広島大学学位請求論文

Taxonomic revision of the genus *Marchantia* L. in Japan

（日本産ゼニゴケ属の分類学的再検討）

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主論文

Taxonomic revision of the genus *Marchantia* L. in Japan

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Summary

The genus *Marchantia* L., included in family Marchantiaceae of Marchantiidae, is one of the most familiar genera of all liverworts due to the inclusion of the prevalent model plant *Marchantia polymorpha*. L. By the end of the twentieth century, 130 species or intraspecific taxa have been recognized in Asia and the Pacific region including Japan, due to the high morphological plasticity. In subsequent studies, many of these taxa were synonymized, and it was interpreted that only six species are distributed in Japan. However, previous taxonomic studies were based on limited field work and morphological comparison of specimens. The taxonomic validity of previous studies needs to be revalidated through the comparison of more specimens collected in intensive fieldwork and molecular phylogenetic studies. Since traditional taxonomy in the genus was based on very limited morphological traits with plasticity (e.g. width of thallus, morphology of ventral scales), the search for new morphological characters was also an important issue. I conducted the first comprehensive taxonomic revision of *Marchantia* in Japan by morphological examination of specimens including types and molecular phylogenetic analysis.

In chapter 1, I proposed the morphology of gemmae as a new taxonomic character of *Marchantia*. Several characters of the gemmae, including size, shape, morphology of marginal cells, and the presence or absence of mucilage hairs were useful in species. Morphological similarity of gemmae between *M. polymorpha* and *M. paleacea*, as well as between *M. emarginata* and *M. pinnata*, was consistent with the results of molecular phylogenetic analyses.

In chapter 2, taxonomic reevaluation on Japanese taxa belonging to sect. *Papillatae* Bischl. of subg. *Chlamidium* (Corda) Bischl. was conducted. The molecular phylogenetic analysis showed that Japanese plants belonging to sect. *Papillatae* should be partitioned into two distinct clades. The plants belonging to the two clades were distinguishable by the presence or absence of a dark median band on the thallus and the morphology of the appendage of ventral scales and gametangiophores. Geographic distribution and ecological habits in Japan also support the partitioning into two distinct clades. We proposed *M. emarginata* Reinw. Blume et Nees subsp. *cuneiloba* T.X.Zheng & M. Shimamura comb. et. stat. nov. and *M. papillata* Raddi. subsp. *grossibarba* (Steph.) Bischl. as appropriate taxonomic names for the plants belonging to each clade. The species previously described from Japan (e.g., *M. radiata* Horik., *M. tosana* Steph. and *M. tosayamensis* Steph.) were synonymized for either of them.

In chapter 3, The species of the genus *Marchantia* distributed in Japan were

taxonomically revised based on morphological examination. The following eight species were recognized as Japanese species, *M. polymorpha* subsp. *polymorpha*, *M. polymorpha* subsp. *ruderalis*, *M. paleacea* subsp. *paleacea*, *M. paleacea* subsp. *diptera*, *M. emarginata* subsp. *cuneiloba*, *M. papillata* subsp. *grossibarba*, *M. pinnata* and *M. quadrata*. The morphological definition of each taxon was circumscribed and illustrated. Distribution, habitat, taxonomic notes, distinguishing characters, and a key to the species of the genus *Marchantia* were also provided.

This study comprehensively resolved the taxonomic ambiguity of the Japanese species of *Marchantia*. Some newly discovered taxonomic characters in this study, such as the gemma morphology and the dark median band on the thallus, will be significant as a new method for reconstructing the classification system of *Marchantia* in the world.

General Introduction

Bryophytes, which include three phyla, liverworts (Marchantiophyta), mosses (Bryophyta) and hornworts (Anthocerophyta) have been considered as the most primitive extant land plants of ca. 20000 species (Patiño & Vanderpoorten 2018; Shaw et al. 2011). These groups are characterized by sharing (1) dominant generation of gametophyte in its life cycle, (2) unbranched sporophyte with single spore producing tissue attached permanently to maternal gametophyte, (3) simple vascular tissue without lignin and (4) dependence on water for fertilization. Although it is widely accepted that bryophyte is the earliest divergent group of land plants, the interrelationship between the three major lineages of bryophyte has been controversial. Previous molecular phylogenetic studies indicated the paraphyly of bryophytes and basal-most position of liverworts among land plants (Friedman & Cook 2000; Growth-Malonek & Knoop 2005; Qiu et al. 2006, 2007; Shaw et al. 2011). Recent morphological (Renzaglia et al. 2018) and phylogenomic evidence (Cox et al. 2014; Harris et al. 2020; Leebens-Mack et al. 2019; Wickett et al. 2014) has supported a challenging view that bryophytes are monophyletic and hornworts diverged earlier than liverworts and mosses (Setaphyta).

The estimated species number of liverworts are over 7200 worldwide, which is second to ca. 12000 species of mosses but ahead of ca. 220 of hornworts (Söderström et al. 2016). Historically, due to the striking diversity in gametophyte form, liverworts were classified into: (1) simple thalloids, without differentiation of conspicuous internal tissue, (2) complex thalloids, with differentiation of internal tissue, such as ventral storage and dorsal photosynthesis layers and (3) leafy liverworts, with two lateral and one ventral (sometimes absent) rows of leaves developing along longitudinal and parallel lines. Based on recent morpho-phylogenetic evidence, liverworts have been subdivided into three classes: Jungermanniopsida, Haplomitriopsida and Marchantiopsida (Crandall-Stotler et al. 2009), which do not perfectly correspond to the previous classification based on gametophyte form. Jungermanniopsida comprises leafy liverworts (subclass Jungermanniidae, *Pleurozia* of Metzgeriidae and *Noteroclada* of Pelliidae) and simple thalloids (remaining taxa of Metzgeriidae and Pelliidae), including most liverworts species. Haplomitriopsida is considered as the earliest diverging group comprising leafy form (Haplomitriidae) and intermediate form between thalloid and leafy (Trubiidae) (Forrest et al. 2006). Marchantiopsida represents a complex thalloid with approximately 400 species, which can be further subdivided into two subclasses, Blasiidae and Marchantiidae.

The genus *Marchantia* L., included in family Marchantiaceae of Marchantiidae, is one of the most familiar genera of all liverworts due to the inclusion of the prevalent model plant *Marchantia polymorpha*. L. which has been recognized and utilized by humans since the ancient Greek era (Bowman 2016; Shimamura 2016). The earliest certain diagnosis of *M. polymorpha* is found in Liber de Simplicibus, which was compiled by Rinio in 1419 and illustrated by Amadio (Pächt 1950). In 1542, Fuchs et al. first described *M. polymorpha* in printed literature. Due to the wide morphological variation of *M. polymorpha* L., most early studies including *Marchantia* taxa were carried out mainly to discuss its taxonomic treatment. Moreover, plants corresponding to *M. polymorpha* were also treated as many independent or intraspecific taxa during its long research history (Bauhin 1623; Schmidel 1747; Micheli 1729; Dellenius 1741). It is worth noting that Marchant (1713) originally named the genus as *Marchantia* in memory of his father and described the species *M. stellata* to represent female *M. polymorpha*.

Linnaeus (1753) adopted "*Marchantia*" as the genus name and established the nomenclatorially valid inception of *Marchantia* L. [type: *M. polymorpha* L.] to accommodate seven complex thalloid species. In 1818, Raddi amended the definition of genus by retaining *M. polymorpha* and *M. chenopoda* L. in situ and transferring others of Linnaeus's species to their own newly established genus. This treatment has been widely accepted by subsequent bryologists. Corda (1829) published *Chlamidium indicum* Corda. (= *M. chenopoda*) and erected genus *Chlamidium* Corda. which was later treated as sect. *Chlamidium* of genus *Marchantia* by Nees von Esenbeck (1838) although Lindley (1836) accepted its generic rank. Lehmann (1832) reviewed the collection made from India by Wallich and reported 3 new species, *M. linearis* Lehm. et Lindenb., *M. nitida* Lehm. et Lindenb and *M. nepalensis* Lehm. et Lindenb. In 1838, Nees von Esenbeck newly recognized sect. *Astromarchantia* Nees, which was also followed by Evans (1917) and Hässal de Menédez (1962).

After that, numerous taxa were added to the genus with the increase in expeditions especially conducted in East and Southeast Asia. Reinwardt et al. (1824), Montagne (1838), Gottsche et al. (1846), Lehmann (1857) and Schiffner (1893, 1898) newly reported nearly 30 taxa from Indonesia (Java). In 1861, Mitten summarized the previous records of liverworts from East India (Gottsche et al. 1846; Griffith 1849) and recognized seven *Marchantia* species from this region including a new taxon *M. subintegra* Mitt. Bescherelle (1892, 1894) enumerated Vietnamese and Japanese liverwort taxa determined by Stephani, in which four Marchantian names were invalidly published. The largest input was made by Stephani (1894, 1897, 1899) who reported over 70 *Marchantia* taxa, 29 of which were collected or previously recorded from Asia. Herzog (1930) organized the specimens collected from Southwestern China and reported 3 infraspecific and one independent taxa. Horikawa (1934) reviewed the liverworts from Japan and its adjacent region and described *M. formosana* Horik. which is endemic to Taiwan Province of China. Chopra (1938a, 1938b) and Hattori (1966) researched liverworts from south India and the Himalayas and proposed three new species, *M. indiaca* Kash., *M papulosa* Amak. and *M. togashii* Amak. In 1943, Burgeff conducted unprecedented genetic research on European and tropical *Marchantia* and originally proposed nine taxa from the Philippines and Indonesia. In 1953, Bonner published 17 Asian *Marchantia* taxa described by Stephani. Grolle (1976) enumerated liverworts and hornworts in Europe and its neighbouring regions and re-instated the name "*Marchantia*" for sect. *Astromarchantia* due to the inclusion of type of the genus, *M. polymorpha* in the section. In 1982, Bischler compared the spore morphology and modes of germination between sect. *Marchantia* and sect. *Chlamidium* and elevated them both to subgeneric level. Gao and Chang (1982) proposed a new genus *Marchantiopsis* C. Gao & K.C. Chang based on the *Marchantiopsis stoloniscyphula* C. Gao & K.C. Chang collected from Tibet of China and this species was transferred to *Marchantia* by Piippo (1990). Nevertheless, its taxonomic status is still in doubt since no critical examination on its type specimen was made hitherto (Söderström et al. 2016). Schuster (1985) newly erected an anomalous subg. *Protomarchantia* Schust. In 1989, Bischler-Causse firstly revised *Marchantia* in Asia and recognized three subgenera, five sections and 17 taxa in the region. Recently, Long et al. (2016) transferred species of *Bucegia* Radian and *Preissia* Corda to *Marchantia* based on an earlier multi-loci phylogenetic analysis (Villarreal et al. 2016). The only new discoveries in the 21st century, *M. longii* R.L. Zhu, Y.L. Xiang et L. Shu and *M. platycarpa* D.G. Long & Crand.-Stol. were both described based on Chinese materials (Xiang et al. 2016; Long & Crandall-Stotler 2020).

Although studies on Asian *Marchantia* species conducted by Bischler-Causse (1989) were based on very limited field work and morphological comparison of specimens selected by contemporary foreign bryologists or collectors, subsequent almost all studies conducted in Asian regions were carried out accordingly based on her taxonomic interpretations. (Alam et al. 2016; Bakalin et al. 2017; Ho 2013; Katagiri & Furuki 2018; Kürschner & Frey 2019; Lai et al. 2008; Long & Grolle 1990; Long & Rubasinghe 2014; Lu & Huang 2017; Piippo et al. 1998; Ruklani et al. 2015; Xiang et al. 2016). Moreover, the taxonomic validity of Bischler-Causse's species needs to be revalidated through the comparison of more specimens collected in intensive fieldwork and molecular phylogenetic studies. Since traditional taxonomy in the genus was based on very limited morphological traits with plasticity (e.g. width of thallus, morphology of ventral scales), the search for new morphological characters is also an important issue.

Here, I conduct the first comprehensive taxonomic revision of *Marchantia* in Japan by morphological examination of specimens including types and molecular phylogenetic analysis. In chapter 1, morphology of gemmae is originally proposed as a new taxonomic character of *Marchantia*. In chapter 2, taxonomic reevaluation on Japanese taxa belonging to sect. *Papillatae* Bischl. of subg. *Chlamidium* (Corda) Bischl. was conducted. In chapter 3, morphological circumscription, distribution, ecological characteristics, identification point and taxonomic notes of each *Marchantia* species in Japan are provided.

Chapter 1

Morphology of gemmae, an overlooked taxonomic trait in the genus *Marchantia* L. (Marchantiaceae)

Introduction

Asexual reproduction is a fundamental reproductive mechanism recognized in bryophytes (Frey & Kürschner 2011). As one type of specialized asexual propagules, gemmae show considerable morphological diversity in bryophytes (Cavers 1903; Imura 1994; Imura & Iwatsuki 1990). In some case, morphological differences in gemmae help to identify species, even among closely related species (Bastos 2008; Borges 2006; Evans 1910; Iwatsuki & Deguchi 1981). In complex thalloid liverworts, many species belonging to the genus *Lunularia, Neohodgsonia* and *Marchantia* produce multicellular gemmae in cup-shaped structures called "gemma cups" (or "cupules"). In *Marchantia*, the gemmae are multicellular discoid structures with two laterally placed apical notches. The central part of the gemma is several cells thick and becomes gradually thinner toward the one-celled margin (Bischler-Causse 1989; Shimamura 2016). The germination of the thallus from gemmae in *Marchantia* has been used as an experimental system in which to study physiological responses of plants to various environmental factors and the gene functions in morphogenesis (Bowman 2016; Eklund et al. 2018; Equihua 1987; Furuya et al. 2018; Mirbel 1835; Naramoto et al. 2019; Shimamura et al. 2017; Solly et al. 2017; Suzuki et al. 2020) and microbiome studies (Kobae et al. 2019; Nelson et al. 2018).

Since the establishment of the genus *Marchantia* (Linnaeus 1753), various attempts have been made to define the taxa at the subgeneric, species and subspecies level based on the morphological characters, such as number of ventral scales rows, morphology of the appendage of the median ventral scales, gemma cup margins, spore ornamentation and alternative patterns of archegoniophores lobes and involucres (Arnell 1963; Bischler 1984; Bischler-Causse 1989, 1993; Bischler-Causse et al. 2005; Burgeff 1943; Gradstein & Costa 2003; Horikawa 1930; Lu & Huang 2017; Schuster 1992). However, no attention has been paid to the morphological characters of gemmae as taxonomic traits. In general, it is assumed that the morphology of gemmae is very uniform throughout the genus *Marchantia* and it does not helpful to identify the species (Bischler-Causse 1989, 1993; Evans 1917). Recently, Zheng & Shimamura (2019a) in a comparison of gemmae morphology of *M. polymorpha* and *M. pinnata* have suggested that morphological diversity of gemmae is worthy of re-consideration as a taxonomic character that has been overlooked. I now have undertaken a comparative study of gemma morphology of six Japanese *Marchantia* taxa and explored its systematic significance of my findings in light of recent molecular phylogenetic analyses. Based on my study, I propose that gemma morphology is a useful taxonomic character to separate *Marchantia* taxa.

Material and Methods

Plant materials

The thalli bearing gemma cups of the following six taxa of *Marchantia* were collected from several natural populations around Japan: *Marchantia polymorpha* L. subsp. *polymorpha*; *M. polymorpha* subsp. *ruderalis* Bischl. et Boissel.-Dub.; *M. paleacea* Bertol. subsp. *paleacea*; *M. paleacea* subsp. *diptera* (Nees & Mont.) H. Inoue; *M. emarginata* Reinw., Blume et Nees subsp. *tosana* (Steph.) Bischl. and *M. pinnata* Steph. In addition, *Lunularia cruciata* (L.) Dumort. ex Lindb. was also used for morphometric analyses and phylogenetic analyses as an outgroup. The thalli of *M. quadrata* Scop. (≡ *Preissia quadrata* (Scop) Nees), which never produces gemma cups and gemmae, were also used for phylogenetic analyses (see **Appendix A.**). All specimens are identified following Bischler-Causse (1989).

Morphological comparison.

Mature gemmae present in gemma cups were picked out with forceps and observed under optical microscope (Nikon ECLIPSE 80i) equipped with digital camera (Nikon DS-Ri1). Small gemmae with stalk attached were interpreted to be at an immature stage and excluded from observation and measurement. Each gemma was measured for width (W) and length (L) as shown in **Fig.1.1** by using NIS-Elements BR 4.20.00 (Nikon) software under the same equipment set as above. The measured data were summarized using R v. 3.6.2 and its package *ggplot2* v. 3.3.0 (Wickham 2016). Altogether, 2453 gemmae from 83 specimens were examined, which included 119 gemmae from *M. polymorpha* subsp. *polymorpha*, 844 from *M. polymorpha* subsp. *ruderalis*, 266 from *M. paleacea* subsp. *paleacea*, 724 from *M. paleacea* subsp. *diptera*, 246 from *M. emarginata* subsp. *tosana*, 225 from *M. pinnata* and 29 from *L. cruciata*.

Molecular phylogenetic analyses.

Four phylogenetic markers were selected for analysis, chloroplast *rbc*L, *rps*4, *trn*TUGU-*trn*LUAA-*trn*FGAA (*trn*T-L-F) and nuclear ITS. The protocol for total DNA extraction followed Tsubota et al. (2005) or Suzuki et al. (2013). The DNA was extracted from gemmae or a part of the parent thallus margin to minimize contamination from symbiotic fungi in the center of the thallus. The PCR conditions for all markers followed Inoue & Tsubota (2014). Primers for PCR and DNA sequencing followed earlier publications (*rbc*L: Masuzaki et al. 2010; Tsubota et al. 1999; Inoue et al. 2011; *rps*4: Souza-Chies et al. 1997; Masuzaki et al. 2010; Inoue et al. 2012; Inoue & Tsubota 2014; *trn*T-L-F: Taberlet et al. 1991; Tsubota et al. 2015; ITS: Oguri et al. 2003). PCR products were purified by using NucleoSpin Gel and PCR Clean-up kit (Macherey-Nagel, Duren) following the manufacturer's protocols. Purified PCR products were sequenced by Macrogen Japan Corp. Newly obtained sequences have been submitted to DDBJ. The voucher information is shown with accession numbers in **Appendix A.**

Sequences of the four markers were aligned separately by using the program MAFFT ver. 7.452 (Katoh & Standley 2013) with some manual adjustment on the sequence editor of MEGA ver. 7 (Kumar et al. 2016). Gaps were treated as missing data. Prior to combining chloroplast and nuclear data, topological incongruences were examined between the two datasets (*rbc*L+*rps*4+*trn*T-L-F and ITS) using maximum likelihood (ML) inference under GTR + Γ model. No conflict was detected between topologies which differed only at poorly supported nodes. Thus, the alignments were treated as a single matrix. The final data matrix consisted of 19 OTUs. Phylogenetic reconstruction was performed based on a ML and Bayesian inferences. Kakusan4 (ver. 4.0.2016.11.07, Tanabe 2011) was used to determine the appropriate substitution model and partitioning scheme based on AICc (Sugiura 1978). For ML analysis, RAxML ver. 8.2.9 (Stamatakis 2014) was used under the separate model (GTRCAT for all codon positions of *rbc*L and *rps*4, *trn*T-L-F, and ITS) with 10,000 heuristic searches and 10,000 bootstrap analyses. For BI analysis, MrBayes ver. 3.2.7a (Ronquist et al. 2012) was used under the proportional model (F81 + Invariant for 1st and 2nd codon positions of *rbc*L, and 2nd codon position of *rps4*; GTR + Γ for 3rd codon position of *rbc*L, and ITS; HKY85 + Invariant for 1st codon position of *rps*4; F81 + Homogeneous for 2nd codon position of *rps*4; GTR + Invariant for 3rd codon position of *rps*4; HKY85 + Γ for *trn*T-L-F) with 10,000,000 generations, sampling trees every 1,000 generations. Convergence was assessed using Tracer ver. 1.6 (Rambaut et al. 2014). A 50% majority-rule consensus tree was calculated after the convergence of the chains and discarding 25% of the sampled trees as burn-in. All *Marchantia* taxa in Japan were used as the ingroup, and *L. cruciata* was selected as outgroup based on the resolution in other studies as a lineage that lies outside *Marchantia* (Forrest et al. 2006; He-Nygren et al. 2006; Villarreal et al. 2016).

Results

Morphometric analyses.

A discoid shape with two opposing apical notches, one stalk trace and scattered oil cells were common to all taxa. However, overall size, outer shape, presence or absence of mucilage hairs in the notches and papillae on the marginal cells distinguished 2 types. Gemmae of *Marchantia polymorpha* and *M. paleacea* were larger than those of *M. emarginata* and *M. pinnata* (**Fig. 1.2**). Although gemmae of *M. polymorpha* and *M. paleacea* had a nearly circular shape, those of *M. emarginata* and *M. pinnata* had an ellipsoidal to obovate shape in which length was longer than width (**Fig. 1. 3**). Mucilage hairs in the notches were observed in *M. polymorpha* and *M. paleacea.* No mucilage hairs were observed in *M. emarginata* and *M. pinnata* (**Figs. 1. 2**). The gemmae morphology of *L. cruciata* was similar to that of *M. polymorpha* and *M. paleacea* in having mucilage hairs and a nearly circular shape with length equal to width. The size of the gemmae was intermediate of the two types found in *Marchantia* **(Fig. 1. 4, Table 1.1)**. Japanese plants of *M. quadrata* had no gemma cups and gemmae, as previously reported (Schuster 1992). The width of gemmae (W) ranged from 289.89–634.21 µm for *M. polymorpha* subsp. *polymorpha*; 192.03–690.52 µm for *M. polymorpha* subsp. *ruderalis*; 234.23–631.4 µm for *M. paleacea* subsp. *paleacea*; 226.15–664.37 µm for *M. paleacea* subsp. *diptera*; 106.68–282.59 µm for *M. emarginata* subsp. *tosana*; 99.13–264.25 µm for *M. pinnata* (**Fig. 1.3A**). The length of gemmae (L) ranged from 368.01–728.85 µm for *M. polymorpha* subsp. *polymorpha*; 292.05–719.85 µm for *M. polymorpha* subsp. *ruderalis*; 356.68–835.83 µm for *M. paleacea* subsp. *paleacea*; 321.68–840.39 µm for *M. paleacea* subsp. *diptera*; 177.26–424 µm for *M. emarginata* subsp. *tosana*; 167.44–356.93 µm for *M. pinnata* (**Fig. 1.3B**). The difference of overall shapes between the two type of gemmae were clearly distinguishable without overlapping in measured values which fall within one standard deviation from the mean (**Fig. 1.3C**). Detailed descriptions of species are presented in **Table 1.1**.

In my observations, no gemmae with mucilage hairs were observed in the gemma cups of *M. emarginata* subsp. *tosana* and *M. pinnata*. However, in the geminating gemmae that spilled out from gemma cups, mucilage-hairs were observed in the bottom of the notches without exception (**Fig. 1.5**).

Phylogenetic analysis.

The concatenated data matrix had a total length of 4,514 bp, of which 1,286 (28%) were variable, and 839 (65% of the variable sites) were parsimony-informative. The same topologies were inferred by ML and BI analyses as shown in **Fig. 1.6**. The monophyly of the family Marchantiaceae (*Marchantia*) was strongly supported (100/1.00) and the species of *Marchantia* are clearly separated into two clades: *M. polymorpha*-*M. paleacea* (100/1.00), and *M. emarginata* subsp. *tosana*- *M. pinnata*-*M. quadrata* (100/1.00). The former corresponds to the subgenus *Marchantia* including part of the subg. *Chlamidium* (Corda) Bischl. (*M. paleacea*) and the latter corresponds to the subg. *Chlamidium* (*M. emarginata* subsp. *tosana* and *M. pinnata*) and subg. *Preissia* (Corda) D.G.Long, Crand.-Stotl., L.L.Forrest & J.C.Villarreal (*M. quadrata*). *M. polymorpha* subsp. *ruderalis* and *M. paleacea* subsp. *diptera* had relatively high genetic diversity and were resolved into two subclades, respectively.

Discussion

In this chapter, morphological characters of gemmae that reflect the phylogenetic relationship in the genus were summarized using Japanese *Marchantia* species. Through the analyses, two morphological types of gemmae were recognized. One is the large (W >ca. 350 and L >ca. 400 µm) and nearly round gemmae with mucilage hairs covering the notches. This type (Type 1) was observed in *M. polymorpha* (**Fig. 1.2A-H**) and *M. paleacea* (**Fig. 1.2I-P**). The other type (Type 2) is small (W <ca. 350 and L <ca. 400 µm) and elliptic to obovate without mucilage hairs. This type was typically observed in *M. emarginata* subsp. *tosana* (**Fig. 1.2Q-T**) and *M. pinnata* (**Fig. 1.2U-X**). The monophyly of each species group producing Type 1 and Type 2 gemmae was also supported by molecular analysis (**Fig. 1.6**). It suggests that the morphology of gemmae might be an effective taxonomic trait that reflects phylogenetic relationships.

The taxa of *Marchantia* including the four subspecies examined here were each supported as monophyletic groups. The subspecies of *M. polymorpha* and *M. paleacea* growing in Japan were originally described as distinct species (Bertoloni 1817; Burgeff 1943; Montagne 1843) and later revised as infraspecific taxa (Bischler-Causse & Boisselier-Dubayle 1991; Inoue 1989). Similarity of gemma morphology and phylogenetic analyses also support the close phylogenetic affinity of these subspecies. Although my analysis was based on limited sampling from Japan, *M. polymorpha* subsp. *ruderalis* and *M. paleacea* subsp. *diptera* had relatively high genetic diversity and were resolved into two subclades, respectively. *M. polymorpha* subsp. *ruderalis* is distributed all over the world and grows in disturbed or man-made habitats (Bischler 1989; Schuster 1992). The broad distribution via artificial dispersal may contribute to the relatively high genetic diversity. Bischler (1986a) described the morphology of the archegonial receptacle of *M. paleacea* subsp. *diptera* as small with inward-bent rays, and the initially arising two rays seemed to interfere with successful fertilization. She speculated that the promotion of asexual reproduction by gemmae due to poor fertilization efficiency may have triggered the speciation of *M. paleacea* subsp. *diptera* in east Asia. However, the high relative genetic diversity of this subspecies does not support the hypothesis. In fact, in a mixed wild colony of male and female plants of *M. paleacea* subsp. *diptera*, sporophyte formation occurs without any problems (Zheng & Shimamura 2019b).

Many previous studies have indicated that the Lunulariaceae is an early divergent group in Marchantiidae and diverged just before the diversification of the Marchantiaceae (Forrest et al. 2006; He-Nygren et al. 2006; Villarreal et al. 2016). In the present study, the gemmae morphology of *L. cruciata* showed close affinity with that of the Type 1 gemmae of *Marchantia,* in terms of shape and presence of mucilage hairs. However, the size of the gemmae was intermediate between the two types and the morphology of peripheral cells with mamillae is similar to that of Type 2 gemmae (**Fig. 1.4**). More sampling and an analysis of character state evolution are needed to reveal the ancestral traits of gemmae in Marchantiidae. *Neohodgsonia*, which is another early divergent genus in Marchantiidae, may have a completely different form of gemmae from *Marchantia* and *Lunularia*. According to Campbell (1954), gemmae of *Neohodgsonia* have a single notch at the anterior end, either in a median position or set obliquely and the two laterally placed apical notches is not normal.

Shimamura (2016) indicated that developing small gemmae of *M. polymorpha,* before the detachment from the stalk, have an ellipsoid shape and no mucilage hairs like Type 2 gemmae. This similarity of the Type 2 gemmae with developing small gemmae of *M. polymorpha* indicates that the Type 2 gemmae formation is due to the heterochronic change in gemmae development. When they are in the gemma cup, the gemmae are dormant and do not grow beyond a certain size. The phenomenon suggests that the gemma cup produces an inhibitor of germination of gemmae (Eklund et al. 2018; Molisch 1922). The occurrence of mucilage-hairs in germinating gemmae that spill out of the gemma cup (**Fig. 1.5**) supports the idea that Type 2 gemmae stop growing at an earlier stage in the development process due to a strong inhibitory signal of the gemma cup compared to *M. polymorph*a and *M. paleacea.* In addition, the notch of Type 2 gemmae with no mucilage hair seems to be shallow compared to *M. polymorph*a and *M. paleacea* (**Fig. 1.2**). The presence of shallow notches may be related to a low cell division activity around the apical cells. The germinating Type 2 gemmae have deeply closed notches like Type 1 gemmae (**Fig. 1.5**).

In the genus *Marchantia*, the current species identification is mainly based on the morphology of specialized sexual branches (archegoniophore and antheridiophore) and ventral scales. Although sexual branches are relatively species-specific, the plants showing only vegetative propagation with no sexual branches can be difficult to identify. I here present a key for identification of Japanese *Marchantia* species using only gemmae morphology. Morphology of gemmae provides an additional character to delimitate species based on vegetative thallus. I propose that the morphology of gemmae should be used as a new taxonomic character in *Marchantia*.

Key to Japanese *Marchantia* species based on gemma morphology

1. Gemma cups and gemmae absent……………..……...............................***M. quadrata***

1. Gemma cups and gemmae present…..…………………......………………………..…2

2. Gemmae large (W>ca. 350 and L>ca. 400 µm), circular shaped, with mucilage hairs in notch......................................……..………..……………...………..……3

2. Gemmae small (W <ca. 350 and L <ca. 400 µm), circular to obovate, without mucilage hairs………..…………………………………………….………..………...…4

3. Margin of gemmae entire; marginal cells without papillae and mamillae ....***M. polymorpha***

3. Margin of gemmae entire; marginal cells with mamillae.............................***M. paleacea***

4. Margin of gemmae entire or dentate; marginal cells with mamillae ....***M. emarginata* subsp. *tosana***

4. Margin of gemmae dentate; marginal cells with mamillae and small papillae .... ***M. pinnata***

Appendix A.

List of voucher specimens for morphological comparison and molecular phylogenetic analysis, with locality, specimen number and accession numbers if necessary (*rbc*L/*rps*4/*trn*L-F/ITS). All specimens are deposited in Herbarium of Hiroshima University (HIRO).

