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Once Again on the Distribution of *Syzygiella* (Adelanthaceae, Marchantiophyta) in Indochina

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Abstract: The distribution of known *Syzygiella* taxa in Indochina was reviewed. Currently, four species are known in Indochina: *S. autumnalis*, *S. elongella*, *S. nipponica*, and *S. securifolia*. This genus is reported for the first time in the flora of Cambodia, and *S. securifolia* is newly recorded for Vietnam. Herein, a description of oil bodies for *S. securifolia* is provided for the first time. A morphological description of the species and intravital photographs, as well as line-art illustrations, are provided along with the identification key to the *Syzygiella* taxa known in Indochina. A comparison of the climatic parameters of the collection sites for four known species showed that three of them occupy a relatively marginal position in the flora of Indochina as a whole and are known from colder biomes on the very northern edge of the peninsula. The locations of *Syzygiella securifolia* are scattered not only on the geographical map of Indochina but also on the bioclimatic scatterplot; these locations are likely an underestimation of the distribution of this taxon in Indochina, although it is generally rare worldwide. A comparison of lists of liverworts across the countries of Indochina will help identify groups of taxa for further targeted searches with the purpose of obtaining more comprehensive knowledge of the biodiversity of still poorly studied Indochina countries.

Keywords: *Syzygiella*; Southeast Asia; Cambodia; Vietnam; liverworts; Hepaticae

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1. Introduction

Syzygiella is one of a few exceptions among liverwort genera that has undergone a change in scope based on molecular genetic research over the past 20 years. While several traditionally recognized large genera have been split into several smaller units [1–5], *Syzygiella* has expanded [6,7] in scope with the inclusion of a number of previously almost universally recognized genera, such as *Cryptochila* R. M. Schust., *Jamesoniella* (Spruce) F. Lees, and *Roivainenia* Pers. [8–10].

There are currently 33 species known within the genus *Syzygiella* [11]. The genus is subdivided into 5 subgenera, the largest of which is *Syzygiella*, which includes 14 species [11]. The center of taxonomic diversity of the genus is in the Southern Hemisphere [8,12,13]. Only a few representatives of the genus are found in the Northern Hemisphere [14,15].

On the Southeast Asian mainland (Indochina Peninsula, Indochinese Floristic Province [16]), there are four representatives of the genus, and according to the literature, they include *Syzygiella securtifolia*, which is known in Thailand [17], as well as *Syzygiella autumnalis* (DC.) K. Feldberg et al., *Syzygiella elongella* (Taylor) K. Feldberg, Váňa, Hentschel et Heinrichs, and *Syzygiella nipponica* (S. Hatt.) K. Feldberg, Váňa, Hentschel et Heinrichs, which are known from the northernmost tip of North Vietnam [18–20]. It is worth mentioning that all three listed species are known from the Hoàng Liên Sơn Range, and *Syzygiella autumnalis* is known from one additional location in Hà Giang (Quản Bạ district) of Vietnam.

Of those listed, *Syzygiella securtifolia* is the most morphologically distinctive, which is also reflected in its placement in the oligotypic subgenus *Pseudoplagiochila*. Representatives of the latter subgenus are indeed quite similar to *Plagiochila* due to the peculiarly curved insertion line, which results in a 'plagiochiloid' habit. The scope and status of the subgenus, among other things, were also supported by recent topologies [6]. We found this species in Vietnam and Cambodia during research over the last decade. Since these collection locations are near the northern border of the species' global range and expands the understanding of its distribution, we aimed to describe those novelties in the present account. Since our study was based on living plants, we were able to collect information on the intravital coloration of the plants, as well as on the morphological parameters of the oil bodies; this information is also presented here. The available data [21] do not permit us to make any statements about the value of oil bodies in this genus due to the lack of information for many taxa. Therefore, now is the time to accumulate data that would be useful for the subsequent analysis. In addition, we provided an annotated list of *Syzygiella* species known from Thailand, Vietnam, and Cambodia, expanding our understanding of the distribution of this genus in Indochina.

