses coming from the Pacific and thereby promote the formation of a dry and cold climate in the area of the collection.

Morphological and molecular study

The morphological traits of the specimen (V.A. Bakalin & K.G. Klimova China-46-2-17) were studied at VBG1, and the molecular investigation conducted at KPABG based on a duplicate of the collection (herbarium codes following Thiers continuously updated).

DNA was extracted from dried liverwort tissue using the NucleoSpin Plant Kit (Macherey-Nagel, Germany). Amplification and sequencing were performed using primers given by White et al. (1990) for ITS1–2, Taberlet et al. (1991) for trnL–F and Kress & Erickson (2007) for rbcL.

PCR was carried out in 20 µL volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s at 94°C, 40 s at 56°C, 60 s at 72°C) and 2 min of final extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by ethidium bromide staining, purified using the GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences, USA), and then used as templates for sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

Phylogenetic analyses

ITS1–2 nrDNA and trnL–F cpDNA were initially targeted to assesses based on BLAST outcomes (http://blast.ncbi.nlm.nih.gov/Blast.cgi) to clarify its morphological identification sequence similarity to those of other species of *Plagiochila*. To determine the phylogenetic affinities of the potential new species, relationships were inferred from analyses of partial *rbcL* cpDNA and ITS1–2 sequences based on datasets published by Renner et al. (2017), minus the *rps4* cpDNA sequences.

The implemented phylogenetic estimation of 160 Plagiochilaaceae and related taxa by the Bayesian method (BA) with MrBayes v. 3.2.1 (Ronquist et al. 2012) estimated the Chinese specimen to be related to a clade composed by representatives from sections *Trabeculatae* S.Hatt. ex Inoue and *Fruticosae* Inoue of *Plagiochila*. Later the entire ITS1–2 and *rbcL* sequence data were downloaded from GenBank for 27 and 24 *Plagiochila* specimens, respectively, distributed among six sections (Patzak et al. 2016; Jamy et al. 2016; Renner et al. 2017): *Plagiochila*, *Trabeculatae*, *Fruticosae*, *Peculaires* Schiffn., *Vagae* Lindenb. and *Poeiitae* Inoue. The recently described *Plagiochila sikhaitensis* (Bakalin & Vilnet 2017) was also included, and *P. andina* was chosen as the outgroup (table 1).
| Taxon                                                 | Specimen voucher | GenBank accession numbers |
|------------------------------------------------------|-------------------|--------------------------|
| Plagiochila abietina (Nees) Nees & Mont.             | Fiji, Renner et al. 5464 (NSW) | KX090150 KX090162 |
| Plagiochila andina Steph.                            | Bolivia, Heinrichs & Müller 4046 (GOET) | DQ194028 DQ194111 |
| Plagiochila asplenoides (L.) Dumort.                 | Italy, Schaefer-Verwimp & Verwimp 35859 (M) | KT992544 KT992617 |
| Plagiochila austinii A. Evans                        | USA, Kentucky, Risk 10849 (DUKE) | AJ748130 DQ439699 |
| Plagiochila britannica Paton                         | United Kingdom, Rycroft 00015, B.E.G.P. 199 (GOET) | AY275162 DQ194119 |
| Plagiochila carringtonii subsp. lobuchensis Grolle   | Bhutan, Long 28857 (GOET) | AJ414631 DQ194121 |
| Plagiochila elegans Mitt.                            | China, Long 33675 (GOET) | AM180599 No data |
| Plagiochila flexuosa Mitt.                           | Japan, Kurita 147 (HIRO) | AY550138 DQ194140 |
| Plagiochila frondescens (Nees) Lindeb.               | Indonesia, Schaefer-Verwimp 20704 (GOET) | AY438237 DQ194141 |
| Plagiochila fruticosa Mitt.                          | India, Long 23002 (GOET) | AY438235 No data |
| Plagiochila hakkodensis Steph.                       | Japan, Yamaguchi 12277 (HIRO) | AY275164 DQ194149 |
| Plagiochila korthalsiana Molk. ex Sande Lac.         | Indonesia, Mt. Gedeh, Java, Gradstein 10258 (GOET) | DQ194049 DQ194156 |
| Plagiochila magna Inoue                              | Japan, Kyushu, Kurita 258 (HIRO) | AY275167 DQ194162 |
| Plagiochila orbicularis (S.Hatt.) S.Hatt.            | Japan, Kurita 132 (HIRO) | AY275168 DQ194167 |
| Plagiochila ovalifolia Mitt.                         | Japan, Ohnishi 5723 (HIRO) | AY275169 No data |
| Plagiochila peculiaris Schiffn.                      | Bhutan, Long 28832 (GOET) | AY550141 DQ194176 |
| Plagiochila poeltii Inoue & Grolle                   | Australia, Renner 880483 (NSW) | KY051315 KY050816 |
| Plagiochila porelloides (Torr. ex Nees) Lindemb.     | India, Long 22802 (GOET) | AY550142 DQ194177 |
| Plagiochila pulcherrima Horik.                        | Portugal, Schaefer-Vervimp 31246 (M) | KT992543 KT992616 |
| Plagiochila renitens (Nees) Lindemb.                 | Japan, Kyushu, Ohnishi 5771 (HIRO) | AY438239 DQ194179 |
| Plagiochila satoi S.Hatt.                            | Malaysia, Schaefer-Vervimp 18736/A (GOET) | AY569441 DQ194184 |
| Plagiochila semidecurrens (Lehm. & Lindemb.) Lehmb.  | Japan, Ohnishi 5720 (HIRO) | AY550144 DQ194192 |
| Plagiochila sichotensis Bakalin & Vilnet             | Nepal, Long 21348 (GOET) | AY275172 DQ194194 |
| Plagiochila xerophila Bakalin & Vilnet               | Russia, Primorsky Territory, Bakalin 1-25-13 (VGBI), 118477 (KPABG) | MF947695 MF947696 |
| Plagiochila sp.                                      | Australia, Renner 855503 (NSW) | KY051508 KY051015 |
| Plagiochila trabeculata Steph.                       | Japan, Kyushu, Kurita 257 (HIRO) | AY550146 DQ194204 |
| Plagiochila trapezoidea Lindemb.                     | Australia, Renner 897031 (NSW) | KY051545 KY051055 |
| Plagiochila xerophila Bakalin & Vilnet               | China, Sichuan Prov., V.A. Bakalin & K.G. Klimova China-46-2-17 (VGBI) | MK121889 MK123265 (trnL-F cpDNA: MK123266) |
RESULTS