Chapter 2

Taxonomic reevaluation of the Japanese *Marchantia* taxa belonging to sect. *Papillatae* of subg. *Chlamidium* (Marchantiaceae)

Introduction

Since the establishment of the genus *Marchantia* L. by Linnaeus (1753), numerous morphologically similar species and infraspecific taxa have been published due to its worldwide distribution and inadequate evaluation of morphological variability (Bertoloni 1817; Bonner 1953; Gao & Chang 1982; Gao et al. 1981; Horikawa 1930, 1934; Reinwardt et al. 1824; Stephani 1894, 1897, 1898–1900). The genus *Marchantia* is subdivided into four subgenera: subg. *Marchantia*, subg. *Chlamidium* (Corda) Bischl., subg. *Protomarchantia* Schust., and subg. *Preissia* (Corda) D.G.Long, Crandall-Stotler, L.L.Forest & Villarreal (Bischler 1982; Long et al. 2016; Schuster 1985, 1992). Among them, the subgenus *Chlamidium,* with a distribution center including many species in Asia and Oceania, is defined as morphologically plastic (Bischler-Causse 1989). Especially, sect. *Papillatae* Bischl. of subg. *Chlamidium* which is one of the most difficult groups for taxonomic interpretation and identification due to its broad species definition and ambiguous inter- and intra-specific delimitation (Bischler-Causse 1989; Inoue 1976; Zheng & Shimamura 2020; Zheng et al. 2020). In the revision of Asian and Oceanic *Marchantia*, Bischler-Causse (1989) revised 36 previously described taxa in the section into two species, *M. emarginata* Reinw. Blume et Nees and *M. papillata* Raddi. The two species were further subdivided into three and two subspecies, respectively. However, this treatment is needed to be carefully reviewed because morphological examination of specimens from a broad geographic range and molecular phylogenetic analyses of these taxa have not been undertaken.

In Japan, since the revision by Bischler-Causse (1989), it has been thought that only *M. emarginata* subsp. *tosana* (Steph.) Bischl. is recognized for the section. *Marchantia emarginata* subsp. *tosana* was originally described as *M. tosana* Steph. based on the specimen collected from Tosa Province (now Kochi Prefecture) of Japan (Stephani 1897). Since then, this species has been repeatedly recorded, illustrated, and discussed by many researchers as a species widely distributed in the southern part of the Japan (Hattori 1944, 1952; Horikawa 1930, 1934, 1939; Iwatsuki & Mizutani 1972; Kawamatsu 1961; Tatuno 1941; Yoshinaga 1898). Although the morphologically similar taxa to *M. tosana* described from Japan have not been re-examined for a long time, Bischler (1987) reviewed Japanese *Marchantia* described by Stephani and selected *M. tosana* as a valid taxonomic name with two synonyms, *M. cuneiloba* Steph. and *M. tosayamensis* Steph.

Two years later, Bischler (1989) published new combinations at a new rank of subspecies as *M. emarginata* subsp. *tosana,* with synonymization of eight additional taxa, including *M. radiata* Horik. described from Japan. Detailed taxonomic notes of each synonym were given in a subsequent monograph (Bischler-Causse 1989). However, possibly owing to the fact that the study was based on limited field work and morphological comparison of aged herbarium specimens, the morphological diversity of the synonymized species, including the ventral scale appendages and dark median band on the dorsal surface of the thalli, were ignored. Moreover, an over-broad definition of subsp. *tosana* not only contributed to morphologic ambiguities in subsequent regional studies but also hampered the recognition of related taxa (Bischler & Piippo 1991; Ho 2013; Piippo & Koponen 2013; Singh & Singh 2013; Xiong & Cao 2018). As an additional taxon of sect. *Papillatae* in Japan, I recently reported *M. papillata* subsp. *grossibarba* (Steph.) Bischl. It is distinguished from the plants that are recognized as typical *M. emarginata* subsp. *tosana* by the continuous dark median band on the dorsal surface of the thallus, hyaline thallus margins, and triangular to pentagonal, yellowish to reddish ventral scale appendages with unicellular or no marginal teeth (Zheng & Shimamura 2020).

In the present study, I conduct critical morphological examination and molecular phylogenetic analysis to reevaluate *M. emarginata* subsp. *tosana* and all its related taxa from Japan. Based on my study, two distinct phylogenetic groups and corresponding morphological discontinuities were recognized in Japanese plants belonging to sect. *Papillatae*. As a taxonomic treatment for the two taxa, I propose the designation of the names *M. emarginata* subsp. *cuneiloba* (Steph.) T.X.Zheng & M. Shimamura *stat. et. comb. nov.* and *M. papillata* subsp. *grossibarba*, respectively.

Material and Methods

Molecular phylogenetic analysis

Sampling for molecular phylogenetic study was based mainly on specimens collected during my recent field work on *Marchantia* growing in Japan (Tohoku, Honshu, Shikoku, Kyushu, and Okinawa) from 2018 to 2021. Species identification followed the original interpretations (Bonner 1953; Horikawa 1930; Stephani 1894, 1897, 1985) prior to the synonymization in Bischler (1987), Bischler (1989) and Bischler-Causse (1989). My collection also includes the specimens of *M. cuneiloba*, *M. tosana* and *M. tosayamensis* collected from their type localities and the morphological characteristics of these specimens were comparable to their types. There were no available *M. radiata* specimens for molecular study. The specimens that may correspond to *M. radiata* were included in *M. cuneiloba*.

Four phylogenetic markers *rbc*L, *rps*4, *trn*T$_{\text{UGU}}$-L$_{\text{UAA}}$-F$_{\text{GAA}}$, and nrITS were selected, and the molecular method described by Zheng et al. (2020) was followed. Sequences obtained in the present study have been submitted to DNA Data Bank of Japan (DDBJ, https://www.ddbj.nig.ac.jp). The information of voucher specimens with accession numbers are shown in **Appendix B.**

The sequences of the four phylogenetic markers were separately aligned using MAFFT 7.471 (Katoh & Standley 2013), with some manual adjustment on the sequence editor of MEGA ver. 7 (Kumar et al. 2016). Gaps were treated as missing data, and the final data matrix consisted of 66 OTUs.

Analysis using concatenated sequences of the four markers was performed based on a maximum likelihood and Bayesian inferences. Prior to the reconstruction, Kakusan4 (ver. 4.0.2016.11.07, Tanabe 2011) was used to determine the appropriate substitution model and partitioning scheme for my data based on the corrected Akaike information criterion (AICc: Sugiura, 1978). For ML inference, RAxML ver. 8.2.9 (Stamatakis 2014) was used under the equal rate model (GTR + Γ for all codon positions of *rbcL, rps4*, *trn*T-L-F, and ITS) with 10,000 heuristic searches and 10,000 bootstrap analyses. The Bayesian inference was determined using MrBayes ver. 3.2.7a (Ronquist et al. 2012) with BI method using the proportional model among codon positions (F81 + Γ for 1st codon positions of *rbcL*, SYM + Γ for 2nd codon positions of *rbcL*, HKY85 + Γ for 3rd codon positions of *rbcL*, JC69 + Γ for 1st codon positions of *rps4*, JC69 + Homogeneous for 2nd codon positions of *rps4*, HKY85 + Γ for 3rd codon positions of *rps4*, HKY85 + Γ for *trn*T-L-F, and GTR + Γ for nrITS) with 10,000,000 generations, sampling trees every 1,000 generations. Convergence was assessed using Tracer ver. 1.7.1 (Rambaut et al. 2018). A 50% majority-rule consensus tree was calculated after converging the chains and discarding 25% of the sampled trees as burn-in.

Morphological examination

In order to find stable morphological characters that reflect the phylogeny, all the specimens used in the phylogenetic analysis, along with additional specimens, were examined. Approximately 200 specimens, including type specimens, were borrowed from G, HIRO, NICH, PE and TNS. I was unable to locate the original specimens of *M. radiata* in HIRO. It is possible that it may have been destroyed in WWII. However, some ordinary specimens collected and identified by the original author were found and examined in this study. All newly collected materials from Japan have been deposited at HIRO. Morphological observations were based on the characteristics commonly used to classify the genus *Marchantia* at species or infraspecific level (Bischler 1984, 1989; Bischler-Causse 1989; Zheng & Shimamura 2019a, 2019b, 2019c, 2020; Zheng et al. 2020). They include size of thallus, occurrence of dark median band on the thallus, color of thallus margin, morphology of ventral scales, gemmae, gemma-cups, air-pores, involucres, stalks of archegoniophores and antheridiophores, and lobes of receptacles.

Specimen examinations were performed using a dissecting microscope (Leica MZ16) and a biological microscope (Nikon ECLIPSE 80i), equipped with digital cameras Leica MC170 HD and Nikon DS-Ri1 digital cameras, respectively. Specimen information are listed in **Appendix B.**

Results

Molecular phylogenetic analysis

The concatenated data matrix had a total length of 4,596 bp (1398, *rbcL*; 609, *rps4*; 817, *trn*T-L-F; 1772, nrITS), of which 1,145 (24.9%) were variable (138, *rbcL*; 64, *rps4*; 166, *trn*T-L-F; 777, nrITS), and 852 (74.4% of variable sites) were parsimony informative (97, *rbcL*; 37, *rps4*; 87, *trn*T-L-F; 631, nrITS). No topology conflict was detected between ML and BI trees, which differed only at poorly supported nodes. Figure 3.1 shows the ML tree depicted by 80% condensed topology with supporting values from bootstrap and Bayesian posterior probabilities (BP/PP).

The inferred topologies were consistent with those of previous phylogenetic studies in that the species of *Marchantia* L. were largely separated into three clades: *M. polymorpha*-*M. paleacea*, the part of the subg. *Chlamidium* (Corda) Bischl. excluding *M. paleacea* Bertol., and subg. *Preissia* (Corda) D.G.Long, Crandall-Stotler, L.L.Forrest & Villarreal (*M. quadrata* Scop.). (Forrest et al. 2006; Villarreal et al. 2016; Zheng et al. 2020).

Each analyzed taxon formed moderately- to well-supported clades. Among them, the monophyly of sect. *Papillatae* Bischl. was strongly supported (100/1.00; BP/PP), in which two clades are clearly recognized—*M. cuneiloba* (100/1.00; BP/PP) (clade 1) and *M. papillata* subsp. *grossibarba*-*M. tosana*-*M. tosayamensis* (100/1.00; BP/PP) (clade 2). No clear monophyletic group corresponding to the morphologically recognized species was found in clade 2. Clade 2 had relatively high genetic diversity compared with clade 1 and was resolved into four subclades (**Fig. 2.1**).

Morphology

Some morphological characters had a clear correspondence with the two clades shown in the molecular phylogenetic analysis. The margin of ventral scale appendages had multicellular teeth (2–3 celled) in *M. cuneiloba* (**Figs. 2.2A & B**) and *M. radiata* (**Figs. 2.2C**) whereas those of *M. tosayamensis* (**Figs. 2.2G, H, I**) and *M. papillata* subsp. *grossibarba* (**Figs. 2.2J, K, L**) were crenulate or had unicellular teeth. Although both multicellular and unicellular toothed margins are observed in *M. tosana,* (**Figs 2.2D, E, F**), the unicellular margin of the ventral scale appendages seem to characterize clade 2 plants. The dark median band was absent in *M. cuneiloba* (**Fig. 2.3A & B**), discontinuous in *M. tosana* (**Fig. 2.3C & D**), and continuous in *M. tosayamensis* (**Figs. 2.3E**) and *M. papillata* subsp. *grossibarba* (**Figs. 2.3F**). The number of female receptacle lobes was up to 13 in *M. cuneiloba* (**Fig. 2.4A**) and *M. radiata* (**Fig. 2.4B**) but only 5–8 in *M. tosana* (**Fig. 2.4C**) and *M. tosayamensis* (**Fig. 2.4D**). In *M. cuneiloba,* the divergence angle of the basal sinus (arrows heads in **Fig. 2.5**) of the male receptacle was 30–180° (**Fig. 2.5 A & B**), while it was about 180° in *M. tosana* (**Fig. 2.5C**) and *M. tosayamensis* (**Fig. 2.5D**). The plants of *M. radiata* bearing antheridiophores and *M. papillata* subsp. *grossibarba* with gametangiophores were not available for the present study. The morphological differences are summarized in **Table 2.1**.

Geographic distribution and ecological habitats in Japan

It was revealed that the plants belonging to clade 1 and clade 2 have different geographic distribution patterns and ecological requirements in Japan. The clade 1 species, *M. cuneiloba* and *M. radiata*, are unevenly distributed in the southern part of the Japanese archipelago. *M. cuneiloba* and *M. radiata* are distributed in Okinawa (Ryukyu Islands in southwestern Japan), South Kyushu, Chugoku, and along the south coast of Honshu Island (**Fig. 2.6A**). These species typically grow on soil near anthropogenically modified regions and seldom on boulder near natural streams (**Fig. 2.7A**). The clade 2 species, *M. tosana*, *M. tosayamensis,* and the typical plants of *M. papillata* subsp. *grossibarba* are distributed in North Kyushu, Shikoku, Chugoku, and along the shore of Honshu Island. These species were never found in the Ryukyu Islands (**Fig. 2.6B**). They prefer to grow in damp areas, such as on boulders near streams and on the walls of artificial waterways (**Fig. 2.7B**, **Table 2.1**).

Discussion

Phylogenetic analysis

Although some large-scale molecular phylogenetic analyses involving multiple species of *Marchantia* have been carried out (Forrest et al. 2006; He-Nygrén et al. 2006; Villarreal et al. 2016), few studies have been conducted to clarify the problem of classification for the genus *Marchantia*. Asian and Oceania taxa of sect. *Papillatae* in particular, were not adequately analyzed. Here, I presented the first attempt of a molecular phylogeny to reevaluate the taxonomic status of taxa of sect. *Papillatae* based on a large number of specimens. The analysis strongly supported the monophyly of sect. *Papillatae*, comprising two clades.

In the present study, I recognized four morphological groups in Japanese plants of sect. *Papillatae*. One of the four morphological groups formed clade 1 in the molecular phylogenetic tree. Based on the examination of specimens, including type specimens, the plants of clade 1 were equivalent to *M. cuneiloba,* described by Stephani (1897) from Okinawa (Ryukyu Islands, southwestern Japan). The morphological groups observed in the other three species formed clade 2 in the molecular phylogenetic tree. The three morphological groups were equivalent to *M. tosana* (≡ *M. emarginata* subsp. *tosana*), *M. tosayamensis* (= *M. emarginata* subsp. *tosana*), and *M. papillata* subsp. *grossibarba*. Contrary to my expectations, no clear monophyletic group corresponding to the morphologically recognized species was found within clade 2. However, clade 2 was resolved into several subclades, and each subclade includes several species. The morphological features that define these species may be morphological variations within the same genetic group. There was slightly high genetic variation among the five specimens of *M. tosayamensis* collected from its type locality, *T.-X. Zheng 380*, *1201*, *1232*, *1217* and *1234*. However, the morphological characters of the five specimens are well consistent with those of the holotype of *M. tosayamensis*. Although based on a very limited number of species and samples, the phylogenetic analyses including representative taxa of sect. *Papillatae* by Xiang et al. (2016) also indicated the close phylogenetic relationship of *M. emarginata* subsp. *tosana* and *M. papillata* subsp. *grossibarba* in the section. It is also worth noting that in the analyses of taxa of sect. *Papillatae* in the present study, nucleotide variation was observed in the non-coding region of *trn*T-L-F and the nrITS region, whereas the sequences of *rbcL* and *rps4* genes are almost identical (data not shown). This may also suggest that taxa of sect. *Papillatae* included in the present study share a closer phylogenetic relationship than currently defined.

Morphological observations and taxonomic implications

Morphologically identifiable taxa were polyphyletic in clade 2. The results indicated that some morphological characteristics previously used to identify the taxa do not reflect the phylogeny, and that the definition of those taxa needs to be revised. Based on my examination, I found several morphological characteristics that define the plants included in clades 1 and 2. All the plants of clade 1 had multicellular-toothed ventral scale appendages, whereas most specimens of clade 2 had unicellular toothed appendages (**Fig. 2.2**). The dark median band on the thallus was absent in all plants of clade 1, whereas there are continuous or discontinuous dark median lines in the plants of clade 2. (**Fig. 2.3).** A previous study determined that *M. papillata* subsp. *grossibarba* can be distinguished from other taxa based on the continuous dark median band on the dorsal surface of the thallus, hyaline thallus margins, and triangular to pentagonal appendages of the ventral scales with smooth, crenulate or unicellular toothed margins (Zheng & Shimamura 2020). These characteristics do not reflect the phylogeny, instead the presence of the dark band on the thallus, even a discontinuous presence, appears to characterize the plants of clade 2. The number of lobes in female receptacles was up to 13 in the plants of clade 1 and only 5–8 in those of clade 2 (**Fig. 2.4**). Although a small number of lobes can be also formed in the plants of clade 1, in such case, the morphological identification can be achieved by the combination of other characters. The divergence angle of basal sinus of the male receptacle in the plants of clade 1 varies from 30–180° in single plant or colony. However, in the plants of clade2, the divergence angle of basal sinus is always about 180° (**Fig. 2.5**). The toothed margin of the appendages of ventral scales was observed only in typical plants of *M. papillata* subsp. *grossibarba* with continuous dark median bands. This characteristic may be linked to a continuous dark line. The morphological differences of the previously recognized taxa and the plants corresponding to clades 1 and 2 are summarized in **Table 2.1**. Based on these results, I propose a reorganization of the Japanese taxa of sect. *Papillatae* into two taxa. However, since these taxa have a complex historical background, this reorganization should be considered carefully.

Prior to the establishment of *M. emarginata* subsp. *tosana* (Bischler 1989), its basionym, *M. tosana* was considered to be a distinct species by some Japanese researchers, and many illustrations and descriptions that reflect the characteristics of the type have been presented (Horikawa 1930, 1939; Inoue 1976; Iwatsuki & Mizutani 1972; Magohuku & Yamada 1964). However, with the increasing number of synonyms, the morphological definition of the taxon *M. tosana* (≡ *M. emarginata* subsp. *tosana*) has become ambiguous. Now, *M. tosana* (≡ *M. emarginata* subsp. *tosana*) is considered to have 11 heterotypic synonyms, of which six are from China; three from Japan; and two from Vietnam (Bischler 1987, 1989; Bischler-Causse 1989, 1993).

In order to eliminate the taxonomic ambiguity caused by the synonyms of *M. tosana* (≡ *M. emarginata* subsp. *tosana*), I need to redefine taxonomic affiliations. For example, one synonym, *M. radiata*, was originally described based on specimens collected from west Japan to Taiwan of China (Horikawa 1930). In the original description, Horikawa noted that *M. radiata* was distinct from *M. tosana* in terms of its more southerly distribution in Japan and bearing a larger number of lobes in female receptacle (up to 13). However, Hattori (1944) disregarded these differences and synonymized *M. radiata* under *M. tosana* without providing the list of specimens examined. Moreover, their geographical distribution was also combined, which led to the distribution of *M. tosana* being extended to Okinawa and its adjacent region. This conclusion was adopted in almost all subsequent studies (Bischler-Causse 1989; Furuki 2012; Hattori 1952; Inoue 1976; Iwatsuki & Mizutani 1972). In 1989, since there were no original type specimens of *M. radiata* available in HIRO, Bischler-Causse followed Hattori (1944) with a comparison of the original description. I have been unable to confirm whether Hattori had examined the original type materials of *M. radiata*. However, from my morphological examination of the old collection of *M. radiata* made by Horikawa and the newly collected specimens from Japan, none of the specimens showed all the characteristics illustrated in the original description of *M. radiata*. Based on extant materials collected and identified by Horikawa, I consider *M. radiata* conspecific with *M. cuneiloba*. Since none of its original type materials survived, I here designated the relatively intact material, *Y. Horikawa 3863* (HIRO 264759) as the neotype.

Bischler (1987) considered *M. cuneiloba* and *M. tosana*, published in the same article (Stephani 1897) as taxonomically synonymous species and formally synonymized *M. cuneiloba* under *M. tosana* according to Art. 57 of the *International Code of Botanical Nomenclature* (Voss et al. 1983). However, the present study suggests that this synonymy is inappropriate and that it erroneously expanded the morphological delimitation of *M. tosana*, specifically in terms of ventral scale appendages (**Fig. 2.2**), blackish median band (**Fig. 2.3**) and the morphology of gametangiophores (**Fig. 2.4 & 2.5**), so that the illustration of *M. emarginata* subsp. *tosana* in Bischler (1989, p. 70, figs 6) and Bischler-Causse (1989, p. 200–202, figs 57 & 58) were virtually closer to the characteristics of *M. cuneiloba* than to those of *M. tosana.*

Marchantia tosayamensis can be readily distinguished from *M. tosana* by the continuous dark median band and minor appendage of ventral scales (Bonner 1953; Stephani 1897, 1985). In 1954, Hattori examined the type specimen of *M. tosayamensis* and annotated that "*Marchantia tosayamensis* Steph. is identical with *M. tosana* Steph.".

Later, Bischler (1987) considered *M. tosayamensis* as an “etiolated specimen” of *M. tosana* and formally treated it as a conspecific name with *M. tosana*. The ambiguity in the recognition of the morphological characteristic of the dark median band would be attributable to this synonymy.

In Bischler's series of studies, the treatment of the characteristic of the dark median band was not clearly defined and consistent (Bischler 1984, 1989; Bischler-Causse 1989, 1993). *Marchantia emarginata* subsp. *tosana* was defined as distinct from *M papillata* subsp. *grossibarba* owing to the absence of the dark median band. On the other hand, several Asian taxa with a dark median band, such as *M. tosayamensis*, *M. angusta* Steph. and *M. rugulosa* Steph., were still synonymized under subsp. *tosana* (Bischler 1989; Bischler-Causse 1989) based on the interpretation that this characteristic is an intraspecific variation induced by a moist environment (Bischler 1984). This treatment also appears to cause confusion in interspecific delimitation and species identification in sect. *Papillatae* (Bischler & Piippo 1991; Ho 2013; Lu & Huang 2017; Piippo & Koponen 2013; Xiang et al. 2016). As previously mentioned, my molecular evidence suggests that the dark median band may be used as an effective taxonomic characteristic.

When Bischler (1989) described *M. emarginata,* she defined three subspecies with strict geographical segregation (subsp. *emarginata* for South Asia and India; subsp. *tosana* for East Asia and subsp. *lecordiana* (Steph.) Bischl. for Oceania). However, excluding the *M. emarginata* subsp. *emarginata* with distinct epidermal papillae, I was not able to distinguish the specimens of subsp. *lecordiana* and subsp. *tosana* from each other unless they were labeled with their locality.

Through the present study, current interspecific circumscription between *M. emarginata* and *M. papillata* and the morphological definition of their subspecies were proved to be ambiguous and problematic. Here, I partly clarified their delimitation by synonymizing *M. tosana* (≡ *M. emarginata* subsp. *tosana*) and *M. tosayamensis* (= *M. emarginata* subsp. *tosana*) under *M. papillata* subsp. *grossibarba*. To give a comprehensive revision on sect. *Papillatae*, integrative study involving more specimens from a wider geographical range in Asia and Oceania will be conducted in the future.

Conclusion

Here, I make a taxonomic interpretation based on the integrative study on the plants belonging to sect. *Papillatae* Bischl. in Japan. I propose *Marchantia emarginata* subsp. *cuneiloba* (Steph.) T.X.Zheng & M. Shimamura. *comb. et. stat. nov* and tentatively treat *M. tosana* Steph. and *M. tosayamensis* Steph. as synonyms of *M. papillata* subsp. *grossibarba* (Steph.) Bischl. Some taxa synonymized under *M. emarginata* subsp. *tosana* in Bischler's series of studies, have also been transferred to *M. emarginata* subsp. *cuneiloba*. Due to the lack of specimens of other two subspecies of *M. emarginata*, namely subsp. *emarginata* and subsp. *lecordiana*, prevalent subspecific treatment of *M. emarginata* was also preserved. The two phylogenetic groups corresponding to clade 1 (*M. emarginata* subsp. *cuneiloba*) and clade 2 (*M. papillata* subsp. *grossibarba*) also showed a clear difference in geographical distribution. The different distributions and ecological preferences also support that both taxa are distinct and speciated to adapt to unique environments. This decision is tentative and may be revised in the future as the number of available specimens of sect. *Papillatae* collected from a wider geographic area increases.

Taxonomy

Marchantia emarginata Reinw., Blume et Nees subsp. ***cuneiloba*** (Steph.) T.X.Zheng & M.Shimamura. *comb. et. stat. nov.*

≡*Marchantia cuneiloba* Steph., Bull. Herb. Boissier 5: 98. 1897. TYPE: JAPAN. OKINAWA: Liukiu (Loochoo), Shuri Isl. *H. Kuroiwa s.n.* = *T. Makino herbarium #201* (lectotype [designated by Bischler 1987: 331]), G 112606!; isolectotype, TNS[N.V.]).

= *Marchantia chinensis* Steph. in Bonner, Candollea 14: 103. 1953. TYPE: CHINA. *P.A. Hariot 1* (holotype, G 61018[N.V.]). [synonymy *fide* Bischler (1989)]

= *Marchantia convoluta* Gao & Zhang, Acta Bot. Yunnan. 3: 390. 1981. TYPE: CHINA. XIZANG: Medog Co., ad vias, 13 Sept. 1974, *J.-W. Zhang M7417* (holotype, ISPH[N.V.]). [synonymy *fide* Bischler-Causse (1993)]

= *Marchantia cuneiloba* f. *multiradiata* Herz. in Handel-Mazzetti, Symb. Sin. 5: 6. 1930. *nom. inval.* (Art. 38.1(a), no accompanied description). ORIGINAL MATERIAL: CHINA. KIANGSI (DJIANGHSI): Um das Kohlen-bergwerk Pinghsiang, c. 600 m, 1920, *T.-H. Wang s.n. [Plantes Sinensis 189]* (JE[N.V.]). [synonymy *fide* Bischler (1989)]

= *Marchantia cuneiloba* f. *paucifibrosa* Herz. in Handel-Mazzetti, Symb. Sin. 5: 6. 1930. *nom. inval.* (Art. 38.1(a), no accompanied description). ORIGINAL MATERIAL: CHINA. KWEITSCHON (GUIDSCHOU): Feuchter Mergel in der str. St. im Walde des Baotie-schan bei Gudschou, 500 m, 20 Jul. 1917, *Handel-Mazzetti 10891* (JE[N.V.]). [synonymy *fide* Bischler (1989)]

= *Marchantia esquirolii* Steph. in Bonner, Candollea 14: 106. 1953. TYPE: CHINA. KIOU TCHOU: 14 May 1910, *J.H. Esquirol 2120+2121* [treated as one specimen in protologue and designated as type] (holotype, G 61017[N.V.]). [synonymy *fide* Bischler (1989)]

= *Marchantia fallax* Herz. in Handel-Mazzeti, Symb. Sin. 5: 6. 1930. TYPE: CHINA. NORTHWEST YUNNAN: Triefende Schieferfelsen der wtp. St. am Dschungdjiang-ho gegen Meidsiping se von Dschungdien ("Chungtien"), 2200 m, 21 Jun. 1915, *Handel-Mazzetti 6842 [Diar. Nr. 1220]* (lectotype [designated by Bischler 1989: 78], JE 4007763 [N.V.]; isolectotype, E 49140 [N.V.]), [synonymy *fide* Bischler (1989)]

= *Marchantia radiata* Horik., Sci. Rep. Tohoku Imp. Univ., ser. 4, Biol. 5: 629. 1930. TYPE: JAPAN. TOTTORI: Saihaku-gun, Houkimizoguchi, 20 Jun. 1931, *Y. Horikawa 3863* (**neotype designated here!**, HIRO 264759!), *syn. nov.*

Marchantia papillata Raddi. subsp. ***grossibarba*** (Steph.) Bischl. Cryptog., Bryol. Lichénol. 10: 78. 1989.

≡*Marchantia grossibarba* Steph., Mém. Soc. Sci. Nat. Cherbourg 29: 221. 1894. TYPE: CHINA. YUNNAN: Santscha-Ho, sylva prope, *P.J.M. Delavay s.n.* (lectotype, [designated by Bischler-Caussse 1989: 210]; G 43749!; isolectotype, BM[N.V.], FH[N.V.], PC 103260, 103261, 103262[N.V.]).

= *Marchantia simlana* Steph., Spec. Hep. 1: 173. 1899. TYPE: INDIA. HIMACHAL PRADESH: Himalaya, Simla, *D. Brandis 1250* (lectotype, [designated by Zheng 2021: 117], G 61008!), *D. Brandis 1280* (syntype, G 61007!).

= *Marchantia togashii* Amakawa, Fl. E. Himalaya. 1: 536. 1966. TYPE: INDIA. SIKKIM: Lopchu, 1500 m., *M. Togashi s.n.* (holotype, NICH 201769!; isotype, TI[N.V.]).

= *Marchantia tosana* Steph., Bull. Herb. Boissier 5: 99. 1897.≡*Marchantia tosana* Steph. ex Makino, Bot. Mag. (Tokyo) 10: 209. 1896. *nom. inval.* (Art. 38.1(a), no accompanied description). TYPE: JAPAN. TOSA: Nanokawa, Apr. 1895, *T. Inoue 5* (lectotype [designated by Bischler 1987: 335], G 43739!), *syn. nov.*

= *Marchantia tosayamensis* Steph. in Bonner, Candollea 14: 112. 1953. TYPE: JAPAN. TOSA: Tosayama, 5 Jun. 1904, *Y. Tokihisa 105* (holotype, G 112607!), *syn. nov.*

Appendix B. List of voucher specimens for morphological examination and molecular phylogenetic analysis, with locality, specimen number and accession numbers if necessary (*rbc*L/*rps*4/*trn*T-L-F/ITS). Bold accession numbers indicated newly obtained sequences for present study. All specimens are deposited in Herbarium of Hiroshima University (HIRO).

Chapter 3
Taxonomic revision of the genus *Marchantia* L. in Japan

Introduction

Marchantia L. is one of the most familiar genera of liverworts (Marchantiophyta) due to the inclusion of prevalent model plant *Marchantia polymorpha* L., comprising nearly 40 species worldwide (Söderström et al. 2016). With a cosmopolitan distribution, the genus is best represented in Asia by 19 accepted taxa (Bischler-Causse 1989; Long & Crandall-Stoler 2020; Xiang et al. 2016).