2. Materials and Methods

Syzygiella material was collected during field studies conducted in Vietnam from 2016 to 2023 in several provinces of northern Vietnam to reveal the overall taxonomic liverwort diversity of the country. In total, 13 specimens were collected. All specimens were annotated under their field numbers (like V-7-5-17) provided to the specimen at the time of collection. All the material was transported alive to the laboratory of cryptogamic biota of the Botanical Garden Institute of the Russian Academy of Sciences or to the laboratory of Plant Ecology at the Institute of Ecology and Biological Resources of the Vietnam Academy of Science and Technology. After identification, the collected materials were subsequently transferred to the VBGI herbarium, with duplicate samples transferred to HN (the acronyms are in accordance with the Index Herbariorum [22]). *Syzygiella securifolia* was observed in Cambodia in 2013 during a study of the taxonomic diversity of bryophytes in this country as part of an international project (International Cooperation Unit on Biodiversity and Environmental Conservation supported by NIBR of the Republic of Korea). For a number of specimens, photographs of oil bodies and living habits were taken using digital cameras mounted on Nikon SMZ800N and Olympus BX43 microscopes in the laboratory of Plant ecology at the Institute of Ecology and Biological Resources of the Vietnam Academy of Science and Technology.

In addition, the distribution of *Syzygiella* was reviewed based on published sources, including [17,18], allowing a summary to be compiled of the genus in Indochina as a whole.

To clarify the differences in the requested climatic conditions for all species, data on 19 bioclimatic indices for all localities were obtained from WorldClim [23,24] (Table S1). In addition to Table S1, which includes bioclimates for occurrences of *Syzygiella* in Vietnam and Cambodia, we also included data for the occurrence of *S. securifolia* in Thailand. However, it is worth mentioning that we had to clarify some of the coordinates. The original source [17] (p. 468) reports that the coordinates were at "Mt. Khao Luang, 8°30′ N, 99°45′ E, 1740 m"; however, this height and the mountain itself are approximately 2.24 km from the EES and have coordinates of 8°29′38.26″ N, 99°43′48.49″ E. These coordinates were included in the table when determining bioclimates. The obtained bioclimatic data (Table S1) were subsequently tested via detrended correspondence analysis (DCA) using Past ver. 4.03c [25]. The DCA results were visualized in a three-dimensional grid graph, with the third dimension represented by a color gradient.

After the conditional coordinates of the position of each point in a three-dimensional coordinate system were determined by DCA, we also found the correlation coefficients between the coordinates of the points on each of the axes and the sequences of each of the 19 bioclimates separately. Correlation values were calculated using basic Excel functionality in MS Office. In this case, the coordinates of points in a three-dimensional grid were

determined using both DCA and CCA methods. The modular average values of correlation coefficients for DCA turned out to be higher than those for CCA (49.5% vs. 42.4%), so we subsequently used the correlation coefficients specifically for DCA, although in general, it should be noted that the calculated indicators are generally similar.

3. Results

3.1. Synopsis of Syzygiella Taxa in Indochina

Taxa are arranged alphabetically, and each taxon is annotated with (1) a geographical description of the collection sites within Indochina; (2) the altitudinal range, in meters above sea level; (3) a description of the species habitat in the investigated area; and (4) a brief citation of the literature reports, if any.

Syzygiella autumnalis (DC.) K. Feldberg, Váňa, Hentschel et J. Heinrichs

Northwest Vietnam (Lao Cai and Điện Biên Provinces) and Northeast Vietnam (Hà Giang Province), 1500–3105 m a.s.l. Decaying tree branches in evergreen tropical forests at 1500 m a.s.l., mesic to moist cliffs in evergreen southern subtropical mountain forests up to 2300 m a.s.l., and scattered *Rhododendron* communities with *Sinobambusa* thickets up to 3105 m a.s.l.

Syzygiella elongella (Taylor) K. Feldberg, Váňa, Hentschel et J. Heinrichs

Northwest Vietnam (Lao Cai, Lai Châu, and Điện Biên Provinces) and North Central Vietnam (Nghệ An Province), 1249–3105 m a.s.l. In Northwest Vietnam, the species occupies mesic boulders in an evergreen southern subtropical mountain forest at 1249 m a.s.l., decaying tree branches in evergreen tropical forests at 1500 m a.s.l., living tree trunks and branches, humus covering rocks in evergreen southern subtropical mountain forests up to 2700 m a.s.l., and scattered *Rhododendron* communities with *Sinobambusa* thickets up to 3105 m a.s.l. In North Central Vietnam (Annamite Range), the species was collected on moist shrub branches in mossy *Rhododendron* forests at 2298 m a.s.l.

Syzygiella nipponica (S. Hatt.) K. Feldberg, Váňa, Hentschel et Heinrichs

Northwest Vietnam (Lao Cai Province). Partially shaded moist cliff in scattered *Rhododendron* communities with *Sinobambusa* thickets at 2846 m a.s.l.