The combined ITS1-2+rbcL alignment for 29 specimens of Plagiochila consists of 1416 characters (i.e., 857 for ITS1-2 and 559 for rbcL). The number of invariable sites in the ITS1-2 and rbcL are 564 (65.81%) and 508 (90.88%), respectively, variable positions are 268 (31.27%) and 51 (9.12%), parsimony informative positions are 136 (15.87%) and 24 (4.29%).

The MP analysis with TNT yielded two equally parsimonious trees with a length of 997 steps, a Consistency Index of 0.754941 and Retention Index of 0.762452 calculated in Mega 5.1. The ML calculation resulted in a single tree, the arithmetic means of Log likelihood was -5037.316145. Arithmetic means of Log likelihoods in BA analysis for both runs sampled were -4906.88 and -4906.52.

The tree topologies achieved by the three methods are highly congruent and also consistent with those published in Patzak et al. (2016) and Renner et al. (2017). The most likely topology is presented in fig. 1 with MP and ML bootstrap support values and Bayesian posterior probabilities. All species were distributed among clades corresponding to the six sampled sections currently accepted in Plagiochila. Our unusual Chinese specimen was weakly resolved as sharing a unique common ancestor with two robust sister clades, i.e., section Trabeclulatae and Fruticosae. The ITS1-2 and rbcL sequences of the new specimen diverged from those of species of sections Trabeclulatae and Fruticosae by 6.3–8.8% and 0.7–1.6%, respectively, and thus a degree similar to that between species of these two sections (4.2–6.2% in ITS1-2, 1.1–1.8% in rbcL, table 2).

A new section and a new species

Based on an integrative taxonomic approach based on molecular, morphological, ecological and geographical data we accommodate the population from the arid region of the Kangding area in a new species for science, Plagiochila xerophila, described in the Taxonomic Treatment below.

The phylogenetic position of the new species and its morphological similarity to P. aspericaulis (see below, Relationships) show that this species pair should be placed in a new section named here Xerophilae, described and typified in the Taxonomic Treatment.