Taxonomic studies of genus *Marchantia* in Japan were started by foreign researchers in the late 18th century. The first species record of Japanese *Marchantia* was made by Thunberg (1784) as *Marchantia polymorpha* and *M. chenopoda* L. In 1843, Montagne published a new species *M. diptera* Nees et Mont. based on Japanese material. Mitten (1865, 1891) summarized previous works on liverworts in Japan and newly added *M. nitida* Lehm. et Lindenb. (=*M. paleacea* Bertol. subsp. *paleacea*) and *M. geminata* Nees. to Japanese bryoflora. The largest input was made by Stephani (1897, 1899) who published 10 new species of *Marchantia* from Japan. However, only five of them, *M. calcarata* Steph., *M. cuneiloba* Steph., *M. planipora* Steph., *M. tosana* Steph. and *M. vaginata* Steph. were published during his lifetime (Stephani 1897, 1899) and the remaining five species, *M. alatocapitata* Steph., *M. fauriana* Steph., ***M.*** *pinnata* Steph., *M. pulcherrima* Steph. and *M. tosayamensis* Steph. were posthumously published by Bonner (1953). Among them, *M. calcarata* and *M. vaginata* were earlier invalidly published by Bescherelle (1894).

Since the late 19th century, Japanese researchers started to identify and study the taxa of genus *Marchantia*. Inoue (1894) and Makino (1896) listed several new Japanese *Marchantia* species of Stephani, but these taxa were all nomenclatorially invalid due to the absence of description or diagnosis (Turland et al. 2018). Yoshinaga (1895, 1900, 1903, 1906) conducted field trips in Tosa Province (now Kochi Prefecture) of Japan and recorded the distribution of *Marchantia cuneiloba*, *M. diptera*, *M. polymorpha* and *M. tosana* from the region. In 1908, Okamura studied the regeneration of *Marchantia* antheridiophore and listed 10 species from Japan with a new record of *M. palmata* Reinw., Bulme et Nees. Between 1929 and 1931, Horikawa, the first professional hepaticologist in Japan, published a serial study on Japanese liverworts and proposed a new species *M. radiata* Horik. Tatuto (1941) accepted the species of Horikawa and included only five *Marchantia* species in his karyotype analysis of Japanese liverworts. In 1944, different from above studies, Hattori recognized nine species and questioned the previous record of *M. geminata*, *M. nitida*, *M. palmata* and *M. vaginata*. In 1953, Shimizu and Hattori excluded the above 4 controversial species from Japanese bryoflora and recognized only 4 species, *M. cuneiloba*, *M. diptera*, *M. polymorpha* and *M. tosana* based on reliable records, which laid the foundation for future taxonomic research on Japanese *Marchantia*. In 1954, Horikawa added *M. polymorpha* var. *aquatica* Schiff. (=*M. polymorpha* subsp. *polymorpha*) to Japanese records. In 1957, Hattori investigated the exemplars from Hokkaido of Japan and newly recorded *M. paleacea* Bertol. Subsequent studies (Bischler 1986a, 1987; Inoue 1989; Mizutani & Hattori 1976) were mainly designed to discuss the taxonomic treatment of taxa published previously.

In 1989, Bischler-Causse revised Asian and Oceanic *Marchantia* and recognized 6 taxa in Japan based on very limited field works and morphological comparison of aged herbarium specimens. Nevertheless, this conclusion was still adopted in almost all Japanese studies (Furuki & Mizutani 2004; Shimamura 2012) and no local comprehensive investigation on *Marchantia* was made hitherto. In 2016, based on a multi-loci phylogenetic analysis (Villarreal et al. 2016), Long et al. replaced *Preissia quadrata* (Scop.) Nees to *Marchantia*, which increased the number of Japanese *Marchantia* taxa to seven (Katagiri & Furuki 2018).

Recently, successive progress on *Marchantia* in Japan, such as new taxonomic character gemmae (Zheng & Shimamura 2019a; Zheng et al. 2020), report of *M. papillata* subsp. *grossibarba* (Steph.) Bischl. (Zheng & Shimamura 2020), taxonomic changes in sect. *Papillatae* Bischl. (Zheng & Shimamura 2022) and nomenclatural issue (Zheng 2021) proved that the current taxonomic knowledge of Japanese *Marchantia* does not seem to reflect the actual situation and needs to be revised thoroughly by comparison of more specimens collected in intensive fieldwork.

Here, I present a comprehensive taxonomic revision of genus *Marchantia* in Japan by morphological examination mainly based on type materials and our collection made between 2018–2022. For each species, description, illustration, geographical distribution, habitat and taxonomic notes are summarized.

Materials and Methods

The taxonomic treatment was made mainly based on specimens collected in field work on *Marchantia* growing in Japan (Tohoku, Honshu, Shikoku, Kyushu and Okinawa) during 2018–2022. Approximately 1400 specimens of *Marchantia*, including several type specimens, borrowed from G, HIRO, M, NICH and PE were examined.

Specimen examination was performed under dissecting (Nikon SMZ745) and optical microscopes (Nikon ECLIPSE 80i). Sketch was drawn with the aid of an optical microscope (Nikon Optiphot 2) equipped with Nikon drawing tube.

The morphological definition of genus *Marchantia* and each taxon was circumscribed and illustrated. Distribution, habitat, taxonomic notes, distinguishing characters, and a key to the species of the genus *Marchantia* are also provided.

Taxonomy

In the following description, all specimens are deposited in HIRO unless otherwise indicated. Synonyms listed below are restricted to the Japanese taxa. I follow the Shenzhen Code of Nomenclature (Turland et al. 2018) for nomenclatural elements.

Marchantia L. Spec. Pl. ed. 1: 1137. 1753 (Linnaeus 1753).
Lectotype: *Marchantia polymorpha* L. *fide* Léman (1823).

Description

Thalloid. *Epidermal cells* in 1–2 layers, with thin or slightly thickened wall. *Epidermal pores* compound, with 4–8 rings of cell; upper cells protruding above the epidermis and lower cells projecting into the air-chamber. *Air-chambers* in single layer, with an epidermal pore and several chlorophyllose filaments each. *Compact ventral tissue* multicellular layered in median portion, sometimes with oil-cells, sclerotic cells, mucilage cavities and central colored (fungi colonized) region. *Rhizoids* smooth and pegged. *Ventral scales* in 2–6 rows; median scales with appendage. *Cupule* present or absent, cup-shaped and present on midrib in dorsal side of thallus. *Gemmae* present or absent, discoid, with two opposing apical notches, one stalk trace and numerous scattered oil cells.

Antheridiophore and *Archegoniophore* stalked. Male receptacle stalks with 2–4 rhizoid furrows and filiform scales; band of air-cavities present or not; Female receptacle stalks with 2 rhizoid furrows; receptacles lobed. *Involucre* bilabiate.

Key to the taxa of *Marchantia* in Japan

1. Monoicous; thallus dichotomous and apically ventral innovative; asexual propagule absent; male receptacle unlobed……………………………….…………..….......…*M. quadrata*

1. Dioicious; thallus always dichotomous; asexual propagule present; male receptacle lobed…………………………………………………...……………………...…2

2. Thallus margin lobulate………………………………………………………………..3

2. Thallus margin smooth or slightly crisped……………………………………………..4

3. Thallus usually growing erect, with continuous and distinct dark median band; margin of median scales appendage entire or crenulate, usually bordering with cells smaller than secondary outer layer cells……….............….*M. polymorpha* subsp. *polymorpha*

3. Thallus usually growing prostrate, with discontinuous dark median band; margin of median scales appendage unicellular toothed...…..........*M. polymorpha* subsp. *ruderalis*

4. Gemmae circular or nearly circular, with entire margin and mucilage hair; margin of

cupule and involucre ciliate lobed; appendage of ventral scales with oil-cells……....5

4. Gemmae ellipdoidal to obovate, with dentate margin, mucilage hair absent; margin of cupule and involucre ciliate; appendage of ventral scales without oil-cells…………6

5. Appendage of median scales acute or apiculate apically, usually with toothed or incised margin…………………………...……………..…..*M. paleacea* subsp. *paleacea*

5. Appendage of median scales obtuse apically, usually with entire or crenulate margin ……....….*M. paleacea* subsp. *diptera*

6. Appendage of median scales pinnatifid………………………………...……*M. pinnata*

6. Appendage of median scales unicellular to multicellular toothed…………………..…7

7. Thallus usually with dark median band; appendage of median scales triangular to pentagonal, unicellular toothed; female receptacle with 5–8 lobes; basal sinus of male receptacle nearly 180°…………………………........*M. papillata* subsp. *grossibarba*

7. Thallus usually without dark median band; appendage of median scales ovate, unicellular to multicellular toothed; female receptacle with 5–13 lobes; basal sinus of male receptacle 30–180°……………..…….………….*M. emarginata* subsp. *cuneiloba*

1. ***Marchantia emarginata*** Reinw., Blume et Nees subsp. ***cuneiloba*** (Steph.) T.X.Zheng & M.Shimamura. Bryologist 125: 145. 2022.

≡***Marchantia cuneiloba*** Steph. Bull. Herb. Boissier 5: 98. 1897. Type: JAPAN. Okinawa, Liukiu (Loochoo), Shuri Isl. coll. *Kuroiwa* in herb. *Makino 201* (lectotype: G 112606!, isolectotype: TNS, *non vidi*).

=***Marchantia radiata*** Horik., Sci. Rep. Tohoku Imp. Univ., Ser. 4, Biol. 5: 629. 1930. Type: JAPAN. Honshu, Tottori Prefecture, Saihaku-gun, Houkimizoguchi, 20 June 1931, *Horikawa 3863* (neotype: HIRO 264759!).

Figs. 3.1, **3.2**

Description *Thallus* yellowish green to dark green, prostrate, compact, 1.8–4.2 mm wide, successive dichotomies 3–9 mm apart; dark median band absent; margin entire, hyaline to purplish. *Epidermal pores* 34.1–80.8 µm in diam., bordered by 5–8 cells, inner opening triangular to hexagonal, sometimes circular, bounded by cells with nearly straight or convex inner walls. *Compact ventral tissue* 16–28 cell layered in median portion; central part brown to purplish in old thallus, hyaline in young thallus; sclerotic cells brown, reddish or purplish; mucilage cavities and oil-cells absent; *Ventral surface* green, brown or purplish; scales extending over 45–80% of width. *Ventral scales* in 4 rows; median scales reddish to purplish, sometimes hyaline in part; appendage ovate (width : length = 0.54–1.48; 155–529 × 237–550mm), reddish to purplish, sometimes hyaline in apex of marginal tooth, usually with unicellular to multicellular toothed margin and apiculate apex; oil-cells absent. *Cupule* ciliate. *Gemmae* yellowish green to dark green, ellipsoidal to obovate (width : length = 0.39–1.22 ; 106.7–282.6 × 177.3–498 µm); surface dentate; marginal cells mamillose; mucilage hair absent.

Dioicous. *Antheridiophore* at apex of thallus; stalk 3.5–12 mm long, with 2–4 rhizoid furrows; band of air-cavities 1 or 2 interrupted; scale surrounding base of stalk absent; receptacle 4.6–7 mm in diam., nearly symmetric, shallowly or deeply dissected into 6–10 lobes; lobe yellowish green or grey green, with reddish to blackish midrib-like region extending up to apex, when mature lobe develop into new thallus; lobe margin hyaline to brown, smooth or slightly crenulate, usually inflexed toward the dorsal side; apex obtuse or emarginate; median scale wide ligulate to nearly semicircular, reddish to purplish, with appendage and entire or crenulate margin; basal sinus 30˚–180˚.

Archegoniophore at apex of thallus, stalk 3–20 mm long, with 2 rhizoid furrows; band of air-cavities present; scale surrounding base of stalk absent; receptacle 2.5–5.8 mm in diam., nearly symmetric, deeply dissected into 5–13 lobes, with projection in central part; lobes yellowish green to bright green, spread or convex, usually broadened apically, when young folded toward the ventral side of receptacles; lobe margin hyaline, entire or slightly crenulate, sometimes tinged with reddish or purplish, usually inflexed toward the ventral side of lobes; apex of lobe obtuse, truncate or emarginate; median scale hyaline, reddish or purplish, thread-liked, lobed, with entire or crenulate margin, seldom toothed; involucre hyaline to brown, alternating with lobes, with entire or crenulate margin; oil-cells absent.

Taxonomical notes: *Marchantia emarginata* subsp. *cuneiloba* is distinguished by (1) compact thallus, (2) appendage of ventral scales with unicellular to multicellular toothed margin and (3) up to 13 female receptacle lobes usually with broadened and emarginate apex.

The present subspecies was originally described from Japan by Stephani (1897) as an independent species *M. cuneiloba* which had long been erroneously used to represent *M. pinnata* Steph. in Japan due to the inclusion of *M. cuneiloba* in type specimen of *M. pinnata*. In 1987, Bischler solved this taxonomic confusion and originally reduced *M. cuneiloba* under *M. tosana* based on their close geographical distribution and complementary sexual organs in their original materials. Later, in the protologue of sect. *Papillatae* Bischl. (Bischler 1989), *M. tosana* was treated at a new rank as *M. emarginata* subsp. *tosana* which was then extensively accepted as the name for present group (Bischler-Causse 1989; Katagiri & Furuki 2018; Lu & Huang 2017; Piippo & Koponen 2013; Singh & Singh 2013; Xiang et al. 2016; Zheng et al. 2020).

Recently, Zheng and Shimamura (2022) conducted integrative reevaluation on Japanese taxa belonging to sect. *Papillatae* and reduced *M. tosana* (≡ *M. emarginata* subsp. *tosana*) and *M. tosayamensis* (= *M. emarginata* subsp. *tosana*) to *M. papillata* subsp. *grossibarba* Furthermore, due to that (1) the prevalent morphological definition of *M. emarginata* subsp. *tosana* (Bischler 1987, 1989; Bischler-Causse 1989) was virtually closer to the characteristic of *M. cuneiloba* and (2) *M. cuneiloba* was well resolved into its own monophyletic clade in phylogenetic analysis, the name *M. cuneiloba* was consequently selected to represent the present group. Previously synonymized taxa under *M. emarginata* subsp. *tosana* were also tentatively transferred to present subspecies.

Marchantia radiata Horik. was originally described based on numerous specimens collected from West Japan to China (Horikawa 1930). The species was synonymized under *M. tosana* by Hattori (1944). In 1989, since the original materials of *M. radiata* were not in the Herbarium of Hiroshima University (HIRO) and most probably were destroyed by the explosion of the atomic bomb during WWII, Bischler-Causse followed Hattori (1944) with only referring to the original description. During the taxonomic reevaluation on sect. *Papillatae* in Japan, Zheng & Shimamura (2022) searched the Horikawa collection in HIRO and found some ordinary specimens collected and identified by the original author, based on which this species was newly reduced to *M. emarginata* subsp. *cuneiloba* and neotypified.

Present revision provides the illustration of *Marchantia emarginata* subsp. *cuneiloba* for the first time.

Distribution and **Habitat**: see Zheng & Shimamura 2022.

Specimens examined:

JAPAN. Shizuoka Prefecture: Shizuoka City, Suruga Dist., Hirasawa, *T.-X. Zheng 1543*, *1547*, *1548*; Hiroshima Pref.: Higashi-Hiroshima City, Hara, *T.-X. Zheng 1506*, *1507*, *1508*. Shobara City, Toujou, *T.-X. Zheng 315*; Wakayama Pref.: Higashimuro County, Matsune, *T.-X. Zheng 1536*, *1538*, *1539*, Nabera, *T.-X. Zheng 1524*, *1525*, *1526*, *1527*, *1528*, *1529*, Nishikawa, *T.-X. Zheng 1530*, *1531*; Tottori Pref.: Saihaku Co., Houkimizoguchi, *Y. Horikawa 3863*; Saga Pref.: Karatsu City, Ouchi-cho, Ikisa, *T.-X. Zheng 1145*; Nagasaki Pref.: Minamishimabara City, Fukae-cho, Kou, *T.-X. Zheng 1149*, *1150*, *1151*. Unzen City, Obara-cho, Minamihon-machi, *T.-X. Zheng 1155*; Kumamoto Pref.: Hitoyoshi City, Nishiotsuka-machi, *T.-X. Zheng 1105*, *1108*. Kikuchi City, Shigemi, *T.-X. Zheng 1123*, *1126*; Miyazaki Pref.: Ebino City, Mukae, *T.-X. Zheng 1099*, *1101*. Kushima City, Ohira, *T.-X. Zheng 1042*, *1043*, *1044*. Miyazaki City, Kiyotake-cho, Imaizumi, *T.-X. Zheng 1018*, *1020*, *1021*, Tano-cho, Ko, *T.-X. Zheng 1022*, *1023*, *1024*, *1025*, *1026*. Nichinan City, Hoshikura, *T.-X. Zheng 1053*, *1054*, Kitagou-cho, Kitagawachi, *T.-X. Zheng 1028*, *1029*, Kusubara, *T.-X. Zheng 1055*, *1056*, Obi, *T.-X.*

Zheng 1058, *1059*, *1060*, *1061*, *1062*, *1063*, *1064*, *1065*, *1066*, Saketanikou, *T.-X. Zheng 1067*, *1069*, *1070*, *1071*. Nishiusuki Co., Iwato, *T.-X. Zheng 1002*, *1003*, *1004*, *1005*. Nobeoka City, Kogawa-machi, *T.-X. Zheng 1009*, *1010*, *1011*; Kagoshima Pref.: Aira City, Hiramatsu, *T.-X. Zheng 197*, *198*, Kajiki-cho, Kida, *T.-X. Zheng 226*, *1093*. Hioki City, Fukiage-cho, Nakahara, *T.-X. Zheng 1081*, *1082*, *1083*, Ijuuin-cho, Koinohara, *T.-X. Zheng 1086*, *1088*. Kagoshima City, Hirakawa-cho, *Y. Horikawa 4776*. Kanoya City, Nishihara, *T.-X. Zheng 1073*, *1074*, *1075*. Kimotsuki Co., Nejimeyokobeppu, *T.-X. Zheng 1079*, *1080*, Sataizashiki, *T.-X. Zheng 1084*, *1085*, *1094*, *1095*, Shiromoto, *T.-X. Zheng 1077*. Kirishima City, Hayato-cho, Kareigawa, *T.-X. Zheng 1*, *210*, *211*, *212*, Tougou, *T.-X. Zheng 1110*, Kokubunchuou, *T.-X. Zheng 1096*, *1098*. Kumage Co., Yakushima-cho, *Y. Horikawa 11873*, *Y. Sakamoto 566*. Oshima Co., Inokawa, *M. Higuchi 7706*, Yuwan, *N. Nishimura 6158*. Shibushi City, Matsuyama-cho, Onomi, *T.-X. Zheng 1032*, *1036*, *1037*, *1038*, *1039*. Soo City, Osumi-cho, Tsukino, *T.-X. Zheng 1030*, Takarabe-cho, Minamimata, *T.-X. Zheng 205*, *206*, *208*. Tarumizu City, Shinmido, *Horikawa 4673*; Okinawa Pref.: Ginowan City, Futenma, *T. Yamaguchi 39421*, *39467*. Kunigami Co., Benoki, *Y. Horikawa 13126*, Higashi-son, *T. Yamaguchi 12929*, Kunigami-son, *T. Yamaguchi 13166*, Okuma, *T.-X. Zheng 899*, Tsuha, *T.-X. Zheng 886*, *887*, *888*, *889*, Yona, *T.-X. Zheng 898*, *900*, *901*, *902*. Ishigaki City, Fukai, *T.-X. Zheng 800*, *804*, *805*, *806*, *T. Yamaguchi 2668*, *3118*, *3033*, *3034*, Hirae, *T.-X. Zheng 780*, Mezato, *T.-X. Zheng 781*, *782*, *783*, *784*, *786*, *787*, *788*, *789*, *792*, *793*, *794*, Nagura, *T.-X. Zheng 816*, *817*, *818*, *819*, *820*, Nosoko, *T.-X. Zheng 802*, *803*, Ohama, *T.-X. Zheng 7*, Tonoshiro, *T.-X. Zheng 795*, *796*, *797*, *798*. Nago City, Genka, *Y. Horikawa 2945*, Nago, *T.-X. Zheng 893*, *894*, *895*, *896*, *897*, Taira, *T.-X. Zheng 892*. Nakagami Co., Ogusuku, *T.-X. Zheng 904*, *905*. Naha City, Shurisueyoshicho, *T. Amano 8112* (NICH). Okinawa City, Chibana, *T.-X. Zheng 864*, *865*, *866*. Yaeyama Co., Komi, *T.-X. Zheng 821*, *822*, *823*, *824*, Iriomote, *K. Nishihata 634*, *670*, *834*, *878*, *1247*, *1252*, *T.-X. Zheng 847*, *849*, *850*, *851*, *T. Yamaguchi 346*, *852*, *869*, *2097* Uehara, *T.-X. Zheng 843*, *844*, *845*, Yonaguni, *T. Yamaguchi 4893*.

2.***Marchantia paleacea*** Bertol. Opusc. Sci. (Bologna) 1: 242. 1817.
Type: ITALY. Etruria, et in Liguria orientali a Borgonuovo prope Clavarum, *Bertoloni s.n.* (lectotype: BOLO, *non vidi*).

Description *Thallus* grey green to bright green, slightly coriaceous, prostrate, 2.8–8.5 mm wide, successively dichotomies 6–9.8 mm apart, usually with punctate reddish to purplish pigmentation on dorsal surface; dark median band absent; margin entire, slightly crisped, brown to purplish, usually with colored area sometimes extending up to half width of thallus. *Epidermal pores* 29.52–117.4 μm in diam., bordered by 6–8 cells; inner opening cruciate, sometimes pentacle-shaped. *Compact ventral tissue* 19–26 cells layered in median portion; sclerotic cells and mucilage cavities absent; oil-cells numerous. *Ventral surface* green, brown or purplish; scales extending over 40–60% of thallus width. *Ventral scales* in 4 rows, purplish; appendage reddish to purplish with oil-cells. *Cupule* ciliate lobed, hyaline or yellowish green to purplish, with numerous oil-cells. *Gemmae* yellowish green to dark green, ellipsoidal to circular; surface smooth; marginal cell mamillose; mucilage hair present.

Dioicous. *Antheridiophore* at apex of thallus; stalk 3.5–16.2 mm long, with 2 rhizoid furrows; band of air-cavities absent; scale surrounding base of stalk yellowish to reddish; receptacle 4.2–6.5 mm in diam., nearly symmetric, shallowly dissected into 6–10 lobes; lobe margin hyaline to purplish, entire or slightly crenulate, sometimes crinkled, usually inflexed toward the dorsal side; median scales long ligulate to nearly semicircular, reddish to brown, with apiculate apex or acute appendage; margin entire or crenulate, sometimes toothed.

Archegoniophore at apex of thallus; stalk 10–68 mm long, with 2 rhizoid furrows; band of air-cavities present; scale surrounding base of stalk reddish to purplish, wide ligulate; apex of scale apiculate, sometimes obtuse or truncate; scale margin entire or crenulate, sometimes slightly lobed; receptacle 4.2–8.6 mm in diam., usually symmetric; lobe sometimes apically broadened, emarginate, obtuse or truncate; median scales hyaline to purplish, filiform; involucre hyaline to yellowish, reddish to purplish in marginal part, alternating with lobes, with numerous oil-cells and ciliate lobed margin.

2a subsp. ***paleacea***

= ***Marchantia pulcherrima*** Steph. in Bonner, Candollea 14: 110. 1953. ≡ ***Marchantia pulcherrima*** Steph. ex Hattori, J. Hattori Bot. Lab. 8: 43. 1952, *nom. inval.* (ICN Art. 36.1 (b); published as synonyms). Type: JAPAN. Norikura, *Faurie 1764* (holotype: G 61009!; isotype: FH, PC, KYO *non vidi*); CHINA. Prov. du Kony Tcheou, ruisseau de Pa-oua, *Esquirol 2650* (paratype, not located in G).

Figs. 3.3

Description *Compact ventral tissue* reddish to purplish in central part. *Median scales appendage* elliptical to nearly circular (width : length = 0.4–0.95; 214–756 × 385–889 μm); apex apiculate, rarely obtuse or crenulate; margin crenulate, incised or irregularly toothed. *Gemmae* (width : length = 0.52–0.92; 234–631 × 356–835 μm). *Antheridiophore* basal stalk scales long to wide ligulate, with crenulate margin and apiculate apex. *Archegoniophore* receptacle dissected into 5–9 spread lobes.

Taxonomical notes: *Marchantia paleacea* subsp. *paleacea* is characterized by (1) thallus tinged with reddish or purplish pigmentation, (2) four rows of ventral scales, (3) ciliate lobed margin of cupule and involucre, (4) median scales appendage with acute or apiculate apex and incised margin and (4) present oil-cells in median scales appendage, cupule and involucre.

Marchantia paleacea subsp. *paleacea* was described by Bertoloni based on the collection made from Italy (Bertoloni 1817). Mitten (1865) reported the present taxon as *M. nitida* from Japan. Okamura (1908) also recognized *M. nitida* in his regeneration study. However, the record of *M. paleacea* in Japan was questioned by Hattori (1944) and later this species was treated as a synonym of *M. diptera* (Hattori 1952). In 1957, Hattori recognized the differences in terms of geographical distribution and morphological characteristics between *M. paleacea* and *M. diptera* and since then the taxonomy of *M. paleacea* started to be discussed separately.

Currently, *Marchantia paleacea* is placed into subg. *Chlamidium* by four rows of ventral scales and female receptacles with involucre alternating with lobes (Bischler-Causse 1989, 1993; Bischler & Piippo 1991; Schuster 1992). Due to the unique characters of this subgenus, (1) present oil-cells on cupule, ventral scales appendage and involucre, (2) ciliate lobed margin of cupule and involucre and (3) *M. polymorpha* type spore ornamentation, *M. paleacea* was considered as an isolated species in subg. *Chlamidium* (Schuster 1992) and further placed in its own monotypic sect. *Paleacea* Bischl. (Bischler-Causse 1989, 1993). However, recent phylogenetic studies (Forrest et al. 2006; Villarreal et al. 2016; Zheng & Shimamura 2022) consistently resolved *M. paleacea* in a monophyletic clade sister to *M. polymorpha* which belongs to subg. *Marchantia* rather than subg. *Chlamidium*. This close affinity was also reflected in gemmae morphology (Zheng et al. 2020). Taking the above into consideration, the intrageneric placement of *M. paleacea* needs to be carefully reviewed in the future.

Marchantia pulcherrima Steph. was originally described by Stephani based on materials collected from Japan and China (Bonner 1953). Hattori (1951) invalidly published *M. pulcherrima* as synonym of *M. diptera* In 1954, Hattori annotated that "The type specimen is quite the same as a taxon which I am studying and considering as a new variety of *M. paleacea*" in the original material of *M. pulcherrima*. Bischler (1989) pointed out that its correct identity was *M. paleacea* subsp. *paleacea*. In type specimen of *M. pulcherrima*, appendage of ventral scales is acute or apiculate in apex and toothed or incised in margin, which is identical to *M. paleacea* subsp. *pelacea*.

Distribution: Mainly distributed in northernmost to central Japan (Hokkaido, Iwate, Miyagi, Shizuoka, Tokyo, Toyama, Yamanashi, Nagano and Gifu), sporadically in western Japan (Hiroshima, Miyazaki and Kagoshima) (**Figs. 3.4**).

Habitat: Growing on boulder, soil, concrete or limestone wall in wet or shaded places.

Specimens examined:

JAPAN. Hokkaido: Furano City, Kamigoryou, *H. Ando 1394*, *1396*. Saru Co., Mitsuiwa, *Y. Takahashi 270*; Iwate Pref.: Ichinoseki City, Genbi-cho, *T.-X. Zheng 493*, *494*, *495*, *496*, *497*, *498*; Miyagi Pref.: Kurihara City, Kurikomanumakura, *T.-X. Zheng 474*, *475*, *476*, *477*, *478*, *479*, *480*, *481*, *482*, *483*, *484*, *485*, *486*, *487*, *510*, *511*; Shizuoka Pref.: Shizuoka City, Aoi Dist., Tashiro, *K. Kiryu 37*, *38*; Tokyo: Nishitama Co., Nippara, leg. *H. Inoue s.n.* (Bryophyta Selecta Exsiccata no. 363 in HIRO), leg. *H. Inoue s.n.* (Bryophyta Selecta Exsiccata no. 15 in HIRO); Toyama Pref.: Nakaniikawa Co., Ashikuraji, *K. Honda 5*, *T.-X. Zheng 515*, Midagahara, *T.-X. Zheng 527*, *528*, *529*. Toyama City, Arimine, *H. Ando 15961*; Yamanashi Pref.: Minamiarupusu City, leg. *T. Sato s.n.* (HIRO1038711), leg. *T. Sato s.n.* (HIRO1038712); Gifu Pref.: Ono Co., Shirakawa, *T.-X. Zheng 1601*, *1602*, *1603*, *1605*, *1606*, *1607*, *1608*, *1609*. Takayama City, Asahi-cho, Aoya, *H. Miyauchi 203*, Nyuukawacho-Kute, *H. Miyauchi 966*, *967, 984*, *993*, *T. Yasuhara 2774*, Nyuukawacho-Hiyomo, *T.-X. Zheng 1570*, *1572*; Nagano Pref.: Matsumoto City, Aduzi, leg. *M. Shimamura s.n.* (HIRO1038685), *M. Uzawa 5193*. Shimoina Co., Oshika-mura, Kashio, *T. Katagiri 637*, *772*, *834*, *1645*, *2318*, *2464*, *T. Sato 231*; Hiroshima Pref.: Yamagata Co., Tsushimi, leg. *M. Iwata s.n.* (HIRO1038700), leg. *M. Iwata s.n.* (HIRO1038702); Miyazaki Pref., Higashisuki Co., Shiibason, *H. Ando 12595*; Kagoshima Pref.: Kirishima City, Kirishimataguchi, *T.-X. Zheng 223*. Kumage Co., Anbou, leg. *M. Shimamura s.n.* (HIRO1038705).