Syzygiella securifolia (Nees ex Lindenb.) Inoue

Northwest Vietnam (Cao Bằng Province): open moist cliff in dense evergreen mountain subtropical forest with bamboo thickets in the understory crossed by a park road at 1691 m a.s.l. Cambodia (Kampong Speu Province): living on tree trunk bases in a tropical mountain forest on 1790 m a.s.l. Thailand (Nakhon Si Thammarat Province): lower montane rainforest on 1740 m a.s.l. (without specifying the substrate in [17] (p. 468)).

Key to *Syzygiella* in Indochina

1. Leaves subopposite to approximate and nearly alternate dorsally, opposite and alternate ventrally, oblong lingulate, subtransversely inserted on the most extent of the insertion line, although ventrally insertion line arcuate and leaf shortly decurrent, while on the dorsal side insertion line oblique and decurrent for 1/4–1/3 of stem width, due to insertion line curvature leaves are ob-canaliculate and plants acquire 'plagiochiloid' habit), rhizoids virtually absent . . . *S. securifolia*
1. Leaves distinctly alternate both ventrally and dorsally, insertion line oblique, rhizoids commonly abundant, in mat or unclear fascicles in the ventral side of the stem . . . 2
2. Perianth mouth with one-to-three-celled tooth, plants purplish to purple-green, rarely greenish brownish, leaves longer than wide, ovate, commonly distinctly canaliculate and sheathing the stem . . . *S. elongella*
2. Perianth mouth with cilia 4–10 superposed cells, plant brown, golden-brown, and purple-brown, leaves wider than long or as wide as long, mostly lingulate, nearly plane, not canaliculate nor sheathing the stem 3
3. Leaf cuticle with large hemispherical papillae, leaf surface opaque and commonly golden-colored, hardly moistened (hydrophobic) . . . *S. nipponica*
3. Leaf cuticle virtually smooth to indistinctly papillose, leaf surface more or less glistening (never opaque) easily moistened (hydrophilous) . . . *S. autumnalis*

Specimens examined from the sampled area:

Syzygiella autumnalis VIETNAM, Northwest Vietnam, Lao Cai Province, Hoang Lien Son Range, Hoang Lien National Park, main path to the Phan Xi Pan Peak nearby (22°20′24″ N 103°46′33.6″ E), 1995 m a.s.l., evergreen southern subtropical mountain forest in the stream valley, open moist cliff near stream, 19 April 2017, V.A. Bakalin and K.G. Klimova V-7-5-17 (VBGI, HN); *ibid.* one of the ways to the Phan Xi Pan Peak (22°18′28″ N 103°46′25″ E), 2846 m a.s.l., thickets of *Sinobambusa* with many rocky outcrops and *Rhododendron* trees, open mesic cliff, 3 April 2018, V.A. Bakalin and K.G. Klimova V-17-16-18 (VBGI, HN); *ibid.* area near Phan Xi Pan Peak (22°18′13″ N 103°46′32″ E), 3105 m a.s.l., thickets of *Sinobambusa* with many rocky outcrops and *Rhododendron* trees, open moist cliff on slope, 3 April 2018, V.A. Bakalin and K.G. Klimova V-18-11-18 (VBGI, HN); Điện Biên Province, Mường Nhé Nature Reserve, Pờ Nhù Khò Mt. (22°22′24.5″ N 102°11′32.7″ E), 1501 m a.s.l., subapical part of unnamed mountain covered with evergreen tropical forest on NW-facing slope, open mesic fallen decaying tree branch, 4 April 2022, V.A. Bakalin and M.H. Nguyễn V-2-14a-22 (VBGI, HN); Northeast Vietnam, Hà Giang Province, Tay Con Linh Range, Tay Con Linh Nature Reserve (22°47′53″ N 104°48′33.5″ E), 2296 m a.s.l., evergreen southern subtropical mountain forest with large conglomerate cliffy massif, open moist cliff 22 March 2020, V.A. Bakalin and K.G. Klimova V-15-12-20, V-15-12a-20 (VBGI, HN).