Plagiochila habitats

Unlike in South America, where many species of Plagiochila occur above 4000 m a.s.l. (Gradstein 2016), not many species exhibit an altitudinal range exceeding 4000 m a.s.l. in East Asia. The following species were listed by So (2001): P. aspericaulis Grolle & M.L.So (above 4760 m), P. biondiana C.Massal. (to 4300 m), P. delavayi Steph. (to 5000 m), P. duthiana Steph. (to 5000 m), P. carringtonii (Balfl. ex Carrington) Grolle (to 5100 m), P. poeltii Inoue & Grolle (to 5100 m), P. pseudopoeltii Inoue (to 4030 m), P. recurvata (W.ENicholson) Grolle (to 4800 m), P. retusa Mitt. (to 4200 m), and P. semidecurrens (Lehm. & Lindenh.) Lindenh. (to 4500 m). Most of the taxa are mesophytic and occur in forests, and only a few are characterized by densely-leaved shoots and occurrence in arid habitats (see table 3).

The distinctly xerophilous habitat deviates from the ecological preference of the overwhelming majority of Plagiochila taxa. The most ‘xeric’ taxa of the genus from East Asia are found in sect. Poeltiae and sect. Peculiares (including the former sect. Zonatae). The morphologically similar taxa from both sections are nevertheless more water-depending than P. xerophila and more brightly coloured with well-developed secondary brown pigmentation. The greenish coloration of P. xerophila is indeed unexpected, as in the

DISCUSSION
Table 2 – P-distances ITS1-2/rbcL, % for the species from sections Trabeculatae, Fruticosae and the new species.
- : non calculated value due to lack of DNA for specific locus.

| Section   | Species        | Trabeculatae | Fruticosae | Xerophilae |
|-----------|----------------|--------------|------------|------------|
|           |                | P. trabeculata | P. flexuosa | P. austini | P. pulcherrima | P. fruticosa | P. frondescens | P. xerophila |
| Trabeculatae | P. trabeculata | 0.5/0.2      |            |            |            |            |            |            |
|            | P. flexuosa   | 5.7/0.7      | 5.8/0.5    |            |            |            |            |            |
|            | P. austini    | 4.2/1.8      | 4.3/1.6    | 6.1/1.8    |            |            |            |            |
|            | P. pulcherrima| 4.5/1.1      | 4.7/1.3    | 6.2/1.4    | 2.3/1.4    | 2.3/-      |            |            |
| Fruticosae | P. fruticosa  | 4.2/-        | 4.3/-      | 6.1/-      | 0.3/-      |            |            |            |
|            | P. frondescens| 6.5/0.9      | 6.6/0.7    | 8.8/0.9    | 6.3/1.6    | 6.3/-      | 7.0/1.3    |            |

Figure 1 – Phylogram obtained in a maximum likelihood calculation for the selected sections of the genus Plagiochila based on combined nucleotide sequences dataset of ITS1-2 nrDNA and rbcL cpDNA. Bootstrap support values under maximum parsimony, maximum likelihood, and Bayesian posterior probabilities > 50% (0.50) are indicated.
| Species                        | Section      | Colour                  | Hialoderm in stem | Paraphyllia-like structures | ‘Vitta’ cells in the leaf base | Leaf dentation | Leaf position | Ecology                     |
|-------------------------------|--------------|-------------------------|-------------------|-----------------------------|-----------------|----------------|---------------|-----------------------------|
| *P. caulimammillosa* Grolle & M.L.So | sect. *Peculiare* Schiffn. | pale brown to dark brown | present           | absent                       | present          | present        | laterally spreading | mesophyte, epiphytic       |
| *P. biondiana* C.Massal.      | sect. *Poeltiae* Inoue | dark brown              | absent            | absent                      | absent           | present, rather coarse | laterally appressed | mesophyte, epiphytic       |
| *P. carringtoni* (Balf. ex Carrington) Grolle | sect. *Poeltiae* Inoue | reddish brown           | absent            | absent                      | absent           | absent or very few | laterally appressed | meso-hygrophyte, epilithic, damp mossy mats |
| *P. duthiana* Steph.          | sect. *Poeltiae* Inoue | yellowish brown         | absent            | absent                      | absent           | absent or inconspicuous | laterally spreading | mesophyte, epilithic to epigeric and epiphytic |
| *P. poeltii* Inoue & Grolle   | sect. *Poeltiae* Inoue | dull brown              | absent            | present, lamelliform, entire | absent           | present, coarse | laterally appressed | mesophyte epixylic         |
| *P. recurvata* (W.E.Nicholson) Grolle | sect. *Poeltiae* Inoue | reddish brown           | absent            | present lamelliform, entire | absent           | absent or inconspicuous | laterally appressed to somewhat spreading | meso-hygrophyte, epilithic to epigeric |
| *P. delavayi* Steph.          | sect. *Plagiochina* | brown                   | absent            | absent                      | absent           | present         | laterally spreading | mesophyte                  |
| *P. aspericaulis* Grolle & M.L.So | sect. *Xerophila* Bakalin & Vilnet | brown to dark brown     | absent, but overgrowth (paraphyllia) very thin-walled in cross section | present, inconsistently lamelliform, dentate | present | present, coarse | appressed to somewhat spreading | mesophyte, forest floor |
| *P. xerophila* Bakalin & Vilnet | sect. *Xerophila* Bakalin & Vilnet | yellowish greenish to greenish brownish | absent           | present, inconsistently lamelliform, dentate | absent           | present, sparse | laterally appressed | xerophyte, epilithic       |