2b subsp. ***diptera*** (Nees et Mont.) Inoue, J. Jap. Bot. 64: 194. 1989.

≡ ***Marchantia diptera*** Nees et Mont. in Montagne, Ann. Sci. Nat. Bot. (sér. 2), 19: 243. 1843.≡ ***Marchantia paleacea*** var. ***diptera*** (Mont.) Hatt., J. Hattori Bot. Lab. 18: 79. 1957. ≡ ***Marchantia paleacea*** subsp. ***diptera*** (Mont.) Hatt. in Mizutani et Hattori, J. Hattori Bot. Lab. 40: 342. 1976. *nom. inval.* (ICN Art. 41.5; no indicated basionym and reference). Type: JAPAN. coll. *Bussenil* in *Nees 291* (lectotype: PC, *non vidi*; isolectotype: G 265185!).

= ***Marchantia alatocapitata*** Steph. in Bonner, Candollea 14: 102. 1953. ≡ ***Marchantia alato-capitulata*** Steph. ex T. Inoue, Bot. Mag. (Tokyo) 8: 293. 1894, *nom. inval.* (ICN Art. 38.1(a); no accompanied description). Type: JAPAN. Tosa, *Inouë 12* (holotype: G 265176!; isotype: BM, *non vidi*).

= ***Marchantia calcarata*** Steph., Bull. Herb. Boissier 5: 98. 1897. ≡ ***Marchantia calcarata*** Steph. ex Bescherelle, Rev. Bryol. 21: 26. 1894, *nom. inval.* (ICN Art. 38.1(a); no accompanied description). Type: JAPAN. Yokoska, bei Yokohama, *Savatier s.n.* (lectotype: G 43746!; isolectotype: BM, FH, PC, *non vidi*).

= ***Marchantia planipora*** Steph., Bull. Herb. Boissier 5: 98. 1897. ≡ ***Marchantia planipora*** Steph. ex Makino, Bot. Mag. (Tokyo) 10: 209. 1896, *nom. inval.* (ICN Art. 38.1 (a), no accompanied description). Type: JAPAN. Kigo, *Ahlburg s.n.* (lectotype: G 43748!).

Figs. 3.5

Description *Compact ventral tissue* hyaline to brown in central part, sometimes reddish to purplish. *Median scales appendage* ovate to nearly circular (width : length = 0.84–1.22; 259–1019 × 378–879 µm); apex obtuse, seldom slightly apiculate; margin entire or crenulate; marginal cells partly narrowed. *Gemmae* (width : length = 0.39–1.18; 226–664 × 321–840 µm). *Antheridiophore* basal stalk scales long ligulate to nearly circular, with entire or crenulate margin and obtuse or apiculate apex, sometimes toothed in lower part. *Archegoniophore* unfertilized receptacle with 2 spread lobes located on both side of basal sinus, other 6–7 lobes folded toward the ventral surface of receptacle; fertilized receptacle with 3, 8 or 9 spread lobes.

Taxonomical notes:

Marchantia paleacea subsp. *diptera* shares (1) thallus tinged with reddish or purplish pigmentation, (2) four rows of ventral scales, (3) ciliate lobed margin of cupule and involucre and (4) present oil-cells in median scales appendage, cupule and involucre with subsp. *paleacea*, but it can be easily distinguished from the latter by (1) median scales appendage with obtuse apex and entire or crenulate margin and (2) unfertilized female receptacle with two spread lobes located on both side of basal sinus.

Separation of the two subspecies in Japan is also supported by geographical distribution: subsp. *diptera* is mainly distributed in western Japan at altitudes below 500m while subsp. *paleacea* is usually found in central and northeastern Japan (Zheng & Shimamura 2019b).

Marchantia paleacea subsp. *diptera* was originally published as *M. diptera* by Montagne (1843) from plants collected in Japan. Since then, various authors treated it in different taxonomic rank. Horikawa (1930), Tatuno (1941), Hattori (1944, 1951) and Suzuki (1966) considered it as an independent species. Hattori (1955) treated *M. diptera* as a synonym of *M. paleacea* but suggested that *M. diptera* should be regarded as a variety of *M. paleacea*. In 1957, Hattori compared the geographical distribution and morphological characteristics between *M. diptera* and *M. paleacea* and formally published *M. diptera* at varietal rank under *M. paleacea*. Mizutani and Hattori (1976) first proposed the *M. paleacea* subsp. *diptera*, which was proved to be nomenclatorially invalid due to the absence of the indicated basionym and reference (Greuter et al. 1988). Bischler (1986a) compared *M. paleacea* and *M. diptera* with respect to morphology, ecology, karyotype and reproductive strategies and concluded that *M. diptera* should be treated as a subspecies under *M. paleacea*. However, although "subsp. *diptera*" was repeatedly used in subsequent studies on Japanese Marchantias (Bischler 1986a, 1987), the subspecific name of *M. diptera* was not validly published until Inoue (1989).

In the holotype of *Marchantia alatocapitata* Steph., two types of ventral scale appendage are observed, one smooth or crenulate in margin and obtuse in apex, the other slightly toothed in margin and apiculate in apex (Fig. 5B). This species seems to be an intermediate between two subspecies of *M. paleacea*. However, due to the presence of *diptera*-type appendage and its westward type locality in Japan, I agreed with the synonymy of Bischler (1987).

Marchantia calcarata Steph. and *M. planipora* Steph. have been synonymized with *M. paleacea* subsp. *diptera* by Bischler (1987). The plants of their types show a robust form of subsp. *diptera*. This form is usually found near perennial dripping wet environments such as spring water in West Japan at low altitude. Both species are characterized by (1) wide and robust thallus (6–8.5 mm), (2) six rows of ventral scales in the dichotomizing part of thalli and (3) female receptacle with longer stalk (up to 6.8 cm) and spread lobes only. At first glance, their robust appearance led us to consider them as polyploids.

The erroneous type citation of *Marchantia planipora* was noticed and corrected by Zheng (2021).

Distribution: Mainly distributed from central to southern Japan (Toyama, Fukui, Nagano, Shizuoka, Mie, Shiga, Hyogo, Nara, Tottori, Shimane, Okayama, Hiroshima, Yamaguchi, Tokushima, Kagawa, Ehime, Kochi, Fukuoka, Saga, Nagasaki, Oita, Miyazaki, Kumamoto and Kagoshima), sporadically in eastern to northern Japan (Akita, Fukushima, Ibaraki, Chiba, Tokyo and Kanagawa) (**Figs. 3.6**).

Habitat: Growing on stone or soil in shaded or semi-shaded places, anthropogenic region or near the stream.

Specimens examined:

JAPAN. Akita Pref.: Akita City, *T.-X. Zheng 425*, *426*, *427*; Fukushima Pref.: Aiduwakamatsu City, Ikki-machi, Yahata, *T.-X. Zheng 1431*. Fukushima City, Omori, *T.-X. Zheng 16*, Tsuchiyuonsenmachi, *T.-X. Zheng 1413*, *1414*, *1415*, *1416*, *1417*, *1418*, *1419*, Yamagiwa, *T.-X. Zheng 1409*, *1410*, *1411*, *1412*. Kooriyama City, Ouse-machi, Kouzu, *T.-X. Zheng 1341*, *1342*. Yama Co., Oshio, *T.-X. Zheng 1425*, *1426*, *1427*; Ibaraki Pref.: Bandou City, Osaki, leg. *M. Uzawa s.n.* (HIRO-1038689). Higashiibaraki Co., Shimofuruuchi, *M. Uzawa 3540*; Chiba Pref.: Futtsu City, Kanaya, *T.-X. Zheng 50*, *51*, *52*, *53*, *54*. Kamogawa City, Kiyosumi, *T.-X. Zheng 56*, *57*. Kimitsu City, Nutazawa, *K. Nokami 8*; Tokyo: Hachijoushichou, Mitsune, *M. Higuchi 10619*. Oshimashichou, Okata, *H. Ando 8077*; Kanagawa Pref.: Kamakura City, Juuniso, *M. Itouga 1339*, *1340*; Toyama Pref., Nakaniikawa Co., Tateyama-cho, *T.-X. Zheng 514*; Fukui Pref.: Fukui City, Kidonouchi-cho, *S. Kamuro 41*; Nagano Pref.: Matsumoto City, Azumi-inekoki, leg. *M. Shimamura s.n.* (HIRO-1038686); Shizuoka Pref.: Izu City, Odaira, leg. *M. Shimamura s.n.* (HIRO-1038687). Shizuoka City, Suruga Dist., Negoya, *Y. Horikawa 2362*, Hirasawa, *T.-X. Zheng 1545*; Mie Pref.: Ise City, Youkaichiba-cho, leg. *K. Yamada s.n.* (Hepaticae Japonicae Exsiccatae no. 782 in HIRO). Matsuzaka City, Iitaka-cho, Hajisu, *T.-X. Zheng 413*. Inabe Co., *H. Ando 172*. Taki Co., Osugi, *H. Ando 2081*, *2127*; Shiga Pref.: Takashima City, leg. *M. Shimamura s.n.* (HIRO-1038704), *T.-X. Zheng 1516*, *1517*, Katsuno, *T.-X. Zheng 1513*; Hyogo Pref.:Nishinomiya City, *Y. Horikawa 2358*. Tanba City, Aogaki-cho, Touzaka, *T.-X. Zheng 747*, *748*; Nara Pref.: Yoshino Co., Ikari, *T.-X. Zheng 414*, *415*; Wakayama Pref.: Higashimuro Co., Okawa, *T.-X. Zheng 1532*, *1533*, *1534*, *1535*, Matsune, *T.-X. Zheng 1537*; Tottori Pref.: Saihaku Co., Daisen-cho, *Y. Horikawa 3864*. Tottori City, Kokufu-cho, Miyanoshita, *T.-X. Zheng 718*, *719*, *721*, *722*, *724*, *725*, *726*, *727*, *728*, *729*, *730*, Saji-cho, Takayama, *T.-X. Zheng 754*, *756*, *758*, *759*, *762*. Touhaku Co., Misasa-cho, Mitoku, *H. Ando 17551*. Yonago City, Kume-cho, *S. Nokawa 14*, Yodoe-cho, Takaidani, *T.-X. Zheng 703*, *704*, *708*, *709*, *710*; Shimane Pref.: Kanoashi Co., Ushiroda, *T.-X. Zheng 299*, *327*; Okayama Pref.: Maniwa City, Hongou, *T.-X. Zheng 713*, *714*. Okayama City, Kita Dist., Kibitsu, *Y. Tateishi 3033*. Takahashi City, Kawakami-cho, *M. Higuchi 6073*; Hiroshima Pref.: Aki Co., Fuchu-cho, leg. *M. Iwata s.n.* (HIRO 1038693), leg. *M. Iwata s.n.* (HIRO 1038707). Akitakata City, Takamiya-cho, Hasadake, *M. Itouga 2987*, *N. Ohnishi 2489*. Biwa Co., Toujou-cho, Kushiro, *N. Ohnishi 3132*. Fuchuu City, Jouge-cho, *N. Ohnishi 3409*. Hatsukaichi City, Asahara, *T.-X. Zheng 930*, *931*, *932*, *933*, *934*, Miyajima-cho, *K. Sonoyama 2391*, *T.-X. Zheng 65*, *67*, *69*, *76*, *84*, *94*. Higashihiroshima City, Kagamiyama, leg. *M. Iwata s.n.* (HIRO 1038696), leg. *M. Iwata s.n.* (HIRO 1038697), leg. *M. Iwata s.n.* (HIRO-1038710), *T.-X. Zheng 679*, *680*, *681*, *682*, *683*, *T. Yasuhara 416*, *500*. Hiroshima City, Asakita Dist., Asa-cho, Tsutsuse, *N. Ohnishi 6121*, Asaminami Dist., Numata-cho, *M. Itouga 2145*, Odukahigashi, leg. *M. Iwata s.n.* (HIRO 1038690), leg. *M. Iwata s.n.* (HIRO-1038691), leg. *M. Iwata s.n.* (HIRO 1038692), Nishi Dist., Koi, *H. Ando 363*. Jinseki Co., Jinsekikougen-cho, *M. Itouga 2929*, *S. Ideshita 1367*, *1450*. Kure City, Shimokamagari-cho, *M. Higuchi 14614*, *14889*, *14919*, *N. Ohnishi 698*. Miyoshi City, Kimita-cho, Hitsuta, *T. Yasuhara 558*. Otake City, *K. Ure 1370*. Shoubara City, Takano-cho, Koubo, *T. Yasuhara 557*, Toujou-cho, *M. Higuchi 2243*, *2444*, *4968*, *5843*, *7282*, *7283*, *7383*, *M. Itouga 3852*. Takehara City, Nika-cho, *M. Itouga 2893*, *3931*, Tadanoumi-cho, *Y. Sasaki 16*. Yamagata Co., Akioota-cho, Sandankyou, *M. Nakashima 122*, Kake, *M. Nakashima 2406*, *2486*, *2616*, *2677*, *2678*, Togouchi, *N.*

Ohnishi 2676, Tsushimi, leg. *M. Iwata s.n.* (HIRO 1038698), leg. *M. Iwata s.n.* (HIRO 1038699), leg. *M. Iwata s.n.* (HIRO 1038701), leg. *M. Iwata s.n.* (HIRO 1038703), *T.-X. Zheng 171*, *172*, Nakatsutsuga, *T.-X. Zheng 184*, *185*, *186*, *187*, *188*; Yamaguchi Pref.: Mine City, Shuuhou-cho, Akiyoshi, *T. Shiomi 673*, *T.-X. Zheng 421*, Beppu, *T.-X. Zheng 570*. Hagi City, Kawakami, *H. Ando 16660*, *Y. Horikawa 5553*. Ichinoseki City, Houhoku-cho, Tsunoshima, *M. Yoshioka 14*. Iwakuni City, Futashika, *M. Itouga 3831*, Mikawa-machi, Nekasa, *T.-X. Zheng 962*, *963*, Miwa-machi, Kitanakayama, *T.-X. Zheng 949*, *950*, *951*, *952*, *953*, *954*, Nishiki-machi, Fukagawa, *S. Katsui 168*. Shuunan City, Yonemitsu, *T.-X. Zheng 954*, *955*, *956*, *957*, *958*, *959*. Yamaguchi City, Ki-machi, *T.-X. Zheng 419*, *420*, Nihonakagou, *T.-X. Zheng 960*, *961*; Tokushima Pref.: Myouzai Co., Kamibun, *T.-X. Zheng 389*, *392*, *393*, *394*, *396*, *1260*, *1261*, *1262*, Shimobun, *H. Taoda 395*. Naka Co., Kitou, *T.-X. Zheng 1223*, *1224*, *T. Hide 5*, Sakashuu, *T.-X. Zheng 1204*; Kagawa Pref.: Takamatsu City, Shionoe-cho, Yasuharashimo, *T.-X. Zheng 1255*, *1256*; Ehime Pref.: Kamiukena Co., Kuma, *T.-X. Zheng 1183*, *1184*, *1185*, *1186*, Wakayama, *T.-X. Zheng 31*, Yanaigawa, *H. Deguchi 38584*. Matsuyama City, Kawanaka-machi, *T.-X. Zheng 1182*. Niihama City, Tatsukawa-cho, *T.-X. Zheng 335*, *336*, *358*, *360*, *361*, *362*. Saijo City, Fujinoishi, *T.-X. Zheng 597*. Toon City, Kawanouchi, *T.-X. Zheng 39*, *44*, *45*, *60*, *61*, *62*. Yawatahama City, Honai-cho, Miyauchi, *H. Ando 11443*, *11452*, *11453*;Kochi Pref.: Agawa Co., Kazurahara, *T.-X. Zheng 357*, Nanokawa, *T.-X. Zheng 338*, *339*, *343*, *345*, *347*, *349*, *634*, *635*, *651*, *652*, Oya, *H. Deguchi 35224*. Kami City, Kahoku-cho, Birafu, *T.-X. Zheng 1205*, *1206*, Monobe-cho, Befu, *H. Deguchi 34877*, *N. Ohnishi 3498*, *3500*, Kubo, *M. Higuchi 3723*. Kochi City, Godaisan, *N. Ohnishi 522*, *T.-X. Zheng 363*, Eikokuji-cho, *T.-X. Zheng 364*, Tosayamahirose, *T.-X. Zheng 1195*, *1196*, Tosayamashoubu, *T.-X. Zheng 1221*, *1222*. Kounan City, Noichi-cho, Otani, *H. Ando 6281*. Nagaoka Co., Tsuge, *H. Ando 6021*. Shimanto City, Nishitosa, *H. Ando 13386*. Takaoka Co., Furuhatakou, *T.-X. Zheng 605*, *607*, *610*, *614*, *618*, *619*, *621*, *622*, Ochi, *T.-X. Zheng 659*, *660*, Shimanto-cho, *H. Ando 13096*; Fukuoka Pref.: Tagawa Co., Soeda-machi, Hikosan, *S. Ideshita 622*. Yame City, Kurogi-machi, Koya, *T.-X. Zheng 1116*, *1117*, *1118*, Yabe-mura, Kitayabe, *T.-X. Zheng 1120*, *1121*. Saga Pref.: Kashima City, Yamaura, *T.-X. Zheng 1137*, *1138*, *1139*. Saga City, Mitsuse-mura, Mitsuse, *T.-X. Zheng 1141*;

Nagasaki Pref., Shimabara City, Mitsugi-machi, *T.-X. Zheng 1152*, *1153*, *1154*; Kumamoto Pref.: Aso Co., Kitazato. *T.-X. Zheng 987*, *988*, Nakamatsu, *T.-X. Zheng 1130*, *1131*. Hitoyoshi City, Nishiootsuka-machi, *T.-X. Zheng 1106*, *1107*. Kikuchi City, Shigemi, *T.-X. Zheng 1122*, *1124*. Kuma Co., Kounose, *T.-X. Zheng 418*, Sangaura, *T.-X. Zheng 1102*, *1103*, *1104*, *1109*. Tamana Co., Konoha, *H. Ando 12132*; Oita Pref.: Bungoono City, Ono-machi, Tashiro, *T.-X. Zheng 284*, *285*, *286*. Hita City, Kamitsue-machi, Kaminoda, *T.-X. Zheng 1128*. Nakatsu City, Yabakei-cho, *T.-X. Zheng 979*, *980*, Kanayoshi, *T.-X. Zheng 545*, *546*, *547*, *548*, Sogi, *T.-X. Zheng 201*, *202*, Yamakuni-machi, Nakama, *T.-X. Zheng 230*, *231*, *235*, *236*, *237*. Kusu Co., Machida, *T.-X. Zheng 969*, *970*, *971*, *972*, Mori, *T.-X. Zheng 974*, *975*, *977*, *978*. Usa City, Ajimu-machi, Higashishiiya, *T.-X. Zheng 239*. Yufu City, Yufuinn-cho, Kawakami, *T.-X. Zheng 554*, *555*; Miyazaki Pref.: Ebino City, Matsunaga, *T.-X. Zheng 1111*, *1112*, *1113*. Koyu Co., Kawakita, *T.-X. Zheng 16*. Kushima City, Ohira, *T.-X. Zheng 1041*. Nichinan City, Obi, *T.-X. Zheng 261*, *279*, Saketani, *T.-X. Zheng 257*. Nishiusuki Co., Kuraoka, *T.-X. Zheng 997*, *1000*, *1001*, Iwato, *T.-X. Zheng 1006*, Mitai, *T.-X. Zheng 1015*, Mukouyama, *T.-X. Zheng 1013*, Seiunnbashi, *T.-X. Zheng 1007*, *1008*. Nobeoka City, Kitakawa-cho, Kawachimyou, *T.-X. Zheng 983*, *984*; Kagoshima Pref.: Aira City, Hiramatsu, *T.-X. Zheng 195*, *196*, *199*, Kajiki-cho, Kida, *T.-X. Zheng 229*, *1091*. Kirishima City, Kareigawa, *T.-X. Zheng 3*, Kirishimataguchi, *T.-X. Zheng 224*, Makizono-cho, Takachiho, *T.-X. Zheng 1114*. Shibushi City, Matsuyama-cho, Onomi, *T.-X. Zheng 1035*, Shibushi-cho, Uchinokura, *T.-X. Zheng 1047*. Soo City, Takarabe-cho, Minamimata, *T.-X. Zheng 219*.

3 ***Marchantia papillata*** Raddi. subsp. ***grossibarba*** (Steph.) Bischl. Cryptogamie, Bryol. Lichénol. 10: 78. 1989.

≡***Marchantia grossibarba*** Steph. Mém. Soc. Sci. Nat. Cherbourg 29: 221. 1894. Type: CHINA. Yunnan, Sylva prope Santcha-Ho., *Delavay s.n.* (lectotype: G 43749!, isolectotypes: BM, FU, PC, *non vidi*).

=***Marchantia tosana*** Steph. Bull. Herb. Boissier 5: 99. 1897. ≡ ***Marchantia tosana*** Steph. ex Makino, Bot. Mag. (Tokyo) 10: 209. 1896. *nom. inval.* (ICN Art. 38.1 (a), no accompanied description). Type: JAPAN. Tosa, Nanokawa, April 1895, *Inoue 5* (holotype: G 43739!).

=***Marchantia tosayamensis*** Steph. in Bonner, Candollea 14: 112. 1953. Type: JAPAN. Tosa, Tosayama, 5 June 1904, *Tokihisa 105* (holotype: G 112607!).

Figs. 3.7

Description *Thallus* grey green to dark green, 4–6.2 mm wide, successively dichotomies 7–9 mm apart; dark or hyaline median band present on dorsal surface; air-chamber continuously absent in central dorsal surface; margins entire, hyaline to yellowish. *Epidermal pores* 33–82 μm in diam., bordered by 5–6 cells, inner opening triangular to hexagonal, sometimes circular, bounded by cells with straight or slightly convex inner walls. *Compact ventral tissue* 16–22 cells layered in median portion; central part reddish to purplish, hyaline in apical part of thallus; sclerotic cells numerous, dark yellowish to purplish; mucilage cavities absent. *Ventral surface* grey to dark green; scales extending over 30–50% thallus width. *Ventral scales* in 4 rows, reddish to purplish; oil-cells absent; appendage light yellowish to reddish, seldom purplish, ovate, triangular to nearly pentagonal (width : length = 0.61–1.24; 211–405 × 249–461 μm), with obtuse or apiculate apex; marginal teeth absent or unicellular to multicellular, same color as median part of appendages. *Cupule* ciliate. *Gemmae* yellowish to dark green, circular to ellipsoidal (width : length = 0.38–0.87; 137–324 × 292–544 μm); surface dentate; marginal cell mamillose; mucilage hair absent.

Dioicous. *Antheridiophore* usually at apex of short lateral thallus branch; stalk 6–20 mm long, with 2 (seldom 3) rhizoid furrows; band of air-cavity absent or 1 or 2 interrupted; scale surrounding base of stalk absent; receptacle 4–7.6 mm in diam., nearly symmetric, shallowly or deeply dissected into 5–7 lobes; lobe yellowish to dark green, with blackish midrib-like region extending up to apex; lobe margin hyaline to brown, smooth or slightly crenulate, usually inflexed toward the dorsal side; lobe apex obtuse, sometimes slightly broadened apically or emarginate; median scale wide ligulate to nearly semicircular, yellowish, with entire margin and appendage; appendage yellowish, fusiform; basal sinus nearly 180°.

Archegoniophore at apex of thallus, stalk 5–27 mm long, with 2 rhizoid furrows; band of air-cavity present; scale surrounding base of stalk absent; receptacle 4.6–6 mm in diam., nearly symmetric, deeply dissected into 5–8 lobes, with projection in central part; lobes yellowish green to green, when young folded toward the ventral side of receptacles; lobe margin brown, smooth or slightly crenulate, when young inflexed toward the ventral side; lobe apex usually broadened apically and emarginate, sometimes truncate; median scale reddish to purplish, thread-liked; margin of scale crenulate or irregularly incised, seldom toothed; involucre hyaline to yellowish, alternating with lobes, with entire or crenulate margin, without oil-cells.

Taxonomical notes: Present subspecies is characterized by (1) continuous air-chamber absence in central dorsal surface of thallus, (2) distinct blackish median band and (3) triangular to nearly pentagonal median scales appendage with unicellular margin.

Marchantia papillata subsp. *grossibarba* was firstly described in 1894 as an independent species, *M. grossibarba* based on the specimen collected from Yunnan, China (Stephani 1894). In 1989, Bischler provided detailed taxonomic research on sect. *Papillatae* and treated *M. grossibarba* as a subspecies under *M. papillata*. In Japan, specimens of present subspecies had been deposited in herbarium under the name *M. tosana* and overlooked for more than 50 years (*S. Katsui 444*, *T. Shiomi 19*). Zheng and Shimamura (2020) found these exemplars deposited in HIRO and reported *M. papillata* subsp. *grossibarba* new to Japanese bryoflora.

In 2022, Zheng and Shimamura reviewed Japanese taxa belonging to sect. *Papillatae* of subg. *Chlamidium* and synonymized *Marchantia tosana* and *M. tosayamensis* under *M. papillata* subsp. *grossibarba*, which made the morphological definition of present subspecies broader than formerly defined. Recently, I compared the type material of *M. grossibarba* (≡ *M. papillata* subsp. *grossibarba*) and additional newly collected specimens of *M. tosana* and *M. tosayamensis* and found that they are different in number of female receptacle lobes. In holotype of *M. grossibarba*, number of female receptacle lobes is up to 11 while in *M. tosana* and *M. tosayamensis* is always 5–8. Due to the lack of ordinary specimens of present subspecies from its distribution center, I followed the synonymy of Zheng and Shimamura (2022). In the future, additional material and taxonomic studies are necessary to give them a more appropriate treatment.

Distribution: North Kyushu, Shikoku, Chugoku, and along the shore of Honshu Island (**Figs. 3.8**).

Habitat: see Zheng & Shimamura 2022.

Specimens examined:

JAPAN. Saitama Pref.: Saitama City, Nakao, *T.-X. Zheng 1480*, *1481*, *1482*, *1483*, *1484*. Chiba Pref., Kamogawa City, Yomogi, *T.-X. Zheng 328*; Tokyo: Higashikurume City, Gakuen-cho, *S. Kifuji 375*, Ota Dist., Ikegami, T.-X. Zheng 1491, 1492, 1493, Shibuya Dist., Higashi, *M. Uzawa 2336*, *5639*; Ishikawa Pref.: Hakusan City, Chuugu, *T.-X. Zheng 1610*, *1611*, *1612*, *1613*, *1614*, *1615*, Senami, *T.-X. Zheng 1617*, *1618*; Gifu Pref.: Yamagata City, Kanzaki, *T.-X. Zheng 411*, *412*; Shiga Pref.: Maibara City, Samegai, *T.-X. Zheng 1519*, *1520*, *1521*, *1522*, *1523*, Takashima City, Katsuno, *T.-X. Zheng 1509*, *1510*, *1511*, *1512*; Hyogo Pref.: Asago City, Ikuno-cho, *T.-X. Zheng 1497*, *1498*; Shimane Pref.: Kanoashi Co., Kibedani, *T.-X. Zheng 271*, *272*, Machida, *T.-X. Zheng 305*. Hiroshima Pref.: Higashi-hiroshima City, Saijohonmachi, *T.-X. Zheng 923*, *924*, *1167*, *1172*; Yamaguchi Pref.: Iwakuni City, Oze, *S. Katsui 444*, Mine City, Shuhou-cho, *T. Shiomi 19*, *T.-X. Zheng 966*, *967*, *1157*, *1158*; Tokushima Pref.: Myouzai Co., Kamibun, *T.-X. Zheng 398*, *1238*, *1246*, *1251*, *1260*. Naka Co., Sakashū, *T.-X. Zheng 1202*; Kochi Pref.: Agawa Co., Nanokawa, *T.-X. Zheng 350*, Kochi City, Tosayamahirose, *T.-X. Zheng 368*, *1200*, *1201*, Tosayamakajitani, *T.-X. Zheng 380*, *1208*, *1214*, *1217*, Tosayamakuwao, *T.-X. Zheng 1228*, *1232*, *1234*. Shimanto City, Nishitosaniwama, *T.-X. Zheng 1192*; Saga Pref.: Kanzaki Co., Ishinari, *T.-X. Zheng 1136*; Kumamoto Pref.: Kuma Co., Kounose, *T.-X. Zheng 417*; Oita Pref.: Kusu Co., Machida, *T.-X. Zheng 996*. Nakatsu City, Yabakeicho-ōshima, *T.-X. Zheng 539*, *992*, *993*; Miyazaki Pref.: Nishiusuki Co., Mukouyama, *T.-X. Zheng 1014*.

Other specimens examined:

CHINA. Sichuan Province: Yanbian Co., *M.-Z. Wang 20126*, *20128* (PE); Yunnan Prov., Mengla Co., Menglun, *P.-C. Wu 21708* (PE). INDIA. Pubjab, *W. Koelz 4420* (NICH). Uttar Pradesh, *Gollan 4585* (G). West Bengal, *Hartless 3324* (G). MYANMAR. *F. G. Dickason 7325* (NICH).

4 ***Marchantia pinnata*** Steph. in Bonner, Candollea 14: 109. 1953. Type: JAPAN. Kagoshima. *Faurie 711* (lectotype: G 61004!; isolectotypes: FH, BM, PC *non vidi*)
= ***Marchantia pinnato-appendiculata*** Steph. ex Hattori, J. Hattori Bot. Lab. 8: 43. 1952. *nom. inval.* (ICN Art. 36.1(b); published as synonyms). [synonymy *fide* Hattori (1952)].
= ***Marchantia pinnatim-articulata*** Steph. ex Hattori, J. Hattori Bot. Lab. 8: 43. 1952. *nom. inval.* (ICN Art. 36.1(b); published as synonyms) . [synonymy *fide* Hattori (1952)].