Syzygiella elongella VIETNAM, Northwest Vietnam, Lao Cai Province, Hoang Lien Son Range, Hoang Lien National Park (22°20′56.4″ N 103°45′50.4″ E), 1840 m a.s.l., evergreen southern subtropical mountain forest in narrow stream valley, open mesic tree branch, 21 April 2017, V.A. Bakalin and K.G. Klimova V-10-16-17 (VBGI, HN); *ibid.* open mesic tree trunk, 21 April 2017, V.A. Bakalin and K.G. Klimova V-10-41-17 (VBGI, HN); *ibid.* area near Phan Xi Pan Peak (22°18′13″ N 103°46′32″ E), 3105 m a.s.l., thickets of *Sinobambusa* with many rocky outcrops and *Rhododendron* trees, open moist cliff on slope, 3 April 2018, V.A. Bakalin and K.G. Klimova V-18-12-18 (VBGI, HN); Lai Châu Province, Banh Hang Stream valley (22°30′30.2″ N 103°32′47.4″ E), 1249 m a.s.l., evergreen southern subtropical mountain forest, open mesic boulder on slope, 4 April 2019, V.A. Bakalin and K.G. Klimova V-1-8-19 (VBGI, HN); *ibid.* SW-facing slope of Bach Moc Luong Tu Mt. (22°29′59.7″ N 103°34′59.8″ E), 2700 m a.s.l., evergreen southern subtropical mountain forest, open mesic humus covering rocks, 5 April 2019, V.A. Bakalin and K.G. Klimova V-6-4-19 (VBGI, HN); Điện Biên Province, Mường Nhé Nature Reserve, Pờ Nhù Khò Mt. (22°22′24.5″ N 102°11′32.7″ E), 1501 m a.s.l., subapical part of unnamed mountain covered with evergreen tropical forest on NW-facing slope, open mesic fallen decaying tree branch, 7 April 2022, V.A. Bakalin and M.H. Nguyễn V-2-14-22 (VBGI, HN); North Central Vietnam, Nghệ An Province, Annamite Range (19°12′12.1″ N 104°07′51.7″ E), 2298 m a.s.l., ridge line covered by mossy *Rhododendron* forest, open moist shrub branch, 8 June 2023, V.A. Bakalin and M.H. Nguyễn V-86-5a-23 (VBGI, HN).

Syzygiella nipponica VIETNAM, Northwest Vietnam, Lao Cai Province, Hoang Lien Son Range, Hoang Lien National Park, one of the ways to the Phan Xi Pan Peak (22°18′28″ N 103°46′25″ E), 2846 m a.s.l., thickets of *Sinobambusa* with many rocky outcrops and *Rhododendron* trees, partly shaded moist cliff, 3 April 2018, V.A. Bakalin and K.G. Klimova V-17-12-18 (VBGI, HN).

Syzygiella securifolia VIETNAM, Northeast Vietnam, Cao Bằng Province, Phia Oac–Phia Den National Park (22°36′26.6″ N 105°52′02.4″ E), 1691 m a.s.l., open moist cliff in dense evergreen mountain subtropical forest with bamboo thickets in the understory crossed by a park road, open moist cliff, 26 March 2020, V.A. Bakalin and K.G. Klimova V-24-9-20, V-24-16-20 (VBGI, HN).

Not examined in the present study: THAILAND, Nakhon Si Thammarat Province, Mt Khao Luang (8°30′ N, 99°45′ E), 1740 m a.s.l., lower montane rainforest, 5 February 1966, Touw 11818, 11839 (BKF).

3.2. Distribution of Syzygiella Species by Bioclimatic Characteristics

As shown in the scatter plot (Figure 1), the bioclimatic localities of three species of *Syzygiella* (*S. autumnalis*, *S. nipponica*, and *S. elongella*) are limited to the extreme left of the diagram, while three occurrences of *S. securifolia* are scattered throughout the diagram, regardless of concentration.