Table 3 – *Plagiochila* taxa morphologically similar to *P. xerophila*. 
majority of liverworts the occurrence in well exposed places is commonly associated with a brown, red or purple pigmentation (Post 1990; Waterman 2018).

Relationships

The inferred shared ancestry of Plagiochila sect. Xerophilae with sect. Trabeculatae and sect. Fruticosae is also difficult to expect (and explain) from the morphological point of view. The representatives of the two sections, commonly characterized by distinctly longer than wide, somewhat plane and distanced to slightly contiguous leaves (So 2001), are in striking contrast with the densely-leaved shoots with suborbicular leaves in P. xerophila. Members of sect. Poeltiae are morphologically somewhat similar to P. xerophila. All superficially similar taxa of sect. Poeltiae differ by the more distinct secondary pigmentation and other traits (see table 3). Two species of this section, P. poeltii and P. recurvata, resemble P. xerophila by their paraphyllia. Plagiochila poeltii is perhaps the most likely to be confused with P. xerophila due to its dull brown colour. They differ, however, in several traits: 1) nodulate trinodes in the leaf cells of P. poeltii versus concave trinodes in P. xerophila, 2) smooth leaf cuticle versus commonly finely asperulose, 3) well developed lamelliform paraphyllia with entire margins versus paraphyllia inconsistent with dentate to denticate margins. The distance is also shown by the phylogenetic analysis (fig. 1).

Plagiochila xerophila is morphologically most similar to P. caulimammillosa and especially to P. aspericaulis from subsect. Caulimammillosae Grolle & So of sect. Peculiares (see fig. 3). Plagiochila xerophila differs from P. caulimammillosa in plant size (less than 1.5 mm versus to 4.5 mm wide), in leaf areolation (very poorly developed vitta-like area well developed), and, especially, in the hyalodermis (absent, although epidermal stem cells have walls somewhat thinner than inward, but never so thin to be eroded, versus well-developed and composed of thin-walled cells that are commonly eroded in older part of the shoot). Plagiochila caulimammillosa is a peculiar species of the genus in this latter trait (cf. So 2001).

Plagiochila aspericaulis is another taxon morphologically most similar to P. xerophila, but differs by its brown to dark brown color (versus greenish to greenish brownish and dirty green coloration of P. xerophila), its ovate leaves that distinctly longer than wide and prominently dentate (versus rounded and sparsely and obtusely dentate in P. xerophila), its stem diameter reaching 270 µm in width (versus less than 200 µm in P. xerophila (despite copious and well developed material of P. xerophila in our collection contrary to scanty plants of P. aspericaulis in iso- and paratypes), and stem overgrowths commonly reaching two or three cells in height on both the dorsal and ventral side in P. aspericaulis (versus outgrowth on dorsal side only in P. xerophila). Furthermore, the two taxa differ in their ecology: P. aspericaulis grows in mesophytic habitats on the forest floor whereas P. xerophila occurs on fully sun-exposed cliffs. The intricate problem is the distribution pattern differences between P. xerophila and P. aspericaulis. As currently estimated, P. aspericaulis is confined to the forested areas of Tibetan Plateau edges. Whether it penetrates the alpine steppes and, therefore could be a potential competitor with P. xerophila is unknown.