Figs. 3.9

Description *Thallus* grey or yellowish green to dark green, sometimes tinged with reddish to purplish on dorsal surface, prostrate, 2.3–5 mm wide, successively dichotomies 4–11 mm apart; dark median band usually present and continuous, sometimes absent; air-chamber continuously absent in central dorsal surface; margin entire, hyaline to purplish. *Epidermal pores* 33.6–62.16 µm in diam., bordered by 4–6 cells; inner opening triangular to pentagonal, bounded by cells with processes on inner wall. *Compact ventral tissue* 17–23 cells layered in median portion; central part brown, reddish to purplish; sclerotic cells present; mucilage cavities and oil-cells absent. *Ventral surface* green or dark purplish; scales extending over 30–50% of thallus width. *Ventral scales* in 4 rows; median scales purplish; appendage nearly triangular (width : length = 0.54–1.8; 441–784 × 455–800 µm), pinnatifid, reddish to purplish, usually hyaline in apical cell of laciniae; laciniae 4–11, unicellular to multicellular; oil-cells absent. *Cupule* short ciliate, usually brown to purplish. *Gemmae* yellowish green to dark green, ellipsoidal to obovate (width : length = 0.42–0.94 ; 99–264 × 167–357 µm); surface dentate; marginal cell mamillose with small papillae; mucilage hair absent.

Dioicous. *Antheridiophore* at apex of thallus; stalk 5–8.3 mm long; rhizoid furrows two, separate, sometimes fused to one; band of air-cavities absent; scale surrounding base of stalk indistinct or undifferentiated; receptacle 5.6–10.2 mm in diam., nearly symmetric, deeply dissected into 4–9 lobes; lobe yellowish green to green, with hyaline and slightly crenulate margin usually inflexing toward the dorsal side; lobe midrib-like region brownish to blackish, sometimes extending up to apex of rays; apex of lobe obtuse, truncate or emarginate; median scale wide to narrow ligulate, hyaline to reddish, with appendage; appendage filiform, reddish to purplish, sometimes with sinuous or incised margin and sinuous apex; basal sinus 180°–240°.

Archegoniophore at apex of thallus, stalk 4.6–7.4 mm long; rhizoid furrow 2; band of air-cavities 2–3 interrupted; scale surrounding base of stalk indistinct or undifferentiated; receptacle 4.5–5.6 mm in diam., nearly symmetric, shallowly or deeply dissected into 5 lobes; lobe green, located on opposite side of basal sinus, spread or slightly folded toward the ventral side of receptacles; margin hyaline to yellowish, slightly crenulate, usually inflexed toward the ventral side of lobes; apex of lobe broadened, truncate and emarginate; median scales wide filiform, usually hyaline in bottom and reddish to purplish in upper part, with sinuous or incised margin, sometimes pinnatifid in apex; involucre hyaline to yellowish in bottom and reddish to dark purplish in margin, with crenulate to unicellular margin, alternating with lobes; basal sinus 180°–240°.

Taxonomical notes: *Marchantia pinnata* can be readily distinguished from all other Japanese *Marchantia* taxa by (1) pinnatifid median scales appendages, (2) continuous air-chamber absence in the central dorsal surface of thallus, (3) present blackish median band and (4) gemmae with papillose marginal cell (Zheng & Shimamura 2019, Zheng et al. 2020).

Marchantia pinnata was first described by Stephani and posthumously published by Bonner in 1953. As mentioned above, owing to the mixture of two different species in its type specimen, *M. pinnata* had been recognized as *M. cuneiloba* in Japan (Amakawa 1967, Horikawa 1939, Hattori 1952, Mizutani 1984). This taxonomic confusion lasted for a long time until the lectotypification of *M. pinnata* was made by Bischler (1987) with exclusion of *M. cuneiloba* from type material of *M. pinnata*.

An annotation card present in type specimens of *Marchantia pinnata* was made by an anonymous researcher, probably S. Hattori, suggesting that present species should be treated at varietal rank under *M. cuneiloba* Although *M. pinnata* is more or less similar to *M. emarginata* subsp. *cuneiloba* in pinnatifid ventral scale appendages, the former can be readily distinguished from the latter by its present blackish median band, absent air-chamber in central dorsal surface of thallus and habitat. *M. pinnata* is usually found on soil-covered stone walls, whilst subsp. *cuneiloba* usually occurs on flat soil in anthropogenic regions.

Marchantia pinnato-appendiculata Steph. ex Hattori and *M. pinnatim-articulata* Steph. ex Hattori were invalidly published by Hattori (1952) as synonyms of *M. pinnata*. Since then, they have never been formally described. I was unable to locate their original materials from Stephani's collection in G. Although an illustration of *M. pinnato-appendiculata* was shown in Stephani's Icones Hepaticarum (Stephani 1985, n. 6515), less illustrated characters are insufficient to support giving a new synonymy. Taking this into consideration, I followed the synonymy of Hattori (1952) for the time being until their type specimens become available.

Specimens examined:
JAPAN. Kanagawa Pref.: Yokosuka City, Uragou-cho, *T. Yamaguchi 37665*. Zushi City, Ikego, *T. Yamaguchi 37824*, *38072*; Miyazaki Pref.: Nichinan City, Kusubara, *T.-X. Zheng 276*, *277*, Obi, *T.-X. Zheng 242*, *243*, *244*, *246*, *281*, *1063*, *1066*. Kushima City, Ohira, *T.-X. Zheng 1040*; Kagoshima Pref.: Kagoshima City, Korimoto, leg. *C. Mori s.n.* Kanoya City, Nishihara, *T.-X. Zheng 1072*. Kimotsuki Co., Nejimekawaminami, *T.-X. Zheng 1089*, *1090*, Shiromoto, *T.-X. Zheng 1078*. Kirishima City, Hayato-cho, Kareigawa, *T.-X. Zheng 2*, *213*, *1115*, *1465–1479*. Makizono-cho, Shimonagatsugawa, *T.-X. Zheng 214*, *216*, *217*. Shibushi City, Matsuyama-cho, Onomi, *T.-X. Zheng 1034*, Shibushi-cho, Uchinokura, *T.-X. Zheng 1046*, *1048*. Soo City, Takarabe-cho, Kitamata, *T.-X. Zheng 203*, *204*; Okinawa Pref.: Nakagami Co., Ogusuku, *T. Yamaguchi 10297*. Yaeyama Co., Iriomote, *T. Yamaguchi 1924*, *1925*, Yonaguni, *T. Yamaguchi & T. Seki 4524*.
Distribution: Kanagawa, Miyazaki, Kagoshima and Okinawa (**Figs. 3.10**).
Habitat: On soil in shaded or anthropogenic area.

5 ***Marchantia polymorpha* L.** Spec. Pl. ed. 1: 1137. 1753.
Type: Dillenius, Hist. musc. Tab. 76, f. 6E-6F, ‘1741’ 1742 (lectotype), Dillenius, fol. 166 f. 6 (typotype: OXF, *non vidi*).

Description
Thallus yellowish green to dark green; margin lobulate, hyaline to brown. *Epidermal pores* 23.5–74.1 μm in diam., bordered by 4–6 cells; inner opening cruciate, sometimes nearly quadrangular or pentacle-shaped, bounded by cells with processes on inner wall. *Compact ventral tissue* 8–14 cells layered in median portion; central part yellowish to brown; sclerotic cells absent; oil-cells numerous, yellowish to brown. *Ventral surface* yellowish green to dark green, brown or purplish; scales extending over entire surface. *Ventral scales* in 6 rows; median scales hyaline to lightly purplish; appendage circular to reniform, hyaline to purplish, sometimes darken from center toward to marginal part; oil-cells present. *Cupule* ciliate lobed, hyaline; apex usually hyaline to yellowish, sometimes slightly purplish in old plant; oil-cells numerous. *Gemmae* yellowish green to dark green, circular to ellipsoidal; surface smooth; marginal cell with thin wall; mucilage hair present. Dioicous. *Antheridiophore* stalk 7–17 mm long, with 2 rhizoid furrows; band of air-cavities absent; scale surrounding base of stalk wide ligulate to nearly semicircular, yellowish to brown, sometimes reddish to purplish; receptacle 5–11 mm in diam., usually

symmetric, shallowly dissected into 6–9 lobes; lobe thinning out from middle toward to margin; apex of lobe obtuse, usually emarginate; margin entire or crenulate, sometimes crisped, usually inflexed toward the dorsal side of lobe; median scale long ligulate, hyaline to brown, seldom reddish in lower margin, with entire to crenulate margin.

Archegoniophore stalk 11–65 mm long, with 2 rhizoid furrows, band of air-cavities present; scales surrounding base of stalk wide ligulate, hyaline to light brown; receptacle 6.5–11 mm in diam., dissected into 8–12 rays; rays rod-like shaped, slightly clavate; median scales hyaline to reddish, filiform, 1–4 celled wide in apex part; involucre hyaline to yellowish in young plant, brown in aged herbarium specimens, alternating with rays, with ciliate lobed margin; oil-cells numerous.

5a. subsp. ***polymorpha***

Figs. 3.11

Description *Thallus* growing erect, sometimes prostrate in dry environment, 6–14 mm wide, successively dichotomous 7–22 mm apart, with distinct and continuous dark median band on dorsal surface; air-chamber continuously absent in central dorsal surface of thalli. *Compact ventral tissue* sometimes with mucilage cavities. *Median scales appendage* (width : length = 1–1.53; 453–756 × 362–603 µm), with obtuse apex and entire or crenulate margin bordering with cells smaller than secondary outer layer cells. *Gemmae* (width : length = 0.58–0.95; 289–634 × 368–728 µm). *Antheridiophore* and *Archegoniophore* usually at apex of short lateral thallus branch; scales surrounding base of stalk with smooth or crenulate upper margin.

Taxonomical notes: *Marchantia polymorpha* subsp. *polymorpha* is characterized by (1) lobulate thallus margin, (2) distinct and continuous dark median band, (3) continuous air-chamber absence in central dorsal surface of thallus, (4) entire or crenulate margin of median scales appendage and (5) male and female receptacles usually at apex of short lateral thallus branch.

The valid inception of *Marchantia polymorpha s. lat.* was given by Linnaeus in 1753, in which three unnamed infraspecific taxa, α, β and γ were recognized due to the high morphological polymorphism in this complex. Nees von Esenbeck (1838) described 18 infraspecific taxa under *M. polymorpha s. lat*, however, corresponding specimens in his collection were either in bad condition or belong equivocally to his taxa and hence they are not able to support the taxonomic status of these names (Geissler & Bischler 1985; Bischler-Causse 1993). In 1943, through a cross-breeding experiment, Burgeff divided *M. polymorpha s. lat.* into three independent species based on Nee's names: *M. aquatica* (Nees) Burgeff, *M. polymorpha s. str.* and *M. alpestris* Nees. Among them, *M. aquatica* was defined to be with distinct and continuous dark median band on dorsal surface of thalli, *M. polymorpha s. str.* with discontinuous dark median band and *M. alpestris* without dark median band. *M. aquatica* resembles present subspecies best. Schuster (1992) also adopted this specific treatment. However, studies on chromosome number (Haupt 1932) and karyotype (Bischler 1986b) of *M. polymorpha s. lat.* did not provide significant variation to support the segregation of Burgeff (1943). In 1989, Boisselier-Dubayle and Bischler conducted electrophoretic analysis on *M. polymorpha s. lat.*, which proved the existence of three genetic groups in this complex and laid the foundation for subsequent establishment of three corresponding subspecies (Bischler-Causse & Boisselier-Dubayle 1991).

Later, due to (1) some illustration cited in original description of Linnaeus's "α" are similar to the plants which were called as *Marchantia aquatica* (Isoviita 1970; Bischler-Causse & Boisselier-Dubayle 1991), (2) the first unnamed taxa "α" of *M. polymorpha* should be used as the basis for the application of the specific name (Isoviita 1970) and (3) absent original materials of "α" in Linnaeus's herbarium (Grolle 1976), Bischler-Causse and Boisselier-Dubayle (1991) newly treated present group as *M. polymorpha* subsp. *polymorpha* and selected Dillenian illustration (1741) as its lectotype.

Distribution: Miyagi (Zheng & Shimamura 2019c), Fukushima (Horikawa 1954, Katagiri et al. 2015, Kitagawa 1987, Nemoto et al. 2020), Nagano (Yoshidomi et al. 2020), Gifu (**Figs. 3.12**).

Habitat: Growing on wet soil in marsh land or stone near the stream, seldom on wet concrete.

Specimens examined:

JAPAN. Miyagi Pref.: Kurihara City, Kurikomanumakura, *T.-X. Zheng 491*; Fukushima Pref.: Minamiaidu County, Hinoemata-mura, *Y. Sakamoto 1182*, *1183*, Shirasuna-Marsh, *S. Nemoto 840*, *970*, *T.-X. Zheng 431*, *432*, *433*, *434*, *436*, *437*; Niigata Pref.: Uonuma City, Ozagahara, *E. Ozasa 1*, *2*, *H. Ando 9142*, *9143*, *T. Katagiri 3890*, *3891*, *3892*, *Y. Horikawa 15073*, *Y. Inoue 3032*, *Y. Sakamoto 1204, 1205*, *1206*, *1207*, *1208*, *1209*, *1210*; Nagano Pref.: Adumino City, Hotaka, *T.-X. Zheng 1564*, *1565*, *1566*, *1567*. Kamiina Co., Hiraide, *T.-X. Zheng 1317*, *1318*, *1319*, *1320*, Ono, *T.-X. Zheng 1324*, Sawasoko, *T.-X. Zheng 1313*, *1314*, *1315*, *1316*. Kiso Co., Ogiso, *T.-X. Zheng 1321*, *1322*, *1323*. Kitaazumi Co., Hakuba-mura, *T.-X. Zheng 1268*, Kemi, *T.-X. Zheng 1291*, *1293*. Komagane City, Akaho, *T.-X. Zheng 1267*, Shimodaira, *T.-X. Zheng 1271*. Komoro City, Moro, *T.-X. Zheng 1308*, *1309*, *1310*, *1311*, *1312*. Matsumoto City, Nakayama, *T.-X. Zheng 1265*. Nakano City, Mayama, *T.-X. Zheng 1296*. Omachi City, Kitahara, *T.-X. Zheng 1292*, Taira, *T.-X. Zheng 1266*, *1270*, *Y. Matsuda 11041*. Shimoina Co., Yamabuki, *T.-X. Zheng 1263*, *1269*. Shimotakai Co., Kijimadaira-mura, *T.-X. Zheng 1298*, *1299*. Shiojiri City, Kisohirasawa, *T.-X. Zheng 1264*. Suwa City, Konami, *T.-X. Zheng 1287*, *1328*, *1329*, *1330*, Toyota, *T.-X. Zheng 1331*. Suzaka City, Yonako-cho, *T.-X. Zheng 1325*, *1326*. Toumi City, Agata, *T.-X. Zheng 1440*, *1441*; Gifu Pref.: Takayama City, Nyukawacho-Gonbou, *T.-X. Zheng 1574*, Shinosannno-machi, *T.-X. Zheng 1576*, *1577*, *1578*, *1580*, *1581*.

5b. subsp. ***ruderalis*** Bischl. et Boisselier, J. Bryol. 16: 364. 1991. Type: FRANCE. Paris, rive droite du canal Saint Martin, quai de Valmy; muret du canal, pH 7, 3 juillet 1990, *Bischler & Boisselier 90169* (holotype: PC, *non vidi*; isotypes: G 120459!, BM, JE, NY *non vidi*).
= ***Marchantia fauriana*** Steph. in Bonner, Candollea 14: 106. 1953. Type: JAPAN. Sapporo, *Faurie 1923* (holotype: G 265197!).
= ***Marchantia vaginata*** Steph. Spec. Hep. 1: 194. 1899. Type: JAPAN. Yezo, Sapporo, *Faurie 263* (lectotype: G 47478!).

Figs. 3.13

Description *Thallus* usually growing prostrate, 4–13 mm wide, successively dichotomous 4–13.8 mm apart, usually with discontinuous dark median band on dorsal surface. *Compact ventral tissue* without mucilage cavities. *Median scales appendage* (width : length = 0.93–1.5; 420–695 × 324–550 µm) with sharply unicellular toothed margin. *Gemmae* (width : length = 0.53–1.14; 192–690 × 292–719 µm); *Antheridiophore* and *Archegoniophore* usually at apex of thallus, scales surrounding base of stalk with unicellular toothed upper margin.

Taxonomical notes: This species shows a wide range of environment induced variation between population, particular in such characters as thallus orientation, width and length of thallus and blackish median band. When growing in dripping wet habitat, the plants often have an erect and robust thallus with distinct and continuous blackish median band on thallus and are sometimes difficult to distinguish from subsp. *polymorpha* based on these characters. However, subsp. *ruderalis* tends to have median scales appendage with unicellular toothed margin. In common anthropogenic region, subsp. *ruderalis* can be readily distinguished from subsp. *polymorpha* by discontinuous blackish median band and prostrate thallus. In Japan, separation of these two subspecies is also supported by geographical distribution: subsp. *polymorpha* is only distributed in central and northeastern Japan, whilst subsp. *ruderalis* can be readily found all around Japan except Okinawa.

Burgeff (1943) treated present subspecies as *Marchantia polymorpha s.str.*, a putative hybrid species between *M. aquatica* and *M. alpestris* due to its high morphological similarity to their resultant hybrids. This suspected hybrid origin was also adopted by Schuster (1992). In 1991, Bischler-Causse and Boisselier-Dubayle found that present subspecies, one of three genetic groups obtained in former electrophoretic study (Boisselier-Dubayle & Bischler 1989), was morphologically corresponding with Nees's form *M. polymorpha* f. *domestica* best among many previously described names and therefore Nees's name seems to be used for this group. However, due to the poor situation of Nees's specimens mentioned above, the name "*ruderalis*" was newly selected.

The postulation of its hybrid origin was not supported by isozyme electrophoretic (Boisselier-Dubayle & Bischler 1989), genetic (Boisselier-Dubayle et al. 1995) and recent molecular studies (Linde et al. 2020).

Notes on *Marchantia fauriana* Steph. and *M. vaginata* Steph. see Zheng (2021).

During the examination of herbarium materials, I happened to find a specimen collected from Hokkaido (*M. Nakao 6*) that highly resembles *Marchantia polymorpha* subsp. *ruderalis*. However, it differs from the latter only in ventral scale appendage with apiculate apex and sporadic multicellular tooth (Figure 3B). Due to the travel restriction during COVID-19, I am not able to conduct field trip at the locality shown on the specimen label and its adjacent area to collect additional materials for further research. Therefore, I prudently treat this taxon as an intrasubspecific variation of *M. polymorpha* subsp. *ruderalis*. Its taxonomic status will be discussed when more specimens become available.

Distribution: Widely distributed in Japan except Okinawa (**Figs. 3.14**).

Habitat: Often on soil, stone, gravel or wall of drainage channel in anthropogenic region.

Specimens examined:

JAPAN. Hokkaido: Asahikawa City, Kaguraokakouen, *M. Nakao 6*. Furano City, *H. Ando 3126*. Kawakami Co., Kussharo, *T.-X. Zheng 323*, *324*. Obihiro City, Higashiichijouminami, *T.-X. Zheng 321*, *322*. Okushiri Co., Yunohama, *T.-X. Zheng 450*, Tomisato, *T.-X. Zheng 451*, *452*. Sapporo City, Jouzankeionsennishi, *T.-X. Zheng 1333*. Teshio Co., Toyotomi-cho, *M. Higuchi 14129*; Aomori Pref.: Kuroishi City, Nuruyuha, *M. Nakao 16*, Nuruyutsuruizumi, *M. Nakao 17*. Towada City, Okuse, *M. Nakao 14*, *15*; Iwate Pref., Ichinoseki City, Kenbi-cho, *T.-X. Zheng 500*, *501*. Oshu City, Maesawa, *M. Nakao 21*; Miyagi Pref.: Kurihara City, Kurikomanumakura, *T.-X. Zheng 488*, *489*, Kouei, *T.-X. Zheng 471*, *472*, Osaki City, Orikoonsenshinyashiki, *M. Nakao 18*, *19*. Sendai City, Aramaki, *S. Nemoto 1014* (TI), Ichiban-cho, *T.-X. Zheng 453*, Katahira, *T.-X. Zheng 454*, *455*, *456*, *457*, *459*, *460*, *462*, Sakunami, *T.-X. Zheng 502*, *503*, *504*, *505*, *512*, *513*;

Akita Pref., Akita City, Shougunnohigashi, *T.-X. Zheng 319*, *320*. Yuzawa City, Takamatsu, *M. Nakao 20*; Fukushima Pref.: Aiduwakamatsu City, Yahata, *T.-X. Zheng 1428*, *1429*, *1430*. Date City, Ryouzen-machi, Ishida, *T.-X. Zheng 1407*, *1408*. Futaba Co., Namie-cho, *M. Nakao 8*. Iwaki City, Ogawa-machi, Kamiogawa, *T.-X. Zheng 1401*, *1402*. Kouriyama City, Ouse-machi, Kouzu, Nishizawa, *T.-X. Zheng 1336*, *1338*, *1339*, *1340*, Higashinagakura, *T.-X. Zheng 1344*, *1345*, *1346*. Minamisouma City, Haramachi Dist., Shimotakahira, *T.-X. Zheng 1404*, *1405*, *1406*, Odaka Dist., *M. Nakao 9*. Minamiaidu Co., Ouchi, *T.-X. Zheng 1433*, Takizawa *T.-X. Zheng 428*, *429*, *430*. Nihonmatsu City, Tazawa, *T.-X. Zheng 14*. Tamura Co., Ohmachi, *T.-X. Zheng 13*. Yama Co., *H. Ando 14902*, Hibara, *T.-X. Zheng 1420*, *1421*, Inawashiro-cho, *M. Nakao 7*, Sarashina, *T.-X. Zheng 438*, *439*, *440*, *441*, *442*, *443*, *444*, *445*, *446*; Ibaraki Pref.: Ishioka City, Kashiwabara, *T.-X. Zheng 769*, *770*. Kawaraya, *T.-X. Zheng 771*. Tsukuba City, Kannondai, *M. Nakao 29*, *30*, *31*; Tochigi Pref., Tochigi City, Souja-cho, *M. Nakao 33*. Utsunomiya City, *T.-X. Zheng 593*, *594*, *595*, *596*; Gunma Pref.: Maebashi City, *T.-X. Zheng 772*, *773*; Saitama Pref.: Tokorozawa City, *T.-X. Zheng 586*, *587*, *588*, *589*, *590*, *591*, *592*; Chiba Pref.: Kamogawa City, Kiyosumi, *T.-X. Zheng 55*, *169*. Futtsu City, Yamanaka, *T.-X. Zheng 58*, *59*; Tokyo: Hachiouji City, Takao-machi, *T.-X. Zheng 583*; Niigata Pref.: Tsubame City, Niibori, *T. Yamaguchi 36508*, *36510*; Ishikawa Pref.: Hakusan City, *H. Ando 26205*. Komatsu City, Hiyo-cho, *M. Itouga 4050*; Yamanashi Pref.: Hokuto City, Takanecho-Kiyosato, *T.-X. Zheng 1551*, *1552*; Nagano Pref.: Adumino City, Misatoyutaka, *T.-X. Zheng 1563*. Chino City, Tamagawa, *T.-X. Zheng 1286*. Higashichikuma Co., Sakai, *T.-X. Zheng 1294*. Iida City, *N. Nishimura 7441*. Ina City, Tomigata, *T.-X. Zheng 1272*. Matsumoto City, Adumi (Inekoki), *T.-X. Zheng 1568*. Minamisaku Co., Kaize, *T.-X. Zheng 1282*. Omachi City, Yasaka, *T.-X. Zheng 1277*. Shimotakai Co., Ougou, *T.-X. Zheng 1297*, *1300*, *1301*, *1302*, *1303*, *1304*, *1305*, *1306*. Suwa City, Konami, *T.-X. Zheng 1288*, *1289*, *1290*. Suzaka City, Shiogawa, *T.-X. Zheng 1327*. Ueda City, Mitakedou, *T.-X. Zheng 1307*, Sanadamachi-Osa, *T.-X. Zheng 1561*, *1562*; Gifu Pref.: Ena City, Akechi-cho, *M. Nakao 10*. Ono Co., Shirakawa, *T.-X. Zheng 1604*. Takayama City, Nyuukawa-cho, *H. Miyauchi 810*, *T. Yasuhara 2528*, *2594*, *T.-X. Zheng 1569*, Nyuukawacho-Gonbou, *T.-X. Zheng 1573*, *1575*, Okuhidaonsengou-Hirayuu, *T.-X. Zheng 1616*, Shimosannomachi, *T.-X. Zheng 1579*. Toki City, Jourinji, *M. Nakao 11*; Shizuoka Pref.: Fujinomiya City, Hara, *T.-X. Zheng 1549*, Inokashira, *T.-X. Zheng 1550*. Shizuoka City, Hirasawa, *T.-X. Zheng 1544*; Aichi Pref.: Inuyama City, Kitakoken, *M. Nakao 12*; Mie Pref.: Minamimuro Co., Sakamatsubara, *T.-X. Zheng 1542*. Tsu City, Ya-cho, *T.-X. Zheng 410*. Watarai Co., Sazaraura, *M. Nakao 13*; Shiga Pref.: Maibara City, Samegai, *T.-X. Zheng 1518*. Takashima City, Katsuno, *T.-X. Zheng 1514*; Osaka: Osaka City, Karita, *T.-X. Zheng 400*; Hyogo Pref.: Tanba City, Hikami-cho, Koura, *T.-X. Zheng 744*, *745*, *746*, Aogaki-cho, Touzaka, *T.-X. Zheng 749*, *750*, *751*, *752*, *753*; Nara Pref.: Yoshino Co., Nishigawa, *T.-X. Zheng 1496*; Tottori Pref.: Saihaku Co., Kamo, *T.-X. Zheng 716*, *717*. Tottori City, Kokufu-cho, Okudani, *T.-X. Zheng 735*, Miyanoshita, *T.-X. Zheng* 723, Saji-cho, Moritsubo, *T.-X. Zheng 765*, *766*, *767*, Takayama, *T.-X. Zheng 755*, *760*. Yonago City, Yodoe-cho, Takaidani, *T.-X. Zheng 711*, *712*; Okayama Pref.: Asakuchi City, Kosakahigashi, *M. Nakao 1*, *2*. Kurashiki City, Fujito-cho, Fujito, *M. Nakahara 2874*. Ibara City, Kurotada, *M. Nakao 3*. Souja City, Hiwa, *T.-X. Zheng 686*, *687*, *688*. Takahashi City, Takakura-cho, Iibe, *T.-X. Zheng 689*, *690*, *691*, *692*; Hiroshima Pref.: Hatsukaichi City, Tsuta, *T.-X. Zheng 925*. Higashihiroshima City, Kagamiyama, *T. Katagiri 3962*, *T.-X. Zheng 6*, *1619*, Fukutomi-cho, Kamidakeni, *M. Itouga 3693*, Saijo-cho, Jike, *T.-X. Zheng 1175*, *1176*, *1177*, *1178*, *1179*, Akitsu-cho, Kazahaya, *T.-X. Zheng 674*, *675*, *676*, *677*, Saijohon-machi, *T.-X. Zheng 992*. Hiroshima City, Aki Dist., Seno, *H. Ando 2345*, Minami Dist., Dannbara, *Y. Yano 724*, *725*, Hijiyamahon-machi, *Y. Yano 502*, Hiuna-cho, *Y. Yano 370*, Niho, *Y, Yano 372*, Naka Dist., *T. Yamaguchi 2311*, Eno-machi, *R. Yoshioka 755*, Kawara-machi, *Y. Yano 334*, Nobori-machi, *Y. Yano 753*, Teppo-cho, *Y. Yano 756*, Nishi Dist., Kanonhon-machi, *Y. Yano 253*, Saeki Dist., Egedani, *H. Miyauchi 1503*. Jinseki Co., Jinsekikougen-cho, *S. Ideshita 1294*, *1563*. Kure City, Shimokamagari-cho, *M. Higuchi 14900*, Ojizou, *M. Higuchi 15020*. Mihara City, Kui-cho, Sakaibara, *H. Deguchi 36887*. Otake City, *K. Ure 1294*, Moto-machi, *K. Une 2547*, Shin-machi, leg. *M. Iwata s.n.* (HIRO-1038706). Sera Co., Kouzan, *T.-X. Zheng 114*, *115*; Shoubara City, Toujou-cho, *T.-X. Zheng 137*, *138*, *139*, *140*, *141*, *142*, *314*. Yamagata Co., Kake, *M. Nakashima 2749*, Tsushimi, *T.-X. Zheng 180*; Yamaguchi Pref.: Hagi City, Horiuchi, *T.-X. Zheng* 574, *579*. Mine City, Shuuhou-cho, Akiyoshi, *T.-X. Zheng 423*, Beppu, *T.-X. Zheng 569*. Shimonoseki City, Ikurashin-machi, *M. Nakao 34*. Yamaguchi City, Kurokawa, *D. Takenaka 21*, *24*; Tokushima Pref.: Awa City, Sakuranooka, *M. Nakao 24*, *25*. Miyoshi City, Higashiiya, *M. Nakao 26*. Myouzai Co., Kamibun, *T.-X. Zheng 388*, *390*. Yoshinogawa City, Misatonakasuji, *T.-X. Zheng 385*, *386*; Kagawa Pref.: Kita Co., Ikenobe, *M. Nakao 22*. Takamatsu City, Yasuharakamihigashi, *M. Nakao 23*; Ehime Pref.: Kamiukena Co., Kuma, *T.-X. Zheng 1187*. Kita Co., Nakatado, *M. Nakao 27*. Niihama City, Tatsukawa-cho, *T.-X. Zheng 332*, *333*, *334*. Seiyo City, Shirokawa-cho, Oriai, *T.-X. Zheng 1188*, *1189*; Kochi Pref.: Agawa Co., Nanokawa, *T.-X. Zheng 342*, *348*. Kami City, Kahoku-cho, Birafu, *T.-X. Zheng 1207*. Kochi City, Eikokuji-cho, *T.-X. Zheng 366*, Tosayama, *T.-X. Zheng 1209*, *1210*, *1211*. Shimanto City, Warabiokakou, *T.-X. Zheng* 1193. Takaoka Co., Furuhatakou, *T.-X. Zheng 616*, *617*; Fukuoka Pref.: Tagawa Co., Mt. Hikosan, *S. Ideshita 309*. Yame City, Yabe-mura, Kitayabe, *T.-X. Zheng 1119*; Saga Pref.: Kanzaki City, Sefuri-machi, Haramaki, *T.-*

X. Zheng 1140; Nagasaki Pref.: Minamishimabara City, Fukae-cho, Kou, *T.-X. Zheng 1148*. Unzen City, Minamihon-machi, *T.-X. Zheng 1156*; Kumamoto Pref.: Aso Co., Kitazato, *T.-X. Zheng 985*. Nakamatsu, *T.-X. Zheng 1129*, Tateno, *T.-X. Zheng 1132*. Kikuchi City, Shigemi, *T.-X. Zheng 1125*. Kuma Co., Kounose, *T.-X. Zheng 416*; Oita Pref.: Beppu City, Noda, *T.-X. Zheng 563*, *564*. Bungoono City, Akamine, *M. Nakao 5*, Ono-machi, Tashiro, *T.-X. Zheng 287*. Hita City, Kamitsue-machi, Kaminoda, *T.-X. Zheng 1127*. Kusu Co., Mori, *T.-X. Zheng 550*, *976*. Nakatsu City, Kamiikenaga, *M. Nakao 4*. Yufu City, Yufuinn-cho, Kawakami, *T.-X. Zheng 556*; Miyazaki Pref.: Ebino City, Mukae, *T.-X. Zheng 1100*. Koyu Co., Kawakita, *T.-X. Zheng 262*, Kawaminami, *T.-X. Zheng 263*, Takewara, *T.-X. Zheng* 1016. Kushima City, Ohira, *T.-X. Zheng 1045*. Miyazaki City, Kiyotake-cho, Imaizumi, *T.-X. Zheng 1019*. Nichinan City, Obi, *T.-X. Zheng 282*, Saketani, *T.-X. Zheng 251*, *253*, *254*. Nishiusuki Co., Kuraoka, *T.-X. Zheng 998*, *999*. Nobeoka City, Kitakata-machi, Kawazuru, *T.-X. Zheng 1017*, Kitakawa-cho, Kawachimyou, *T.-X. Zheng 981*, *982*; Kagoshima Pref.: Hioki City, Ijuuin-cho, Koinohara, *T.-X. Zheng 1087*. Kagoshima City, Chuzan-cho, *T.-X. Zheng 1489*. Kimotsuki Co., Shiromoto, *T.-X. Zheng 1076*. Kirishima City, Kokubunchuuou, *T.-X. Zheng 1097*, Kirishimataguchi, *T.-X. Zheng 221*. Soo City, Takarabe-cho, Minamimata, *T.-X. Zheng 207*, *209*, Osumi-cho, Tsukino, *T.-X. Zheng 1031*.