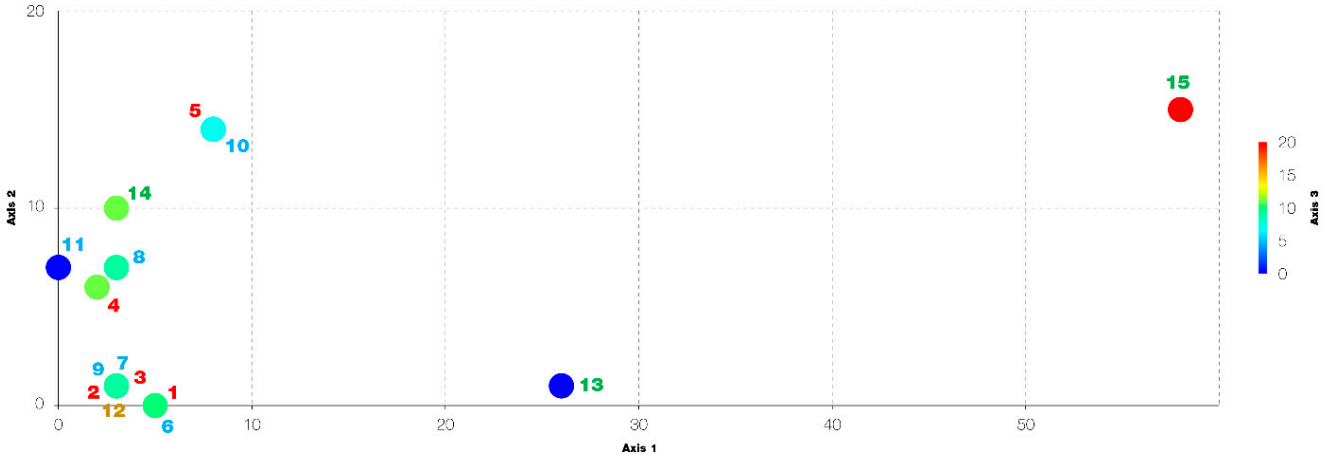

Figure 1. Scatter plot for distribution of *Syzygiella* taxa across bioclimatic parameters based on their collecting localities in Indochina according to Table S1. The numerals near each filled circle correspond to the number of the specimen listed in Table S1. Red numerals—*Syzygiella autumnalis*, blue—*S. elongella*, brown—*S. nipponica*, green—*S. securifolia*.

The distribution of points on the scatterplot according to Table S1 clearly correlates with certain types of bioclimates. So, on the x-axis, the highest direct correlation, exceeding 70%, is observed for BIO3 = Isothermality (BIO2/BIO7) (×100), BIO6 = Min Temperature of Coldest Month, BIO9 = Mean Temperature of Driest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO14 = Precipitation of Driest Month, BIO17 = Precipitation of Driest Quarter, BIO19 = Precipitation of Coldest Quarter. An inverse correlation with the same modular values is observed for BIO4 = Temperature Seasonality (standard deviation ×100), BIO7 = Temperature Annual Range (BIO5-BIO6), BIO15 = Precipitation Seasonality (Coefficient of Variation), and BIO18 = Precipitation of Warmest Quarter.

3.3. Morphological Description of Syzygiella securifolia

Since the most interesting report, as well as the least studied of those listed, is *Syzygiella securifolia*, we provide a morphological description compiled from the studied specimen from Vietnam below, including the first information on the oil bodies of the species. We also provide drawings and photographs of this species and species habitat from Vietnam and Cambodia.

Syzygiella securifolia (Nees ex Lindenb.) Inoue

Description (based on V-24-9-20). Plants green to bright green and brownish green (in alive conditions) becoming brownish and green-brownish in the herbarium, in loose pure patches, erect, more or less rigid, (3.5–)4–5 mm wide and 40–60 mm long (longer shoots commonly decaying in lower part). Rhizoids virtually absent. Stem nearly straight to slightly flexuous, rarely branched (branching ventral), brownish, ventral and dorsal sides not different in color; stem cross-section transversely ellipsoidal, 300–350 μm high and 400–450 μm wide, outer cells oblong along cross-section margin, in 1–2 rows with distinctly thickened brownish walls, 13–23 × 10–13 μm; inward cells become thinner (although never distinctly thin), 5–6-gonal, to 25–33 μm in diameter, trigones small to moderate, concave. Leaves subtransversely inserted on the most extent of the insertion line, although ventrally insertion line arcuate and leaf shortly decurrent, while on the dorsal side insertion line oblique and decurrent for 1/4–1/3 of stem width, due to insertion line

curvature leaves are ob-canaliculate and plants acquire 'plagiochiloid' habit; subopposite both ventrally and dorsally; when flattened on the slide narrowly ovate, widest below the middle, 1.8–2.5 mm long and 1.2–1.5 mm wide, leaf apex rounded, entire to obscurely crispate or obtusely angular. Midleaf cells thin-walled or with slightly and obscurely thickened walls, trigones moderate in size, triangular to slightly convex, subisodiametric to shortly oblong, 27–45 × 20–33 μm; cells along leaf margin 20–25 μm, subisodiametric, thin-walled, with moderate to concave trigones, external wall slightly thickened; cuticle smooth or sometimes slightly striolate in the middle parts of leaves; oil bodies in the midleaf cells 8–18 per cell, granulate, spherical 3–6 μm in diameter, to irregularly oblong, 4–12 × 3–5 μm. Dioicous. Perianth on the main axis, with 1–2 ventral subfloral innovations, ovate to loosely trigonous, 2.0–2.5 × 1.0 mm, gradually contracted to lacinulate-dentate mouth. Female bracts similar in size to the leaves or slightly smaller, commonly one bract is obliquely ovate, with a shortly dentate upper half, while the second is lanceolate with an attenuate apex and several teeth on lateral sides. Female bracteole widely connate with lanceolate bract, nearly triangular with two additional large teeth near the base and several additional small teeth over the margin.