As previously shown by Söderström et al. (2015) and Renner et al. (2017) members of Plagiochila sect. Zonatae subsect. Zonatae belong to Plagiochila sect. Peculiares Schiffn. (cf. Renner et al. 2017: Fig. 1). This ‘Peculiare-Zonatae’ complex is clearly different from the newly described species. Moreover, we estimate that if even we will erect subsect. Caulimammillosae (type species P. caulimammillosa) to the section level, the pair P. aspericaulis-P. xerophila should hardly be referred to that section due to the morphological differentiationd. Unfortunately, three attempts to extract DNA for P. caulimammillosa and P. aspericaulis failed. Therefore, we prefer to retain P. caulimammillosa in sect. Zonatae subsect. Caulimammillosae and to separate P. aspericaulis and P. xerophila in a new section.

The phylogenetic hypothesis (fig. 1) whereby the morphologically similar sect. Xerophilae and Poeltiae are rather distantly related suggest parallel evolution of features such as densely foliated shoots, and rounded leaves with recurved margin or paraphyllia.

Biogeography

The studied area marks the transition between the Tibetan Province of the Irano-Turanian floristic region and the East Asian floristic province (cf. Chang 1981; Takhtajan 1986). Chang (1981) and He et al. (2012) noted the proximity of two different vegetation complexes in the edges of the plateau. The area where Plagiochila xerophila occurs shows drastically contrasting environments that may promote speciation. The same was observed in the Tibetan Plateau in general (Wen et al. 2014) and results in a large proportion of endemic taxa as it was noted for vascular plants in the alpine steppe in other parts of the plateau (Miehe et al. 2011b). Indeed, P. xerophila was collected in the dry alpine steppe, whereas as near as 10–15 km eastward (although behind of range of over 5000 m a.s.l.) more mesophytic communities are abundant and provide the suitable habitats for taxa with Sino-Himalayan distribution. These two vegetation complexes are markedly different in water requirements, with dry steppe plants commonly drought tolerant, and forest taxa, distributed also in the wetter edges of spurs of Tibetan Plateau, being mostly mesophytic and hygro-mesophytic.

Takhtajan (1986) characterized the Tibetan Province as relatively poor in species and relatively young, a consequence of its modern ‘vegetation history’ following the last glaciation. He argued that its vegetation probably originated from the transformation of Central Asian and (in broader view) ancient Mediterranean (~circum Paleo-Tethyan) ancestors. Spicer (2017) argued for a Paleogene origin of the diversity of southern Asia, including the Proto-Tibetan Highland at the northern extreme of the latter (uplifted before final Paleo-Tethys Ocean closure). However, he also confirmed (Spicer 2017) that the East Asian Monsoon, which governs patterns of precipitations, is a Neogene (ca. 22 Ma) phenomenon. The monsoon might be associated with Himalaya uplift, cooling in Central Asia and therefore additional decreasing of precipitation in the Tibetan Highland than it was before the splitting of single Asian monsoon into East
Asian and South-East Asian ones. The latter events drastically changed ecological conditions (for plant growth) in the Tibetan Highlands. These sudden changes in climate resulted in vegetation community movements and changes and could promote speciation in contrasting environments (Herzschuh et al. 2011; Wen et al. 2014).

It is difficult to predict the distribution of *Plagiochila xerophila*. It may be more widely distributed across Tibetan Plateau, at least in its eastern part, because of presence of virtually suitable habitats.

Liverworts provide many examples of mesophytic elements of meta-Himalayan distribution (cf. the term in Bakalin et al. 2018a). Outside of the eastern part of the Himalayas these taxa occur south-eastwards along the large spur that geomorphologically belongs to Tibetan Plateau. Some taxa of the mesophytic vegetation complex (cf. Bakalin et al. 2018b) occur within 10–15 km from the locality of *Plagiochila xerophila*.

Liverworts, related to the xerophilous Tibetan complex are likely rare. *Plagiochila xerophila* may be one of the few rare cases. *Gymnomitron sinense* and *G. crenatilobum* which are associated with *P. xerophila* may also belong to the xerophilous Tibetan complex. The representatives of the two complexes – mesophytic and xerophytic – probably originated in different areas at a different time. By now, the two complexes, however, penetrate one another. The penetration may be especially simple for the taxa of xerophytic nature, since even in generally moist regions (e.g. even along Pacific Ocean Coast), there are substrates that may house taxa distinctly alien to the general flora characteristics. Such evidence was found, e.g. in the distribution of xerophilous *Plagiochasma* in Japan (Bischler 1978) and the distribution of primarily paleo-Tethyan xerophytic *Riccia* in relict habitats of coastal areas in North-Eastern part of the East Asian mainland (Borovichev & Bakalin 2016).