6 ***Marchantia quadrata*** Scop. Fl. Carniol. ed. 2: 355. 1772. ≡ ***Preissia quadrata*** (Scop.) Nees, Naturgesch. Eur. Leberm. 4: 135. 1838. Type: Jugoslawien, Slowenien, Idria, 450m, substrato calcareo, *Leithe s.n.* (Kerner, Fl. Exs. Austro-Hung. no. 745. Wien. 1882). (neotype: M!; isoneotype: B, BM, K, G, H, PRC, *non vidi*)

Figs. 3.15

Description

Thallus grey green to dark green, slightly leathery, prostrate, 4.8–8.2 mm wide, dichotomies and apically ventral innovative; dark median band absent; margin crenulate, sometimes crinkled and inflexed toward the dorsal side; epidermal cell in single layer. *Epidermal pore* 25.94–54.42 μm in diam., bordered by 4–6 cells, inner opening cruciate, bounded by cells with processes on inner wall. *Compact ventral tissue* 20–28 cell layered in median portion; central part hyaline in young thalli and reddish to purplish in old thalli; sclerotic cells sometimes present, brown, reddish or purplish; mucilage cavities and oil-cells absent; *Ventral surface* green in apex part and purplish in old part; scales extending over 35–50% of width. *Ventral scales* in 2 rows; median scales reddish to purplish, seldom hyaline and with blackish margin in young plant; appendage fusiform to wide fusiform (width : length = 0.28–1.28; 59.71–210.77 × 187.56–346.41 μm), slightly reddish to purplish, seldom hyaline, with blackish margin in young plant; margin sinuous, crenulate or seldom irregularly unicellular toothed; oil-cells absent. *Asexual propagule* absent.

Monoicous. *Antheridiophore* at apex of thallus; stalk 3–6 mm long, with 2 rhizoid furrows; band of air-cavities absent; scale surrounding base of stalk absent; receptacle circular to oval, seldom nearly triangular, unlobed, yellowish green in young plant and dark brown in old plant; long axis 3–4.8 mm; margin hyaline to brown, smooth to crenulate, seldom incised, usually inflexed toward the dorsal side.

Archegoniophore at apex of thallus, stalk 30–45 mm long, with 2 rhizoid furrows; band of air cavities 2, interrupted; scale surrounding base of stalk absent; receptacle green to purplish brown, 4–6 mm in diam., nearly symmetric, very shallowly dissected into 4 downward lobes (depending on number of sporophyte) united by 4 convex radiating ridges on dorsal surface; lobe apex hyaline to yellowish, sinuous or irregularly incised; involucre hyaline to slightly yellowish, under the lobes, with entire or crenulate margin, without oil-cells.

Distribution: Hokkaido (Hattori 1957; Hattori & Shimizu 1955; Iwatsuki & Inoue 1972), Saitama (Hattori 1954; Inoue 1960; Tatuno 1955), Yamanashi (Takaki et al. 1970), Nagano (Hattori & Inoue 1959; Inoue 1960) and Tokushima (**Figs. 3.16**).

Habitat: On soil, boulder or wet limestone in alpine region.

Taxonomical notes: *Marchantia quadrata* Scop. can be readily distinguished from all other Japanese *Marchantia* taxa by (1) two rows of ventral scales, (2) monoicy, (3) apically ventral innovation of thallus, (4) unlobed male receptacle, (5) ridged female receptacle and (6) its alpine distribution.

In Japan, *Marchantia quadrata* was recorded under different names (Yamada & Iwatsuki 2006). Yoshinaga (1895, 1901), Stephani (1897) and Tatuno (1941) reported the present species as *Preissia commutata* (Lindenb.) Nees. Horikawa (1929) recorded it as *Chomiocarpon quadratus* (Scop.) Lind. In 1950, Horikawa pointed out its correct name *Preissia quadrata*, which was widely adopted in subsequent Japanese literature (Tatuno 1955; Hattori 1952, 1957; Hattori & Inoue 1959; Takaki et al. 1970; Mizutani 1984; Furuki & Mizutani 2004; Katagiri & Furuki 2012).

In 1985, with the description of subsp. *hyperborea* R.M.Schust. (Schuster 1985), subspecific treatment started to be introduced to *Marchantia quadrata* (Caners 2016; Schuster 1992). However, this classification is consistently noted with “knowledge problem” in recent liverwort checklists (Söderström et al. 2015, 2016) and not accepted universally (Abudurusuli & Erol 2020; Andrejeva et al. 2009; Cérgio & Carvalho 2003; Grolle & Long 2000; Hodgetts et al. 2020; Katagiri & Furuki 2018; Long & Crandall-Stotler 2020; Paton 1999; Şimşek et al. 2014). Furthermore, according to the original description (Schuster 1985) and additional notes (Schuster 1992), subsp. *quadrata* was defined mainly as dioicous and subsp. *hyperborea* was autoicous. However, in subsequent enzyme polymorphism analysis of *M. quadrata* (Boisselier-Dubayle & Bischler 1997), sexual condition was proved to be inappropriate as a diagnostic feature. Therefore, I adopt the specific treatment of *M. quadrata* in this revision.

Marchantia quadrata is a taxonomically peculiar species that is treated to hover between *Marchantia* and *Preissia* Corda. It was originally described as a species of *Marchantia* (Scopoli 1772), then transferred to *Preissia* (Nees von Esenbeck 1838) and recently replaced to *Marchantia* by Long et al. (2016). However, after our perusal of literature and specimen examination, I found that the evidence supporting the last treatment needs to be reviewed carefully.

Long et al. (2016) transferred *Preissia* to *Marchantia* as a new subgenus based on an earlier multi-loci phylogenetic analysis (Villarreal et al. 2016) in which *Preissia quadrata* was resolved in a maximally supported and separate clade that was deeply nested within the lineage of *Marchantia*. Furthermore, an unnamed taxon labeled as "*Marchantia* sp." was also nested in this *Preissia* clade, which seems to further support the inclusion of *Preissia* under *Marchantia*. However, this unknown taxon was not published until Long & Crandall-Stotler (2020), which was described as *Marchantia platycarpa* D.G. Long & Crand-Stotl. and its characters, such as absent asexual propagules, *Preissia*-like spore ornamentation, calcareous substrate and natural distribution clearly indicated that this new species is closely related to *Preissia* rather than *Marchantia*. Probably, Villarreal et al. (2016) misidentified this specimen as "*Marchantia* sp." in sampling of their phylogenetic research and Long et al. (2016) directly cited it as one of the evidences supporting his subgeneric treatment of *Preissia*.

Morphologically, Long et al. (2016) noted that "This synonymy is supported not only by molecular data, but also by the many shared morphological characters of these taxa". However, our specimen examination seems to support a contrary opinion that *M. quadrata* is a highly morphologically isolated species in *Marchantia*. Detailed morphological differences with other residual *Marchantia* taxa are listed in **Table 3.1**. Another two species of subg. *Preissia*, *M. romanica* (Radian) D.G.Long, Crandall-Stotler, L.L.Forrest & Villarreal and *M. platycarpa* will be discussed at some other time because their specimens are not available for present study.

Taking the above into consideration, the transfer of *Preissia* to *Marchantia* as a subgenus is worthy of careful re-consideration. Although, I still adopt the inclusion of *Preissia* to *Marchantia* in this revision and I believe that the status of subg. *Preissia* should be given in the future as a more appropriate interpretation.

It is reported that both monoicous and dioicous plants are observed in *Marchantia quadrata* (Haupt 1926; Paton 1999). Among them, monoicous group is usually found in Arctic while dioicous group are distributed in temperate-boreal region (Long & Crandall-Stotler 2020; Schuster 1972, 1985, 1992). However, according to our experience of intensive field work and examination of specimens, I found that all Japanese *M. quadrata* tend to be monoicous, which is contrary with the prevalent understanding. Here, I also noted a unique growth pattern of thallus observed in Japanese group and this pattern may explains that why so-called dioicous groups were considered common in temperate-boreal area. In spring, thalli with young antheridiophore usually apically initiates from the ventral side of previous thalli with well-stalked female receptacle. In summer, new thallus with archegoniophore occurs in the same way from the underside of the chip of previous thalli with a well-stalked male receptacle and the oldest archegoniophore withers. However, in *M. quadrata*, the stalk of female receptacle does not begin to elongate until the maturity of sporophyte in next spring (Haupt 1926). Therefore, during this period and early spring, the plant seems to only have male or female receptacle, respectively. Moreover, in the neotype of present species, only archegoniophore are present, which may further lead taxonomists to consider *M. quadrata* dioicous.

In *M. quadrata*, it is also noted that (1) female receptacle randomly dissects into 2–5 lobes and (2) each involucre contains 1–multi sporophyte (Bischler 1998; Caners 2016; Schuster 1992). However, our morphological examination found that (1) the number of female receptacle lobes is not random but the same as the number of fertilized sporophyte and (2) each involucre only includes one sporophyte. To give a correct conclusion, careful anatomical research is necessary.

Specimens examined:

JAPAN. Hokkaido: Ashibetsu City, Ashibetsu, *T. Sato 1761*; Yamanashi Pref.: Minamiarupusu City, Ashitasuashikura, *T. Katagiri 2810*, *2820*, *2865*, *2866*, *2868*, *2869*, *2872*, *2873*, *T. Sato 423*, *427*, *429*, *501*, *679*, *755*, *841*, *860*, *885*; Nagano Pref.: Minamisaku Co., Yakoori, *T.-X. Zheng 1553*, *1554*, *1555*, *1556*, *1557*, *1558*, *1559*, *1560*. Shimoina Co., Kashio, *T. Sato 889*, *893*, Sanpukutouge, *T. Katagiri 754*, *2317*, *T. Sato 572*, *580*; Tokushima Pref.: Mima City, Koyadaira, *H. Deguchi 39122*.

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References

Abudurusuli, A. & Erol, O. 2020. Contribution to the liverwort flora of western Tian Shan Mountains. Anatolian Bryology 6: 8–18.

Alam, J., I. Ali, S. Karim, M. Islam & H. Ahmad. 2016. Check list of Anthocerophyta and Marchantiophyta of Pakistan and Kashmir. Plant Science Today 2: 226–236.

Amakawa, T. 1967. A preliminary list of Hepaticae of Ryukius. Biologia Fukuoka 7: 47–51.

Andrejeva, E. N., A. G. Bezgodov, E. A. Borovichev, M. V. Dulin & Yu. S. Mamontov. 2009. Checklist of liverworts (Marchantiophyta) of Russia. Arctoa 18: 1–64.

Arnell, S. 1963. Hepaticae of South Africa. Swedish Natural Science Research Council, Stockholm.

Bakalin, V. A., V. S. Nguyen & E. A. Borovichev. 2017. New liverwort records for Vietnam. Journal of Bryology 50: 68–73.

Bastos, C. J. P. 2008. Vegetative reproduction patterns in species of Lejeuneaceae (Marchantiophyta) and its taxonomic and ecological significances. Brazilian Journal of Botany 31: 309–315.

Bauhin, C. 1623. Pinax theatri botanici, sive Index in Theophrasti Dioscoridis, Phinii et Botanicorum qui a saeculo scipserunt opera.

Bertoloni, A. 1817. Opuscoli Scientifici d'una Società di Professori della Pontifical Università di Bologna 1: 242.

Bescherelle, E. 1892. Énumération des Hépatiques récoltées au Tonkin par M. Balansa et déterminées par M. Stephani. Revue Bryologique 19: 13–15.

Bescherelle, E. 1894. Énumération des Hépatiques récoltées par M. l'abbé Faurie au Japon et déterminées par M. Stephani. Revue Bryologique 21: 25–27.

Bischler, H. 1982. *Marcahntia* L.: morphologie sporale, gemination et rang taxonomique des sections *Marchantia* et *Chlamidium* (Corda) Nees. Cryptogamie, Bryologie, Lichénologie 3: 351–364.

Bischler, H. 1984. *Marchantia* L. The New World Species. Bryophytorum Bibliotheca 26: 1–228.

Bischler, H. 1986a. Geographic variation and species structure in *Marchantia paleacea* Bertol. Hikobia 9: 345–352.

Bischler, H. 1986b. *Marchantia polymorpha* L. *s. lat.* karyotype analysis. Journal of the Hattori Botanical Laboratoty 60: 105–117.

Bischler, H. 1987. The typification and synonymy of Japanese Marchantias described by Stephani. The Bryologist 331–336.

Bischler, H. 1989. *Marchantia* L.: Subg. *Chlamidium* (Nees) Bischl. sect. *Papillatae* Bischl sect. nov. en Asie et en Océanie. Cryptogamie, Bryologie, Lichénologie 10: 61–79.

Bischler, H. 1998. Systematics and evolution of the genera of the Marchantiales. Bryophytorum Bibliotheca 51: 1–201.

Bischler, H. & S. Piippo. 1991. Bryophyte flora of Huon Peninsula, Papua New Guinea. L. *Marchantia* (Marchantiaceae, Hepaticae). Annales Botanici Fennici 28: 277–301.

Bischler-Causse, H. 1989. *Marchantia* L., The Asiatic and Oceanic taxa. Bryophytorum Bibliotheca. 38: 1–317.

Bischler-Causse, H. 1993. *Marchantia* L. The European and African taxa. Bryophytorum Bibliotheca 45: 1–129.

Bischler-Causse, H. & M. C. Boisselier-Dubayle. 1991. Lectotypification of *Marchantia polymorpha* L. Journal of Bryology 16: 361–365.

Bischler-Causse, H., S. R. Gradstein, S. Jovet-Ast, D. G. Long & N. S. Allen. 2005. Marchantiidae. Flora Neotropica Monograph 97: 1–267.

Boisselier-Dubayle, M. C. & H. Bischler. 1989. Electrophoretic studies in *Marchantia polymorpha* L. Journal of the Hattori Botanical Laboratory 67: 297–312.

Boisselier-Dubayle, M. C. & H. Bischler. 1997. Enzyme polymorphism in *Preissia quadrata* (Hepaticae, Marchantiaceae). Plant Systematics and Evolution 205: 73–84.

Boisselier-Dubayle, M. C., M. F. Jubier, B. Lejeune & H. Bischler. 1995. Genetic variability in the three subspecies of *Marchantia polymorpha* (Hepaticae): isozymes, RFLP and RAPD markers. Taxon 44: 363–376.

Bonner, C. E. B. 1953. De Hepatics II. An unpublished section of volume 6 of Stephani's Species Hepaticarum: the genus *Marchantia*. Candollea 14: 101–112.

Borges, A. L. I. 2006. A taxonomic monograph of the genus Prionolejeunea (Lejeuneaceae, Jungermanniopsida). Cuvillier Verlag, Göttingen.

Bowman, J. L. 2016. A brief history of *Marchantia* from Greece to Genomics. Plant Cell Physiol. 57: 210–229.

Burgeff, H. 1943. Genetische Studien an *Marchantia*. Gustav Fischer, Jena.

Campbell, E. O. 1954. The structure and development of *Marchasta areolata* Camp. Transactions of the Royal Society of New Zealand 82: 249–262.

Caners, R. T. 2016. New records of the putative Arctic/ Sub-Arctic/ alpine liverwort *Preissia quadrata* ssp. *hyperborea* R.M. Schust. (Marchantiopsida, Marchantiaceae) in Canada. Evansia 33: 83–91.

Cavers, F. 1903. On asexual reproduction and regeneration in Hepaticae. New Phytologist 2: 121–133.

Cecília, S. & S. Carvalho. Annotated catalogue of Portuguese bryophytes. Portugaliae Acta Biologica 21: 5–230.

Chopra, R. S. 1938a. Notes on Indian hepatics, I. South India. Proceedings of Indian Academy of Sciences. Sect. B 7: 239–251.

Chopra, R. S. 1938b. Notes on Indian hepatics, II. Sikkim Himalayas and Bengal. Proceedings of Indian Academy of Sciences. Sect. B 8: 427–439.

Corda, A. J. C. 1829. Genera Hepaticarum. Pages 643–655. In P. M. Opiz, Beitraege zur Naturgeschichte. Prague.

Cox, C. J., B. Li, P. G. Foster, T. M. Embley & P. Civáň. 2014. Conflicting phylogenies for early land plants are caused by composition biases among synonymous substitutions. Systematic Biology 63: 272–279.

Crandall-Stotler, B., R. E. Stotler & D. G. Long. 2009. Phylogeny and classification of the Marchantiophyta. Edinburgh Journal of Botany 66: 155–198.

Dellenius, J. J. 1741. Historia muscorum in qua circiter sexcentae species veteres et novae ad sua genera relatae descriuntur et iconibus genuinis illustrantur cum appendice et indice synonymorum. Oxonii.

Eklund, D. M., M. Kanei, E. Flores-Sandoval, K. Ishizaki, R. Nishihama, T. Kohchi, U. Lagercrantz, R. P. Bhalerao, Y. Sakata & J. L. Bowman. 2018. An evolutionarily conserved abscisic acid signaling pathway regulates dormancy in the liverwort *Marchantia polymorpha*. Current Biology 28: 3691–3699.

Equihua, C. 1987. Diseminación de yemas en *Marchantia polymorpha* L. Cryptogamie Bryologie Lichenologie 8: 199–217.

Evans, A. W. 1910. Vegetative reproduction in *Metzgeria*. Annals of Botany 24: 271–303.

Evans, A. W. 1917. The American species of *Marchantia*. Transactions of the Connecticut Academy of the Arts and Sciences 21: 201–313.

Forrest, L. L., E. C. Davis, D. G. Long, B. J. Crandall-Stoler, A. Clark & M. L. Hollingsworth. 2006. Unraveling the evolutionary history of the liverworts (Marchantiophyta): multiple taxa, genomes and analyses. The Bryologist 109: 303–334.

Frey, W. & H. Kürschner. 2011. Asexual reproduction, habitat colonization and habitat maintenance in bryophytes. Flora 206: 173–84.

Friedman, W. E. & M. E. Cook. 2000. The origin and early evolution of tracheids in vascular plants: integration of palaeobotanical and neobotanical data. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 355: 857–868.

Fuchs, L., H. Füllmaurer, A. Meyer & V. R. Specklin. 1542. De historia stirpium commentarii insignes. In officina Isingriniana, Basilae.

Furuki, T. 2012. Wonderful moss world, 10. Marchantiaceae (Hepaticae). Bryological Research 10: 268–270.

Furuki, T. & M. Mizutani. 2004. Checklist of Japanese Hepaticae and Anthocerotae, 2004. Bryological Research 8: 296–316.

Furuya, T., K. Hattori, Y. Kimori, S. Ishida, R. Nishihama, T. Kohchi & H. Tsukaya. 2018. ANGUSTIFOLIA contributes to the regulation of three-dimensional morphogenesis and cortical microtubule orientations in the liverwort *Marchantia polymorpha*. Development 145: dev161398.

Gao, C. & K.-C. Chang. 1982. Genus nova bryophytarum. Bulletin of Botanical Research 2: 113–121.

Gao, C., G.-C. Zhang & T. Cao. 1981. Taxa Nova Bryophytarum Tibeticarum. Acta Botanica Yunnanica 3: 389–399.

Geissler, P. & H. Bischler. 1985. Index Hepaticarum vol. 10. Cramer, Vaduz.

Gottsche, C. M., J. B. W. Lindenberg & C. G. Nees von Esenbeck. 1846. Synopsis hepaticarum, fasc. 4. Meissner, Hamburg.

Gradstein, S. R. & D. P. da Costa. 2003. The Hepaticae and Anthocerotae of Brazil. New York Botanical Garden Press, New York.

Greuter, W., H. M. Burdet, W. G. Chaloner, V. Demoulin, R. Grolle, D. L. Hawks-Worth, D. H. Nicolson, P. C. Silva, F. A. Stafleu, E. G. Voss & J. McNeill. 1988. International Code of Botanical Nomenclature. Regnum Vegetabile 118, Königstein.

Griffith, W., 1849 Notulae ad plantas asiaticas. Part II. On the higher cryptogamous plants. C. A. Serrao, Calcutta.

Grolle, R. 1975. Miscellanea Hepaticologica 151–160. Lindbergia 3: 47–56.

Grolle, R. 1976. Verzeichnis der Lebermoose Europas und benechbarter Gebiete. Feddes Repertorium 87: 171–279.

Grolle, R. & D.G. Long. 2000. An annotated check-list of the Hepaticae and Anthocerotae of Europe and Macaronesia. Journal of Bryology 22: 103–140.

Growth-Malonek, M. & V. Knoop. 2005. Bryophytes and other basal land plants: the mitochondrial perspective. Taxon 54: 293–297.

Harris, B. J., C. J. Harrison, A. M. Hetherington & T. A. Williams. 2020. Phylogenomic evidence for the monophyly of bryophytes and the reductive evolution of stomata. Current Biology 30: 2001–2012.

Hässal de Menédez, G. G. 1962. Estudio de las Anthocerotales y Marchantiales de la Argentina. Opera Lilloana Vol. 7. Universidad Nacional de Tucumán, Argentina.

Hattori, S. 1944. Contributio ad Floram Hepaticaeum Astro-Kiushiuensem. Bulletin of the Tokyo Science Museum 11: 1–203.

Hattori, S. 1951. Contribution ad Floram Hepaticarum Yakusimensem, VI. Journal of the Hattori Botanical Laboratory 6: 7–23.

Hattori, S. 1952. Hepaticae of Shikoku and Kyushu, southern Japan (2). Journal of the Hattori Botanical Laboratory 8: 21–46.

Hattori, S. 1954. Hepaticae Japonicae Exsiccatae Ser. 1–6. Journal of the Hattori Botanical Laboratory 12: 76–90.

Hattori, S. 1955. Hepaticae of Hokkaidō. I. On the hepaticae of Southern Hidaka, with special reference to the hepaticae occurring on serpentine on Mt. Apoi. Journal of the Hattori Botanical Laboratory 15: 75–92.

Hattori, S. 1957. Hepaticae of Hokkaido. II. Rishiri and Rebun Islands. Journal of the Hattori Botanical Laboratory 18: 78–92.

Hattori, S. 1966. Bryophyta. Pages 501–591. In: H. Hara, The Flora of Eastern Himalaya. The university of Tokyo Press, Tokyo.

Hattori, S. & H. Inoue. 1959. Hepaticae of Shirouma Mountains, Middle Japan. Journal of the Hattori Botanical Laboratory 21: 104–117.

Hattori, S. & D. Shimizu. 1955. Marchantiales of Japan. IV. Journal of the Hattori Botanical Laboratory 14: 79–107.

Haupt, W. A. 1926. Morphology of *Preissia quadrata*. Botanical Gazette 82: 30–54.

Haupt, G. 1932. Beiträge zur Zytologie der Gattung *Marchantia* (L.) I. Zeitschrife für Induktive Abstammungs und Vererbungslehre 62: 367–428.

He-Nygren, X., A. Juslen, I. Ahonen, D. Glenny & S. Piippo. 2006. Illuminating the evolutionary history of liverworts (Marchantiophyta): Towards a natural classification. Cladistics 22: 1–31.

Herzog T. 1930. Marchantiales. In: Handel-Mazzetti H. Symbolae Sinicae 5. Hepaticae. Wien: Springer; p. 6.

Ho, B.-C. 2013. The liverworts genus *Marcahntia* L. (Marchantiophyta: Marchantiopsida) in Singapore, with a new specie record. Nature in Singapore 6: 187–190.

Hodgetts, N. G., L. Söderström, T. L. Blockeel, S. Caspari, M. S. Ignatov, N. A. Konstantinova, N. Lockhart, B. Papp, C. Schröck, M. Sim-Sim, D. Bell et al. 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. Journal of Bryology 42: 1–116.

Horikawa, Y. 1929. Studies on the Hepaticae of Japan. II. Science Reports of the Tohoku Imperial University, Ser. 4. 4: 395–429.

Horikawa, Y. 1930. Studies on the Hepaticae of Japan. III. Science Reports of the

Tohoku Imperial University, Ser. 4. 5: 623–650.

Horikawa, Y. 1934. Monographia Hepaticarum Australi-Japonicarum. Journal of Science of the Hiroshima University. Series B. Div 2, Botany 2: 101-325.

Horikawa, Y. 1939. Bryophyta. Pages 783–992. In Y. Asahina (ed.) Nippon Inkwasyokubutu Dukan. Sanseido, Tokyo.

Horikawa, T. 1950. Symbolae Florae Bryophytae Orientali-Asiae et Micronesiae XI. Hikobia 1: 30–36.

Horikawa, Y. 1954. Bryophytes of Oze District. Pages480-498. In Scientific Researches of the Ozegahara Moor (ed.), Scientific Researches of the Ozegahara Moor. Japan Society for the Promotion of Science, Tokyo.

Imura, S. 1994. Vegetative diaspores in Japanese mosses. J. Hattori Bot. Lab. 77: 177–232.

Imura, S. & Iwatsuki, Z. 1990. Classification of vegetative diaspores on Japanese mosses. Hikobia 10: 435–443.

Inoue, H. 1960. Studies in spore gemination and the earlier stages of gametophyte development in the Marchantiales. Journal of the Hattori Botanical Laboratory 23: 148–191.

Inoue, H. 1976. Illustrations of Japanese Hepaticae-2. Tsukiji Shokan, Tokyo.

Inoue, H. 1989. Taxonomic miscellany on hepatics (6). The Journal of Japanese Botany 64: 193–198.

Inoue, T. 1894. Tosa-koku san zenigoke-ka shokubutsu. Shokubutsugaku Zasshi 8: 291–293.

Inoue, Y. & H. Tsubota. 2014. On the systematic position of the genus *Timmiella* (Dicranidae, Bryopsida) and its allied genera, with the description of a new family Timmiellaceae. Phytotaxa 181: 151–162.

Inoue, Y., H. Tsubota, H. Kubo, S. Uchida, S. Mukai, M. Shimamura & H. Deguchi. 2011. A note on *Pottia intermedia* (Turner) Fürnr. (Pottiaceae, Bryopsida) with special reference to its phylogeny and new localities in SW Japan. Hikobia 16: 67–78.

Inoue, Y., H. Tsubota, H. Sato & T. Yamaguchi. 2012. Phylogenetic note on *Pachyneuropsis miyagii* T.Yamag. (Pottiaceae, Bryophyta). Hikobia 16: 221–228.

Isoviita, P. 1970. Dillenius' 'Historia Muscorum' as the basis of hepatic nomenclature, and S. O. Lindberg's collection of Dillenian bryophytes. Acta Botanica Fennica 89: 1–28.

Iwatsuki, Z. & H. Deguchi. 1981. Propagules found in *Isoterygium pohliaecarpum* and related species. Hikobia Supplement 1: 105–110.

Iwatsuki, Z. & H. Inoue. 1972. Bryophytes of the Hidaka mountains, Hokkaido, Northern

Japan. Journal of the Hattori Botanical Laboratory 36: 533–546.

Iwatsuki, Z. & M. Mizutani. 1972. Colored Illustrations of Bryophytes of Japan. Hoikusha, Osaka.

Katagiri, T. & T. Furuki. 2012. Checklist of Japanese liverworts and hornworts, 2012. Bryological Research 10: 193–210.

Katagiri, T. & T. Furuki. 2018. Checklist of Japanese liverworts and hornworts, 2018. Hattoria 9: 53–102.

Katagiri, T., Y. Sakamoto, Y. Inoue & M. Shimamura. 2015. *Marchantia polymorpha* L. subsp. *polymorpha* rediscovered in Japan after 60 years. Bryological Research 11: 120–122.

Katoh, K. & D. M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.

Kawamatsu, S. 1961. On the regeneration of *Marchantia tosana* Steph. Miscellanea Bryologica et Lichenologica 2: 111–115.

Kitagawa, T. 1987. *Marchantia polymorpha* var. *aquatica* found in Japan. Proveedings of the Bryological Society of Japan 4: 116–117.