Illustrations in the present paper: Figures 2–4.

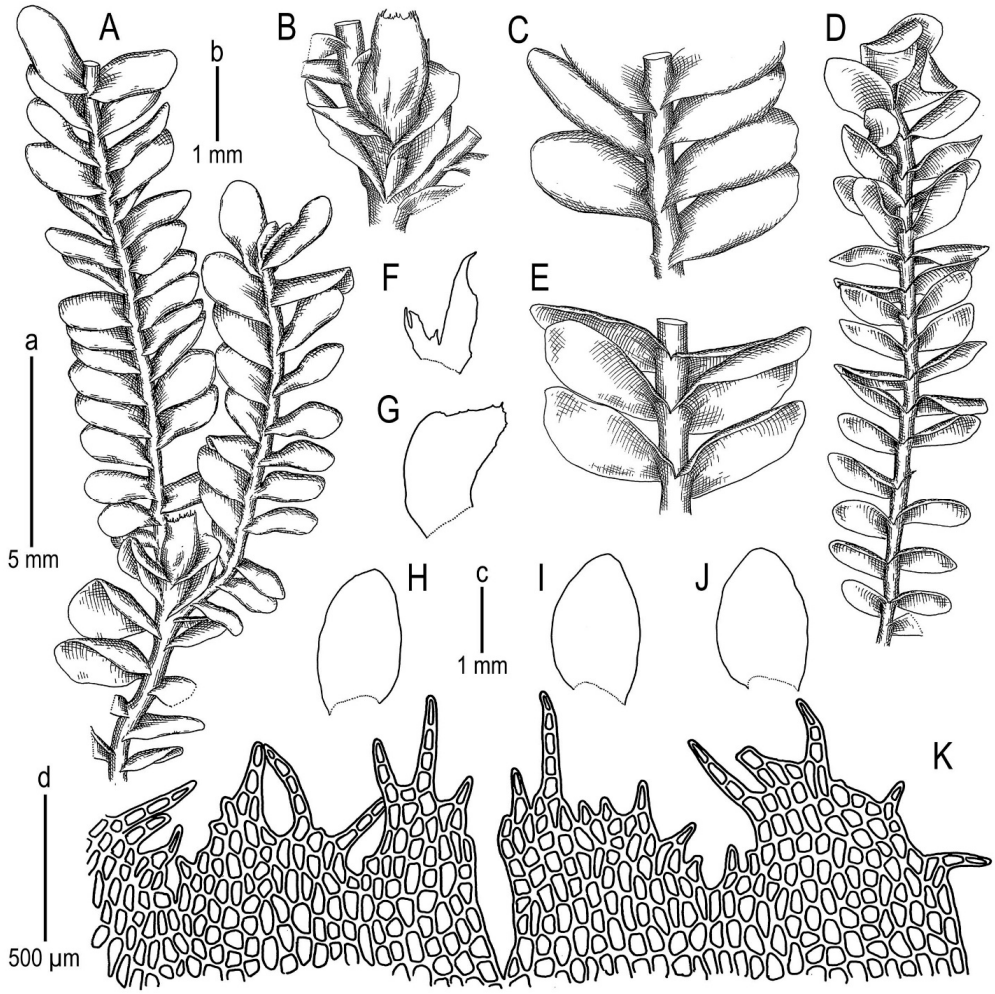

Figure 2. *Syzygiella securifolia* (Nees ex Lindenb.) Inoue: (**A**) perianthous shoot, dorsal view; (**B**) part of shoot with perianth, dorsal view; (**C**) insertion lines of leaves on dorsal side of a shoot, dorsal view; (**D**) shoot, fragment, ventral view; (**E**) insertion lines of leaves on ventral side of a shoot; (**F**,**G**) female bracts; (**H**–**J**) leaves; (**K**) lacinulate-dentate perianth mouth armature. Scales: a—5 mm for (**A**,**D**); b—1 mm for (**B**,**C**,**E**); c—1 mm for (**F**–**J**); d—500 μm for (**K**). All from V-24-9-20 (VBGI).

Figure 3. *Syzygiella securifolia* (Nees ex Lindenb.) Inoue: (**A**) shoot, dorsal view; (**B**) shoot, ventral view; (**C**) insertion lines of leaves on dorsal side of a shoot; (**D**) insertion lines of leaves on ventral side of a shoot; (**E**) lacinulate-dentate armature of the perianth mouth; (**F**) perianthous shoot, fragment; (**G**) stem cross-section; (**H**) cells with oil bodies near leaf margin; (**I**,**J**) midleaf cells with oil bodies. Scales: 5 mm for (**A**,**B**); 3 mm for (**F**); 500 μm for (**C**,**D**); 200 μm for (**G**); 50 μm for (**E**,**H**–**J**). All from V-24-16-20 (VBGI).