**TAXONOMIC TREATMENT**

*Plagiochila* (Dumort.) Dumort.

Sect. *Xerophila* Bakalin & Vilnet, sect. nov.

**Type species** – *Plagiochila xerophila* Bakalin & Vilnet (present paper).

**Description** – Plants of xerophytic habitats, yellowish greenish to greenish brownish, erect in dense patches, 0.8–1.5 mm wide and 3–6 mm long. *Rhizoids* in erect spreading fascicles, grayish. Stem greenish-brownish, sparsely laterally intercalary branched, cross section transversely elliptic, ca. 225 × 175 µm, with mammillose epidermal cell walls or overgrowths 1 or 2(–5) cells high (forming somewhat dentate, lamelliform outgrowths (= paraphyllia) on the dorsal side of the stem), epidermis cells 15–22 µm in diameter, more or less thin-walled, with external wall thick, inward of epidermis cell walls become thicker and forming a 1 or 2 layers of thick-walled cells, further inward to the stem middle cell walls gradually become thin, the innermost cells 17–25 µm in diameter, with small, concave trigones. Leaves transversely inserted, decurrent for 0.5–1.0 of stem width on both sides, strongly ventral, at the first glance looking as incubous, suborbicular when flattened, 0.5–1.0 mm in diameter, dorsal side with strongly recurved margin, apical margin and upper half of ventral leaf margin sparsely and shortly denticate, with wide-based triangular teeth, teeth 1–3 cells long. Midleaf cells 12–25 × 12–20 µm, thin-walled, with moderately sized concave trigones, in larger cells sometimes with intermediate thickenings, cuticle very finely and at times obscurely asperulous, cells near leaf base 30–75 × 12–22 µm, thin-walled with small trigones, bistratose in lower 120–170 µm from base; marginal cells 10–16 µm along leaf margin, thin-walled to with slightly thickened walls, with moderate to small trigones. Generative structures unknown.

**Distribution** – Unknown, perhaps widely distributed across the Tibetan Plateau, at least in its eastern part.

**Habitat** – Poorly known, collected in rocky outcrops in alpine environment.

**SUPPLEMENTARY FILE**

One supplementary file is associated to this paper: Combined ITS1-2 nrDNA + rbcL cpDNA alignment for 29 specimens (Nexus file):

[https://doi.org/10.5091/plecevo.2020.1560.2051](https://doi.org/10.5091/plecevo.2020.1560.2051)

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Figure 2 – A–H. Plagiochila xerophila, from Bakalin & Klimova China-46-2-17 (VBGI). A. Plant habit, dorsal view. B. Plant habit, lateral view. C. Shoot fragment, ventral view. D–G. Leaves (rectangular area at G is increased at H). H. Leaf margin. I. Stem cross section. Scales: 1 (for A, B, D–G) = 1 mm; 2 (for C) = 1 mm; 3 (for H, I) = 100 µm. Drawn by Matvei Bakalin.
Figure 3 – A–E. Plagiochila caulimammillosa, from Long 24304 (JE). A. Dorsal view, perianthous branch. B. Shoot lateral view, fragment. C. Stem cross section, fragment. D, E. Leaves. F–K. Plagiochila aspericaulis, from Zhang Mu 713 (JE). F. Plant habit ventral view. G. Plant habit dorsal view. H. Dorsal view shoot, fragment. I. Stem cross section. J, K. Leaves. L–S. Plagiochila xerophila, from Bakalin & Klimova China-46-2-17 (VBGI). L. Plant, dorsal view. M. Plant, ventral view. N. Plant dorsal view, fragment. O. Stem cross section. P–R. Leaves. S. Cushion. Scales: 1 (for A) = 5 mm; 2 (for B) = 3 mm; 3 (for F, G) = 1 mm; 4 (for H) 500 µm; 5 (for L, M) = 1 mm; 6 (for N) = 500 µm; 6 (for C, I, O) = 100 µm; 8 (for D, E) = 1 mm; 9 (for J–R) = 500 µm.
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