Kobae, Y., R. Ohtomo, S. Morimoto, D. Sato, T. Nakagawa, N. Oka & S. Sato. 2019. Isolation of native arbuscular mycorrhizal fungi within young thalli of the liverwort *Marchantia paleacea*. Plants (Basel, Switzerland), 8: 142. doi: 10.3390/plants8060142.

Kürschner, H. & W. Frey. 2019. Liverworts, mosses and hornworts of Afghanistan-our present knowledge. Acta Musei Silesiae, Scientiae Naturales. 68: 11–24.

Kumar, S., G. Stecher & K. Tamura. 2016. Mega7 Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874.

Lai, M.-J., R.-L. Zhu & S. Chantanaorrapint. 2008. Liverworts and hornworts of Thailand: an updated checklist and bryofloristic accounts. Annales Botanici Fennici 45: 321–341.

Leebens-Mack, J. H., M. S. Barker, E. J. Carpenter, M. K. Deyholos, M. A. Gitzendanner, S. W. Graham, I. Grosse, Z. Li, M. Melkonian, S. Mirarab et al. 2019. One thousand plant transcriptomes and the phylogenomics of green plants. Nature 574: 679–685.

Lehmann, J. G. C. 1832. Novarum et minus cognitarum stirpium pugillus quartus. Meissner, Hamburg.

Lehmann, J. G. C. 1857. Novarum et minus cognitarum stirpium pugillus decimus. Meissner, Hamburg.

Léman, D. S. 1823. *Marchantia*. Pages 113–118. In: Cuvier, F. (ed.), Dictionnaire des Sciences Naturelles. 29. Levrault, Strasbourg & Le Normant, Paris.

Linde, A.-M., W. Sawangproh, N. Cronberg, P. Szövényi & U. Lagercrantz. 2020. Evolutionary history of the *Marchantia polymorpha* complex. Frontiers in Plant Science 11: 829 doi: 10.3389/fpls.2020.00829.

Lindley, J. 1836. A Natural System of Botany. Longman, London.

Linneaus, C. 1753. Species Plantarum, ed. 1. Laurentii Salvii, Holmiae, Stockholm.

Long, D. G. & B. J. Crandall-Stotler. 2020. *Marchantia platycarpa* (Marchantiopsida, Marchantiaceae), a new species from China. Nova, Hedwigia, Beiheft 150: 109–116.

Long, D. G. & R. Grolle. 1990. Hepaticae of Bhutan II. Journal of the Hattori Botanical Laboratory 68: 381–440.

Long, D. G., L. L. Forrest, J. C. Villarreal & B. J. Crandall-Stotler. 2016. Taxonomic changes in Marchantiaceae, Corsiniaceae and Cleveaceae (Marchantiidae, Marchantiophyta). Phytotaxa 252: 77–80.

Long, D. G. & S. C. K. Rubasinghe. 2014. Liverworts and Hornworts of Sri Lanka: a revised checklist. Ceylon Journal of Science (Bio. Sci.) 43: 1–36.

Lu, Y.-W. & S.-F. Huang. 2017. *Marchantia* L. (Marchantiaceae-Marchantiophyta) in Taiwan. Taiwania 62: 55–62.

Magohuku, T. & K. Yamada. 1964. Illustration of Hepaticae of the Ise-Jingû Area. Jingûsityô, Ise.

Makino, T. 1896. Tosa san zenigoke-ka shokubutsu rosshu. Shokubutsugaku Zasshi 10: p209.

Marchant, J. 1713. Nouvelle découverte des Fleurs et des Graines d'une Plante rangée par les Botanistes sous le genre du Lichen. In Histoire de l'Académie Royale des Sciences. Band 35, pp. 229–234. Académie des sciences, Paris.

Masuzaki, H., M. Shimamura, T. Furuki, H. Tsubota, T. Yamaguchi, A. M. Haji Mohamed & H. Deguchi. 2010. Systematic position of the enigmatic liverwort *Mizutania* (Mizutaniaceae, Marchantiophyta) inferred from molecular phylogenetic analyses. Taxon 59: 448–458.

Micheli, P. A. 1729. Nova Plantarum Genera, Florentiae.

Mirbel, C. F. B. de. 1835. Recherches anatomiques et physiologiques sur le *Marchantia polymorpha*, pour servir al'histoire du tissu cellulaire, de l'épiderme et des stomates. Mémoires de l'Académie Royale des sciences de l'Institut de France. 13: 337–373,

Mitten, W. 1865. On some species of Musci and Hepaticae, additional to the floras of Japan and the coast of China. Journal of the Linnean Society, Botany 8: 148–158.

Mitten, W. 1891. An enumeration of all species of Musci and Hepaticae recorded from

Japan. Transactions of Linnean Society of London. (Second series-Botany) 3 153–206.

Mizutani, M. 1984. Check list of Japanese Hepaticae and Anthocerotae. Proceedings of the Bryological Society of Japan 3: 155–163.

Mizutani, M. & S. Hattori. 1976. Hepaticae Japonicae exsiccatae ser. 1–20 alphabetical list of species. Journal of the Hattori Botanical Laboratory 40: 327–353.

Molisch, H. 1922. Pflanzenphysiologie als Theorie der Gärtnerei, Gustav Fischer, Jena.

Montagne, J. F. C. 1838. Centurie de plantes cellulaires exotiques Nouvelles (siute). Annales des Sciences Naturelles, Botanique (sér 2) 9: 38–57.

Montagne, J. P. F. C. 1843. Quatrième centurie de plantes cellulaires exotiques nouvelles. Annales des Sciences Naturelles Botanique, séries 2. 19: 238–266.

Naramoto, S., V. A. S. Jonesb, N. Trozzia, M. Sato, K. Toyooka, M. Shimamura, S. Ishida, K. Nishitani, K. Ishizaki, R. Nishihama, T. Kohchi, L. Dolan & J. Kyozuka. 2019. Lateral organ diversification in plants mediated by the ALOG protein family of transcription factors. PLOS Biology 17: e3000560

Nees von Esenbeck, C. G. 1838. Naturgeschichte der europäischen Lebermoose: mit besonderer Beziehung auf Schlesien und die Oertlichkeiten des Riesengebirgs. 4. Grass & Barth, Brreslau.

Nelson, J. M., D. A. Hauser, R. Hinson & A. J. Shaw. 2018. A novel experimental system using the liverwort *Marchantia polymorpha* and its fungal endophytes reveals diverse and context-dependent effects. New Phytologist. 217: 1217–1232.

Nemoto, S., T.-X. Zheng, M. Shimamura, T. Kurosawa & T. Ohmori. 2020. A new locality of *Marchantia polymorpha* L. subsp. *polymorpha* from Oze, Fukushima Prefecture, Japan. 12: 73–75.

Oguri, E., T. Yamaguchi, H. Tsubota & H. Deguchi. 2003. A preliminary phylogenetic study of the genus *Leucobryum* (Leucobryaceae, Musci) in Asia and the Pacific based on ITS and *rbcL* sequences. Hikobia 14: 45–53.

Okamura, S. 1908. Contributions to the studi of Japanese Bryophyta II. On the regeneration of the antheridial receptacles of *Marchantia* 1. The Botanical Magazine, Tokyo 22: 140–143.

Pächt, O. 1950. Early Italian nature studies and the early calendar landscape. Journal of the Warburg and Courtauld Institutes 13: 13–47.

Patiño, J. & A. Vanderpoorten. 2018. Bryophyte biogeography. Critical Reviews in Plant Sciences 37: 175–209.

Paton, J. A. 1999. The Liverwort Flora of the British Isles. Colchester: Harley Books.

Piippo, S. 1990. Annotated catalogue of Chinese Hepaticae and Anthocerotae. Journal of the Hattori Botanical Laboratory 68: 1–192.

Piippo, S., X.-L. He, T. Koponen, P. J. Redfearn Jr. & J.-X. Li. 1998. Hepaticae from Yunnan, China, with a checklist of Yunnan Hepaticae and Anthocerotae. Journal of the Hattori Botanical Laboratory. 84: 135–158.

Piippo, S. & T. Koponen. 2013. Bryophyte flora of Hunan Province, China. 16. Complex thalloids (Marchantiopsida, Hepaticae). Polish Botanical Journal 58: 179–192.

Qiu, Y.-L., L. Li, B. Wang, Z. Chen, V. Knoop, M. Growth-Malonek, O. Dombrovska, J. Lee, L. Kent, J. Rest, G. F. Estabrook, T. A. Hendry, D. W. Taylor, C. M. Testa, M. Ambros, B. Crandall-Stoler, R. J. Duff, M. Stech, W. Frey, D. Quandt & C. C. Davis. 2006. The deepest divergences in land plants inferred from phylogenomic evidence. Proceedings of the National Academy of Sciences of the United States of America 103: 15511–15516.

Qiu, Y.-L., L. Li, B. Wang, Z. Chen, O. Dombrovska, J. Lee, L. Kent, R. Li, R. W. Jobson, T. A. Hendry, D. W. Taylor, C. M. Testa & M. Ambrost. 2007. A nonflowering land plant phylogeny inferred from nucleotide sequences of seven chloroplast, mitochondrial, and nuclear genes. International Journal of Plant Sciences 168: 691–708.

Raddi, G. 1818. Novarum vel rariorum ex cryptogamia stirpium in agro florentino collectarum. Opuscoli Scientifici (Bologna) 2: 349–361.

Rambaut, A., M. A. Suchard, D. Xie & A. J. Drummond. 2014. Tracer v1.6 http://beast.bio.ed.ac.uk/Tracer

Reinwardt, C. G. C., C. L. Blume & C. G. Nees von Esenbeck. 1824. Hepaticae javanicae. Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosum 12: 181–238.

Renzaglia, K. S., J. C. A. Villarreal & D. J. Garbary. 2018. Morphology supports the setaphyte hypothesis: mosses plus liverworts form a natural group. Bryophyte diversity and Evolution. 40: 11–17.

Ronquist, F., M. Teslenko, P. Van Der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard & J. P. Huelsenbeck. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542.

Ruklani, N. C. S., S. C. K. Rubasinghe & D. G. Long. 2015. Morphological diversity of complex thalloid liverwort genera of Sri Lanka. Ceylon Journal of Science (Bio. Sci.) 44: 27–44.

Schiffner, V. 1894. Ueber exotische Hepaticae, hauptsächlich aus Java, Amboina und

Brasilien, nebst einigen morphologischen und kritischen Bemerkungen über *Marchantia*. Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum. 60: 219–316.

Schiffner, V. 1898. Expositio plantarum in itinere suo Indico annis 1893–1894 suscepto collectarum I. Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse 67: 153–203.

Schmidel, C. C. 1747. Icones Plantarum et analyses partium. Knorr, G. W. Nürnberg.

Schuster, R. M. 1972. Evolving taxonomic concepts in the Hepaticae, with special reference to Circum-Pacific taxa. Journal of the Hattori Botanical Laboratory 35: 169–201.

Schuster, R. M. 1985. Some new taxa of Hepaticae. Phytologia 57: 408–414.

Schuster, R. M. 1992. The Hepaticae and Anthocerotae of North America, Vol. 6. Field Museum of Natural History, Chicago.

Scopoli, J.A. 1772. Flora carniolica. Tom. II. Edition secunda. Joannis Pauli Karuss, Viennae.

Shaw, A. J., P. Szövényi & B. Shaw. 2011. Bryophyte diversity and evolution: windows into the early evolution of land plants. American Journal of Botany 98: 352–369.

Shimamura, M. 2012. An introduction to the taxonomy and morphology of *Marchantia polymorpha*. BSJ-Review 3: 84–113.

Shimamura, M. 2016. *Marchantia polymorpha*: Taxonomy, phylogeny and morphology of a model system. Plant Cell Physiol. 57: 230–256.

Shimamura, M., T. Hanada, M. Iwata & T. Kozuka. 2017. Unequal growth of gemmaling in *Marchantia paleacea* subsp. *diptera* (Marchantiophyta, Marchantiaceae). Hikobia 17: 187–191.

Shimizu, D. & S. Hattori. 1953. Marchantiales of Japan, I. Journal of the Hattori Botanical Laboratory 9: 32–44.

Şimşek, Ö., Canli, K. & Çetin B. 2014. *Preissia quadrata* (Marchantiaceae), new to the liverwort flora of Turkey. Phytologia Balcanica 20: 155–157.

Singh, D. & D. K. Singh. 2013. An appraisal of the genus *Marchantia* in India with a note on *Marchantia emarginata* subspecies *emarginata* in Indian Himalayan region. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences 83: 15–26.

Söderström, L., A. Hagborg & M. Konrat, S. 2015. Liverworts from the largest of the United States: a checklist for mainland Alaska. Arctoa 24: 327–361.

Söderström, L., A. Hagborg, M. Konrat, S. Bartholomew-Began, D. Bell, L. Briscoe, E. Brown, D. C. Cargill, D. P. Costa, B. J. Crandall-Stoler et al. 2016. World checklist of hornworts and liverworts. Phytokeys 59: 1–828.

Solly, J. E., N. J. Cunniffe & C. J. Harrison. 2017. Regional growth rate differences specified by apical notch activities regulate liverwort thallus shape. Current Biology 27: 1–11.

Souza-Chies, T. T., G. Bittar, S. Nadot, L. Carter, E. Besin & B. Lejeune. 1997. Phylogenetic analysis of Iridaceae with parsimony and distance methods using the plastid gene *rps4*. Plant Systematics and Evolution 204: 109–123.

Stamatakis, A. 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313.

Stephani, F. 1894. Hepaticae Chinenses. Mémoires de la Société des Sciences Naturelles et Mathematiques des Cherbourg 29: 207–228.

Stephani, F. 1897. Hepaticae Japonicae. Bulletin de l'Herbier Boissier 5: 76–108.

Stephani, F. 1899. Species Hepaticarum. George & Cie, Genève & Bale.

Stephani, F. 1985. Icones Hepaticarum (microfiche). Jardin Botanique Genève, IDC, Zug.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics-Theory and Methods 7: 13–26.

Suzuki, H. 1966. The germination of gemma in *Marchantia diptera* Mont. and *M. poylmorpha* L. The journal of Japanese Botany 41: 356–362.

Suzuki, H., C. J. Harrison, M. Shimamura, T. Kohchi & R. Nishihama. 2020. Positional cues regulate dorsal organ formation in the liverwort *Marchantia polymorpha*. Journal of Plant Research. 133: 311–321.

Suzuki, T., Y. Inoue, H. Tsubota & Z. Iwatsuki. 2013. Notes on *Aptychella* (Sematophyllaceae, Bryopsida): Yakushimabryum longissimum, syn. nov. Hattoria 4: 107–118.

Taberlet, P., L. Gielly, G. Pautou & J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Molecular Biology 17: 1105–1109.

Takaki, N., T. Amakawa, T. Osada & E. Sakuma. 1970. Bryophyte flora of Mt. Kaikoma, Mt. Senjo and Mt. Kitadake (Southern Japan Alps). Journal of the Hattori Botanical Laboratory 33: 171–202.

Tanabe, A. S. 2011. Kakusan4 and Aminosan: two programs for comparing nonpartitioned, proportional and separate models for combined molecular phylogenetic analyses of multilocus sequence data. Molecular Ecology Resources 11: 914–921.

Tatuno, S. 1941. Zytologische Untersuchungen über die Lebermoose von Japan. Journal of Science of the Hiroshima University Series B, Div. 2. 4: 73–187.

Tatuno, S. 1955. Chromosomen bei einigen Arten von Marchantiales aus Japan. Journal of the Hattori Botanical Laboratory 14: 109–112.

Thunberg, C. P. 1784. Flora Japonica. J. G. Mülleriano, Leipzig.

Tsubota, H., S. Ikeda, Y. Inoue, S. Uchida & S. Mukai. 2015. Current status of *Lysimachia sikokiana* Miq. (Primulaceae) in Hiroshima Prefecture, SW Japan. Hikobia 17: 81–88.

Tsubota, H., N. Nakao, T. Arikawa, T. Yamaguchi, M. Higuchi, H. Deguchi & T. Seki. 1999. A preliminary phylogeny of *Hypnales* (Musci) as inferred from chloroplast rbcL sequence data. Hikobia 7: 233–248.

Tsubota, H., K. Takahashi, M. Nakahara, H. Mohamed & H. Deguchi. 2005. A simple procedure for DNA isolation using small quantities of lichen thallus. Lichenology 4: 25–28.

Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawskworth, P. S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold et al. 2018. Internation Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). Koeltz Botanical Books, Glashütten.

Villarreal, J. C. A., B. J. Crandall-Stotler, M. K. Hart, D. G. Long & L. L. Forrest. 2016. Divergence times and the evolution of morphological complexity in an early land plant lineage (Marchantiopsida) with a slow molecular rate. New Phytologist 209: 1734–1746.

Voss, E. G., H. M. Burdet, W. G. Chaloner, V. Demoulin, P. Hiepko, J. McNeill, R. D. Meikle, D. H. Nicolson, R. C. Rollins, P. C. Silva & W. Greuter (eds.). 1983. International Code of Botanical Nomenclature. Regnum Vegetabile 111: 1–472.

Wickett, N. J., S. Mirarab, N. Nguyen, T. Warnow, E. Carpenter, N. Matasci, S. Ayyampalayam, M. S. Barker, J. G. Bruleigh, M. A. Gitzendanner et al. 2014. Phylotranscriptomic analysis of the origin and early diversification of land plants. Proceedings of the National Academy of Sciences of the United States of America 111: E4859–E4868.

Wickham, H. 2016. Ggplot2: Elegant graphics for data analysis. Springer, New York.

Xiang, Y.-L., L. Shu & R.-L. Zhu. *Marchantia longii* (Marchantiaceae), a new species from northwestern Yunnan, China. The Bryologist 119: 280–289.

Xiong, Y. & W. Cao. 2018. Bryophyte Flora of Guizhou China. Volume 3. Guizhou Science and Technology Publishing House, Guiyang.

Yamada, K. & Z. Iwatsuki. 2006. Catalog of the hepatics of Japan. Journal of the Hattori Botanical Laboratory 99: 1–106.

Yoshidomi, M., T.-X. Zheng & M. Shimamura. 2020. Discovery of male plants of *Marchantia polymorpha* L. subsp. *polymorpha* (Marchantiaceae, Marchantiophyta) in Japan. Hikobia 18: 105–108.

Yoshinaga, T. 1895. Liverworts of Prov. Tosa, ser. 2. The Botanical Magazine 9: 134–135.

Yoshinaga, T. 1898. Twenty-four species of liverworts from Prov. Tosa. The Botanical Magazines 12: 73–74.

Yoshinaga, T. 1900. Some liverworts of Prov. Tosa. The Botanical Magazine 14: 39–41.

Yoshinaga, T. 1901. On the liverworts of Prov. Iyo. The Botanical Magazine 15: 179–182.

Yoshinaga, T. 1903. Hepaticae of the Provinces Tosa and Nikkō. The Botanical Magazine 17: 37–39.

Yoshinaga, T. 1906. Hepaticae of the Provinces Kai and Tosa. The Botanical Magazine 20: 52–54.

Zheng, T.-X. 2021. Nomenclature notes and synonymy of four *Marchantia* L. (Marchantiaceae, Marchantiophyta) species in Asia. Phytotaxa 523: 116–118.

Zheng, T.-X., Y. Inoue & M. Shimamura. 2020. Morphology of gemmae, an overlooked taxonomic trait in the genus Marchantia L. (Marchantiaceae). The Bryologist 123: 601–610.

Zheng, T.-X. & M. Shimamura. 2019a. The gemma of *Marchantia pinnata* (Marchantiaceae, Marchantiophyta). Bryological Research 12: 1–5.

Zheng, T.-X. & M. Shimamura. 2019b. Morphological discrimination of the two subspecies of *Marchantia paleacea* Bertol. (Marchantiaceae, Marchantiophyta) and their geographical distribution patterns in Japan. Hikobia 18: 65–69.

Zheng, T.-X. & M. Shimamura. 2019c. A new locality of *Marchantia polymorpha* L. subsp. *polymorpha* (Marchantiaceae, Marchantiophyta) from Miyagi Prefecture, Japan. Hikobia 18: 61–64.

Zheng, T.-X. & M. Shimamura. 2020. *Marchantia papillata* Raddi subsp. *grossibarba* (Steph.) Bischl. (Marchantiaceae, Marchantiophyta) new to Japan. Hikobia 18: 93–96.

Zheng, T.-X. & M. Shimamura. 2022. Taxonomic re-evaluation of the Japanese *Marchantia* taxa belonging to sect. *Papillatae* of subg. *Chlamidium* (Marchantiaceae). The Bryologist

Tables & Figures

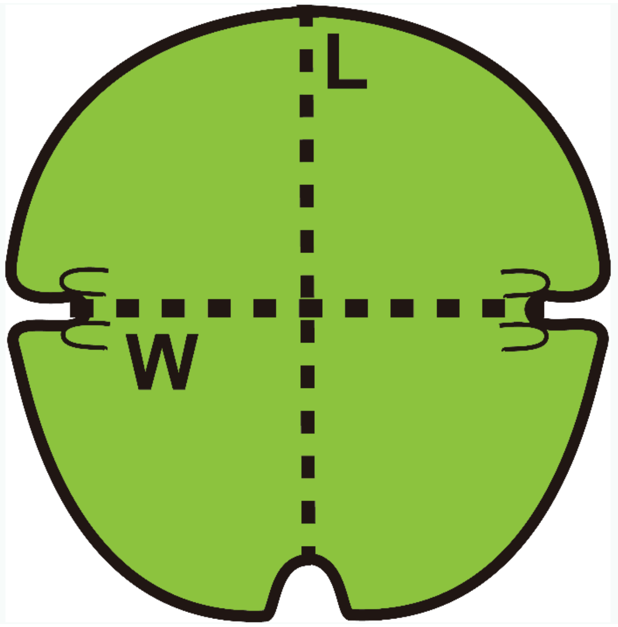


Fig. 1.1. Schemes of gemma measurement. The width (W) and length (L) were defined as the distance of two notches and the vertical line against the line for (W) from the trace of stalk respectively.

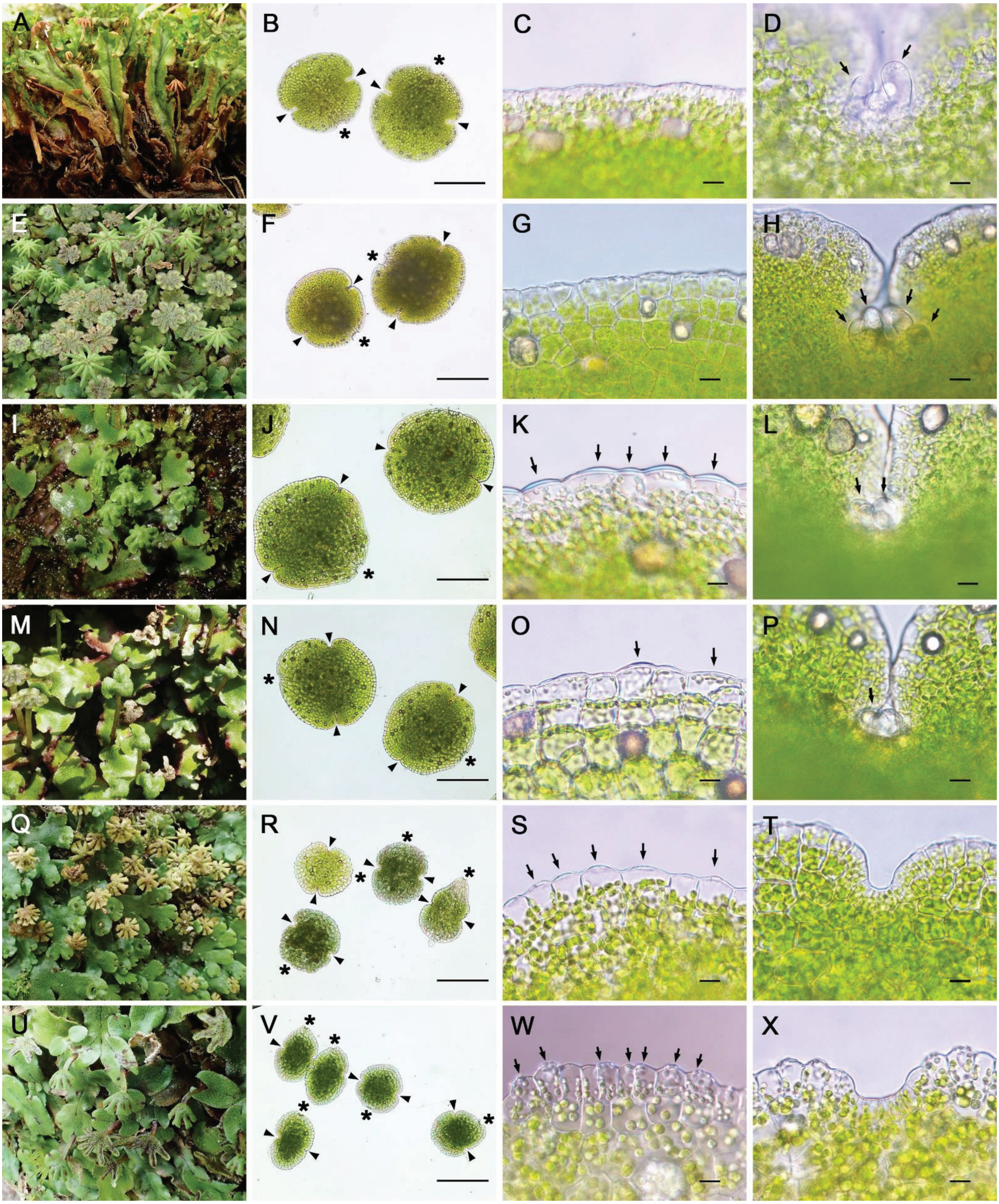


Fig. 1.2. Figure 2. The gemmae of *Marchantia* species. *M. polymorpha* subsp. *polymorpha* (A–D), *M. polymorpha* subsp. *ruderalis* (E–H), *M. paleacea* subsp. *paleacea* (I–L), *M. paleacea* subsp. *diptera* (M–P), *M. emarginata* subsp. *tosana* (Q–T) and *M. pinnata* (U–X). A,E,I,M,Q,U. Thalli. B,F,J,N,R,V. Entire shape of gemmae. Scales = 250 µm. C,G,K,O,S,W. Marginal cells. Scales = 10 µm. D,H,L,P,T,X. Notch. Scales = 10 µm. Asterisks: trace of stalk; Arrow heads: notches. Arrows in K,O,S,W: mamillae or papillae on marginal cell; Arrows in D,H,L,P: mucilage hairs covering notch.

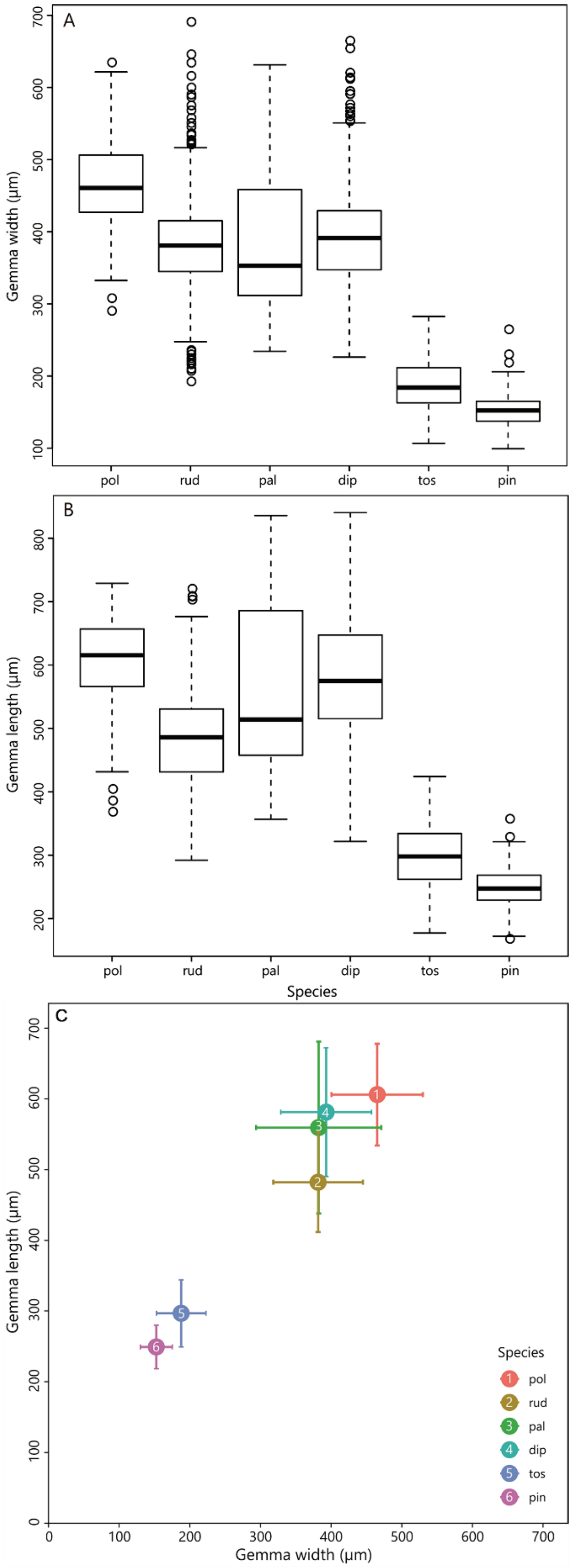


Fig. 1.3. Box plot of width (A), length (B) and scatter plot showing overall shape (C) of gemmae in six taxa of Japanese Marchantia. The maximum and minimum values in (A) and (B) are indicated as short horizontal bars out of the box respectively; upper and lower horizontal broad line of the box show 75th percentile and 25th percentile, respectively; median values are shown as bold line within the box; unfilled circles represent outliers. Scatter plot (C) showing overall width and length of each taxa without outlier. Error bars in (C) represent 61 standard deviation. pol: *Marchantia polymorpha* subsp. *polymorpha*, rud: *M. polymorpha* subsp. *ruderalis*, pal: *M. paleacea* subsp. *paleacea*, dip: *M. paleacea* subsp. *diptera*, tos: *M. emarginata* subsp. *tosana*, pin: *M. pinnata*.