Figure 4. (**A**) Mat of *Syzygiella securifolia* (Nees ex Lindenb.) Inoue in natural conditions (Cambodia, Aoral Mt.); (**B**) Shoots, dorsal view; (**C**) Shoots, ventral view; (**D**) Tropical mountain forest on Aoral Mt. (1790 m a.s.l.)—collection place of *Syzygiella securifolia* in Cambodia (Photos by S.S. Choi, 2013).

4. Discussion

Although the center of diversity of *Syzygiella* is located in the Southern Hemisphere, several species are distributed predominantly in the Holarctic, and three of them (*S. autumnalis*, *S. elongella*, and *S. nipponica*) penetrate the northern tip of the Indochina Peninsula, which is at the southern extreme of their core area. However, it is worth mentioning that they all occur further south. *Syzygiella nipponica*, a predominantly East Asian species, is

known from Southeast Asia in Borneo [8,26]. *Syzygiella autumnalis* is generally a Holarctic species that penetrates somewhat south of the Holarctic border, as is observed in Indochina. In addition to the mentioned penetrations, the species is also known in Latin America (from Mexico to Central America and the northern Andes). According to Gradstein et al. [27], the distribution of the species in the Southern Hemisphere may be the result of recent migration into the Neotropics. *Syzygiella elongella* is distributed in the southern part of the East Asian region (roughly corresponding to the Sino-Himalayan area), and the distribution of this species in the mountains of northern Vietnam is also quite expected. In general, all three of these species indicate the penetration of conditionally 'northern' species into Indochina through mountain systems connected with the Sino-Himalaya. The dense interpenetration of Sino-Himalayan flora to Indochina is also evident from the maps by Takhtajan [16], Welk [28], and several other authors. The same phenomenon was discussed for liverwort taxa previously [29]. All three species are also expected to be found in the mountains of northern Laos and northern Thailand.

Compared to the distribution of taxa briefly discussed above, the distribution of *Syzygiella securifolia* is fundamentally different. As reviewed by Sukkharak [17], the species is found in Indonesia, Malaysia, New Caledonia, Papua New Guinea, the Philippines, the Solomon Islands, Sri Lanka, the Taiwan Province of China, and Thailand. Thus, the distribution of the species as a whole can be characterized as Southeast Asian (including Indochina and Malesia), extending into Melanesia. Along with the Taiwanese localities, the distribution in northern Vietnam is at the northern limit of the species' range. However, the discovery of this taxon in other areas of Indochina is highly anticipated.

Syzygiella securifolia is known from various parts of Indochina, and this is reflected not only in the geographical map but also in the scatter plot (Figure 1). Moreover, the other three species, limited in distribution to the northern tip of Vietnam, exhibited a much smaller spread in climatic conditions and were closely related to each other (Figure 1). In part, this can be interpreted as the distinctness of these three species from Indochina liverwort flora as a whole. The distribution of *Syzygiella* species in Indochina is provided in Figure 5.

According to the obtained bioclimatic parameters and their correlation with the sequence of conditional coordinates in a three-dimensional grid (Figure 1, Table S1) along the abscissa axis (the longest in the diagram), the greatest correlation is observed between the jointly acting and related parameters of isothermality, temperature and humidity seasonality, and the amount of precipitation in the driest and coldest quarters (these are nearly the same quarters in the calendar). Precipitation in the warmest quarter is also of great importance for the spread of *Syzygiella*. Since all points for the three *Syzygiella* species are clearly clustered near the left edge of the scatterplot (Figure 1), the bioclimatic parameters listed above mainly determine the distribution of Syzygiella species in Indochina.

5. Conclusions

The regional floras of Indochina, with some differences of a provincial nature (for example, shown on the map by Welk [28], have close connections with each other [16]. Therefore, the species found outside of the extreme northern region of Indochina (such as the Hoang Lien Son Range in Vietnam) in one country can easily be expected in other countries of Indochina, as again evidenced by the distribution of *Syzygiella securifolia*. We assume that a comparative analysis of the liverwort lists for the countries of Indochina will make it possible to identify several groups of species that are currently known to be from one to two countries but that are likely to be discovered in the future in neighboring countries. This targeted search may provide the basis for further explorations on taxonomic diversity of liverworts in the countries within the Indochinese floristic region of the Paleotropics.

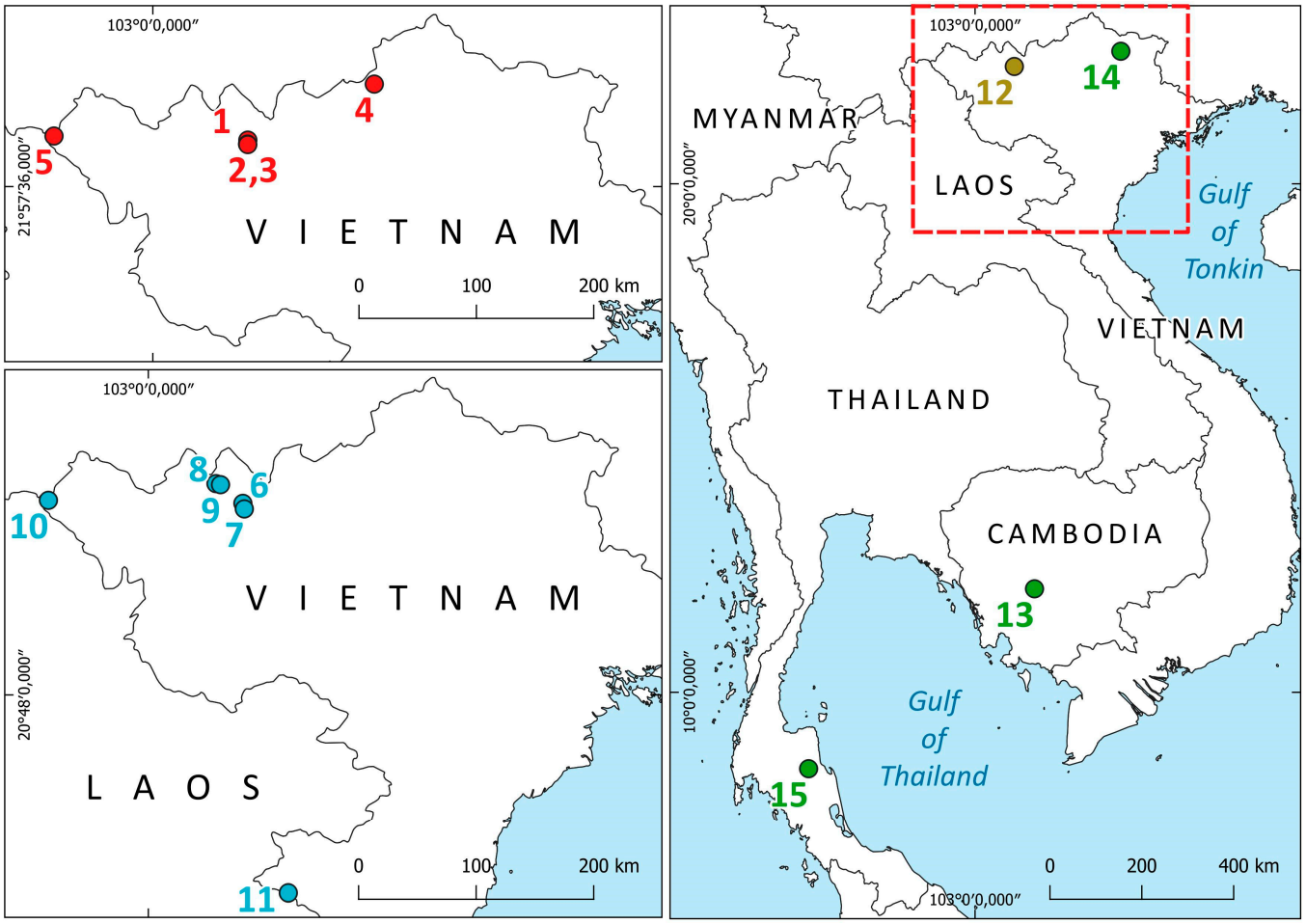

Figure 5. The distribution of *Syzygiella* species in Indochina. Color of numbers and points: red—*Syzygiella autumnalis*, blue—*S. elongella*, brown—*S. nipponica*, green—*S. securifolia*. Numbers and colors correspond to Table S1 and Figure 1. The dashed area in the upper right corner shows the part of the map that has been enlarged on the left side of the picture.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16030149/s1, Table S1: Bioclimatic data, geographic coordinates, field numbers, and elevations of collecting localities (including those from the literature sources) of *Syzygiella* in Indochina supplemented with conditional coordinates in the three-dimensional grid taken from DCA, CCA, as well as correlation coefficients between sequences of point coordinates and their bioclimatic parameters separately for all 19 bioclimates.

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