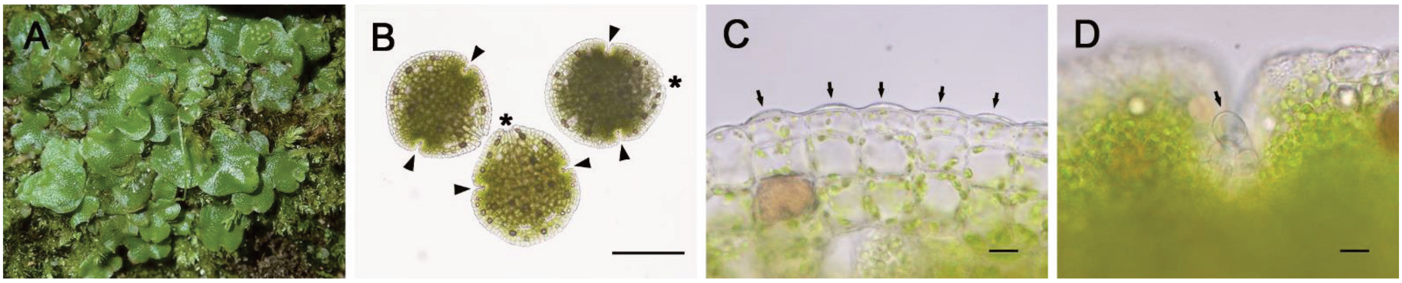


Fig. 1.4. *Lunularia cruciata*. A. Thalli. B. Entire shape of gemmae. Scales = 250 µm. C. Marginal cells. Scales = 10 µm. D. Notch. Scales = 10 µm. Asterisks: trace of stalk. Arrow heads: notches. Arrows in C: mamillae on marginal cell. Arrows in D: mucilage hairs covering notch.

Tab. 1.1 Morphology of gemmae in each taxon.

Taxa	Width (W) Mean ± S.D. (μm)	Length (L) Mean ± S.D. (μm)	Shape	Margin	Cell wall of marginal cells	Mucilage hair
M. polymorpha subsp. *polymorpha*	465.18±64.67	606.09±71.87	Nearly circular	Entire	Uniformly thin-walled	Present
M. polymorpha subsp. *ruderalis*	381.57±63.44	482.24±70.31	Nearly circular	Entire	Uniformly thin-walled	Present
M. paleacea subsp. *paleacea*	382.35±88.55	559.49±121.5	Nearly circular	Entire	Mamillose	Present
M. paleacea subsp. *diptera*	392.93±64.18	581.31±91	Nearly circular	Entire	Mamillose	Present
M. emarginata subsp. *tosana*	187.78±35.01	296.7±47.25	Ellipsoidal to obovate	Dentate	Mamillose	Absent
M. pinnata	152.56±22.53	249.1±30.72	Ellipsoidal to obovate	Dentate	Mamillose with small papillae	Absent
Lunularia cruciata	283.51±28.94	364.37±32.42	Nearly circular	Entire	Mamillose	Present

Fig. 1.5. Mucilage hairs covering notch of a germinating gemma in *Marchantia emarginata* subsp. *tosana*. Scales = 50 µm.

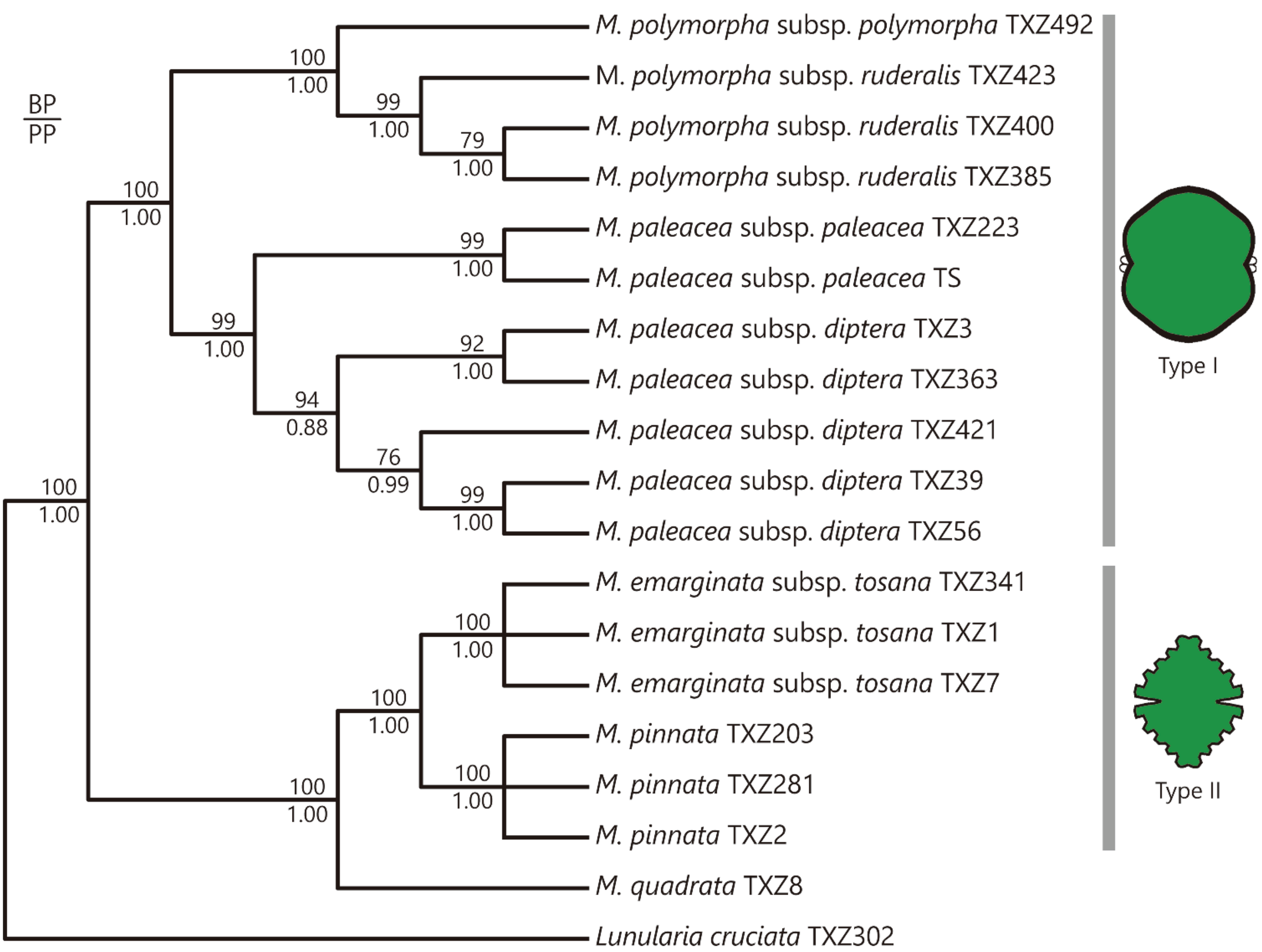


Fig. 1.6. Phylogenetic tree of the genus *Marchantia* based on concatenated sequences of *rbc*L, *rps*4, *trn*T-L-F and nrITS with supporting values (BP/PP).

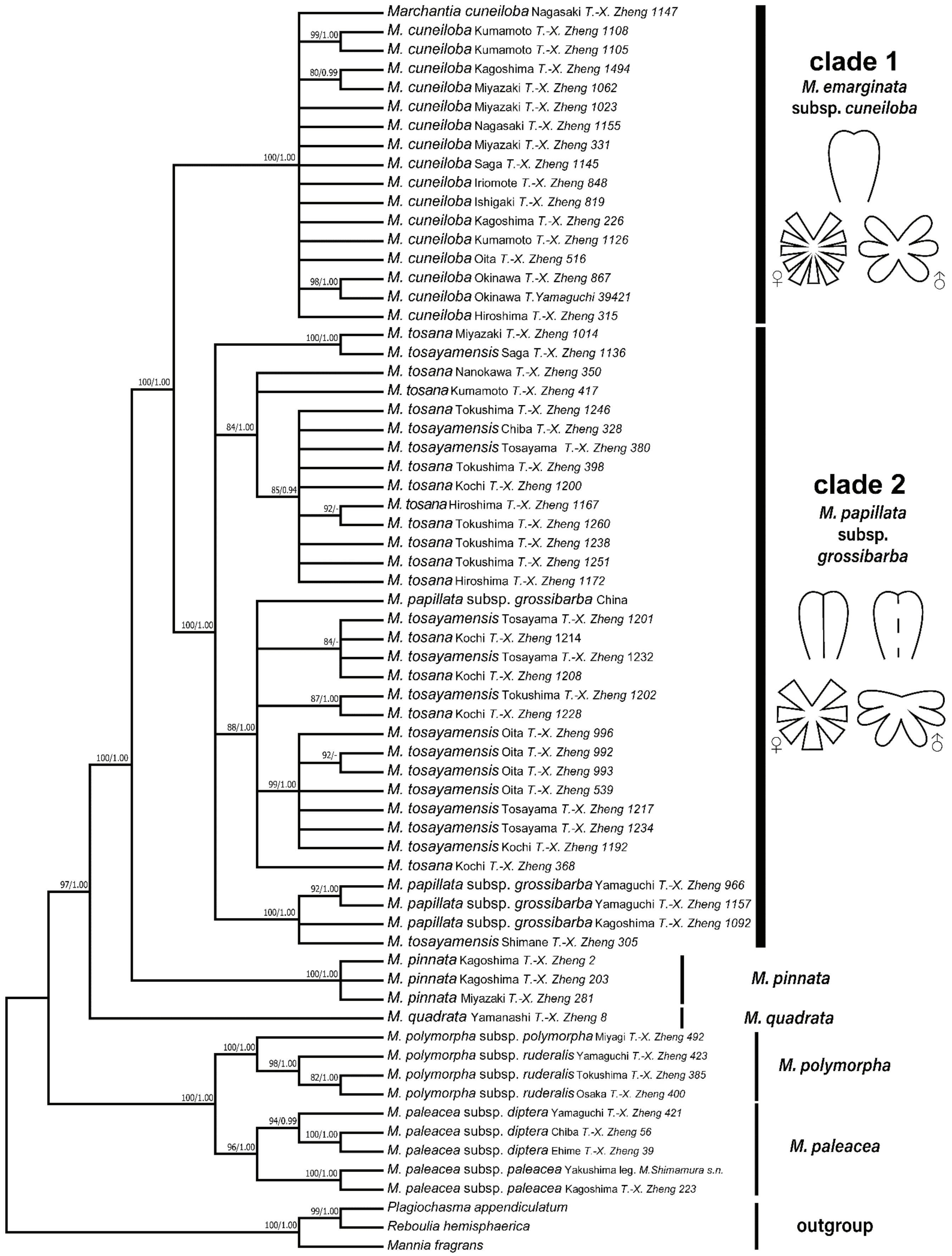


Fig. 2.1. Maximum likelihood tree based on concatenated *rbcL*, *rps4*, *trn*T-L-F and nrITS sequences depicted by an 80% condensed topology. Supporting values for bootstrap probabilities and Bayesian posterior probabilities (PP) are shown on each branch (BP/PP). The schematic diagrams indicate the thallus, male and female receptacle of the typical plants belonging to clade 1 and clade 2, respectively.

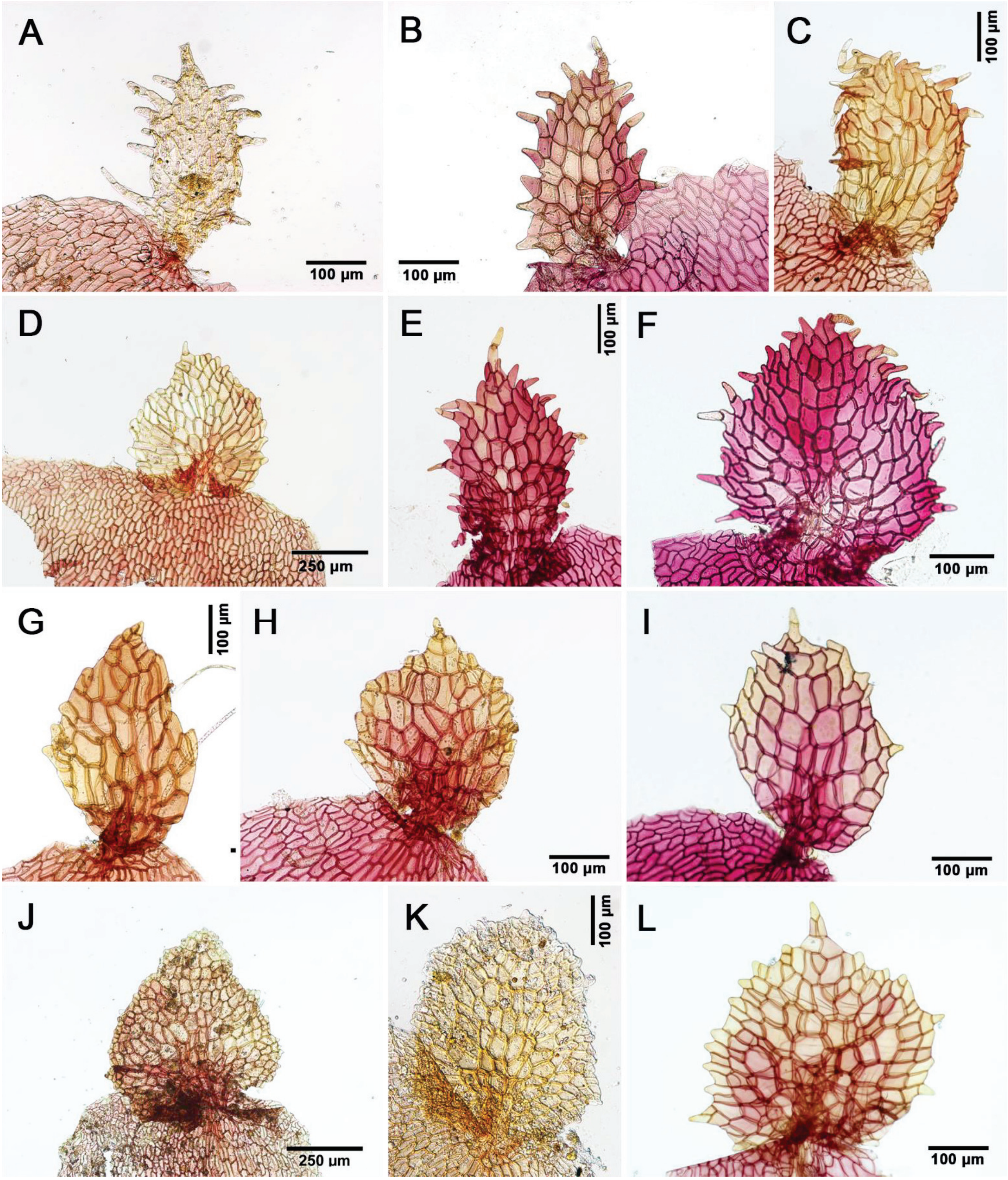


Fig. 2.2 Appendages of ventral scale. **A, B.** *Marchantia cuneiloba*. **C.** *M. radiata*. **D**–**F.** *M. tosana*. **G**–**I.** *M. tosayamensis*. **J**–**L.** *M. papillata* subsp. *grossibarba*. [A. *T. Makino 201* (holotype, G). B. *T.-X. Zheng 819*. C. *Y. Horikawa 3863* (neotype). D. *T. Inoue 5* (holotype, G). E. *T.-X. Zheng 1246*. F. *T.-X. Zheng 1208*. G, H**.** *Y. Tokihisa 105* (holotype, G). I. *T.-X. Zheng 996*. J. leg. *Delavay s.n.* (holotype, G). K. *W. Koelz 4420* (NICH). L. *T.-X. Zheng 1157*.]

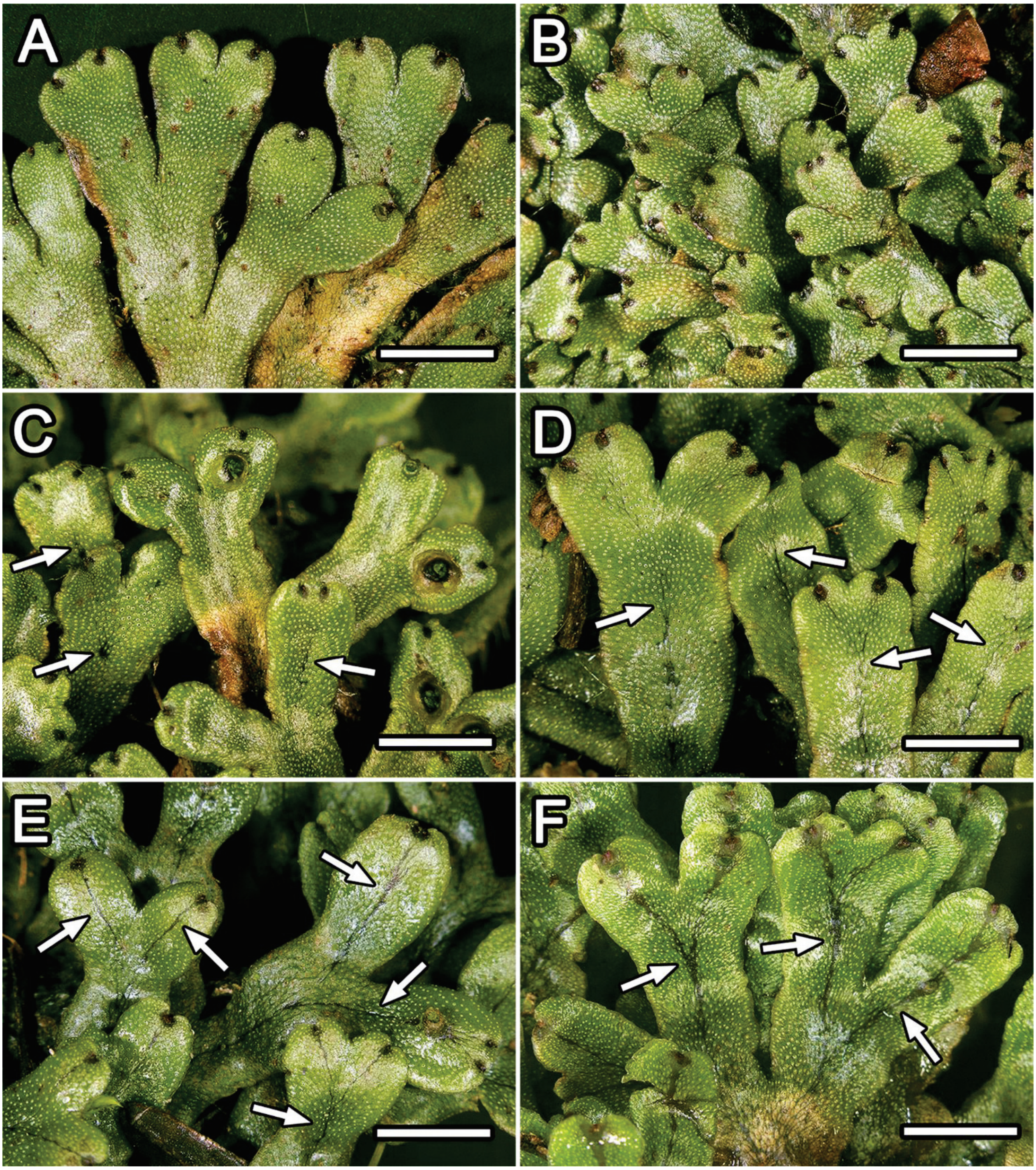


Fig. 2.3. Dorsal surface of thalli. **A, B.** *Marchantia cuneiloba*. **C, D.** *M. tosana*. **E.** *M. tosayamensis.* **F.** *M. papillata* subsp. *grossibarba*. Arrow indicates the dark median band. Scale bar = 5 mm. [A. *T.-X. Zheng 1062*. B. *T.-X. Zheng 1023*. C. *T.-X. Zheng 1172*. D. *T.-X. Zheng 1208*. E. *T.-X. Zheng 1232*. **F.** *T.-X. Zheng 1157*.]

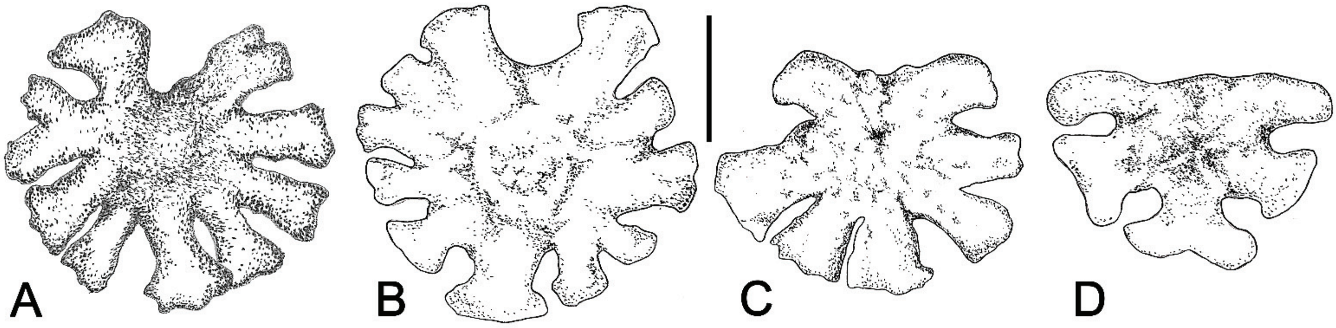
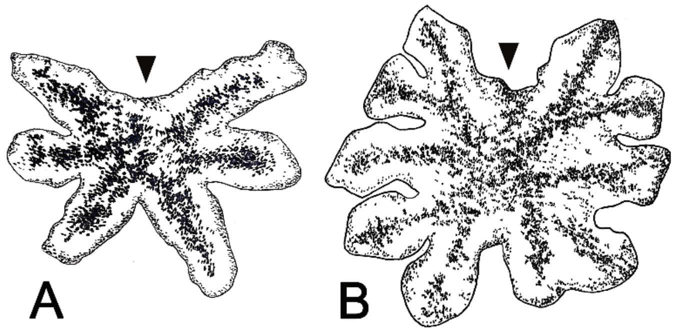


Fig. 2.4. Female receptacle. **A.** *Marchantia cuneiloba*. **B.** *M. radiata*. **C.** *M. tosana*. **D.** *M. tosayamensis*. Scale bar = 2 mm. [A. *T.-X. Zheng 1494*. B. *Y. Horikawa 3863* (neotype). C. *T.-X. Zheng 1208*. D. *Y. Tokihisa 105* (holotype, G).]



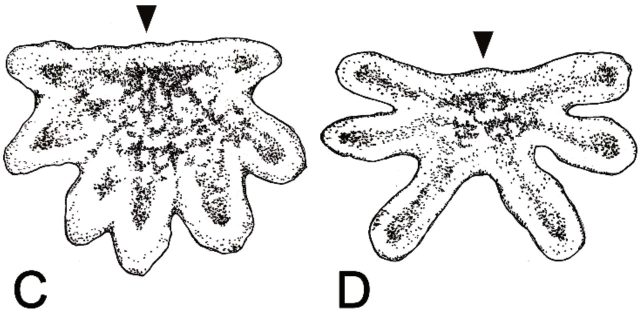


Fig. 2.5. Male receptacle. **A, B.** *Marchantia cuneiloba*. **C.** *M. tosana*. **D.** *M. tosayamensis*. [**A.** *T.-X. Zheng 1105*. **B.** *T.-X. Zheng 1075*. **C.** *T. Inoue 5* (holotype, G). **D.** *T.-X. Zheng 996*.]

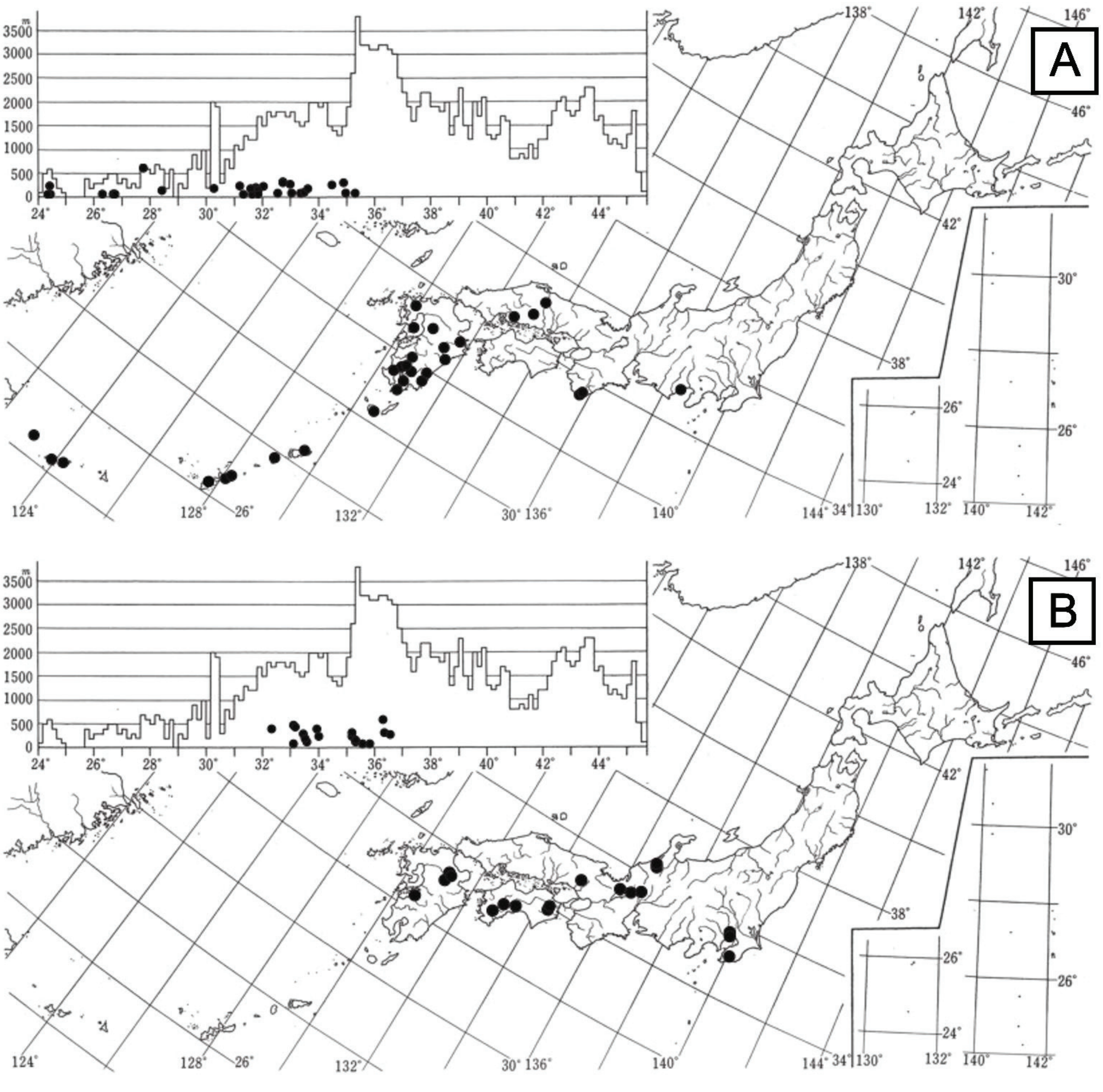


Fig. 2.6. Distribution map and vertical geographic ranges (inset) of the Japanese plants belonging to sect. *Papillatae*. **A.** *Marchantia cuneiloba*-*M. radiata*. **B.** *M. papillata* subsp. *grossibarba*-*M. tosana*-*M. tosayamensis*. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

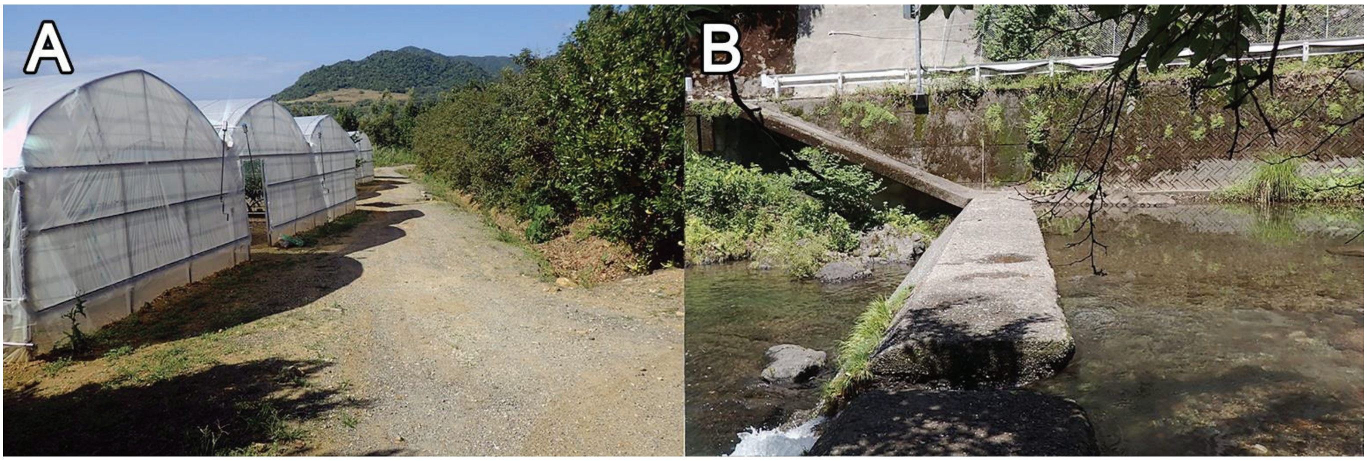


Fig. 2.7. Typical growing environment of the Japanese plants belonging to sect. *Papillatae*. **A.** Collection site of the *Marchantia cuneiloba* (*T.-X. Zheng 819*) growing on the soil of an orchard in Ishigaki Isl., Okinawa Prefecture. **B.** Collection site of the *M. tosayamensis* (*T.-X. Zheng 1217*) growing on a stone wall along the stream in Tosayama, Kochi Prefecture.

Tab. 2.1. Morphological, geographical and ecological differences between the Japanese taxa of sect. *Papillatae* Bischl.

Taxa	Margin of ventral scale appendages	Blackish median band on thalli	Number of female receptacle lobes	Basal sinus of male receptacle	Distribution	Ecological habitats
M. cuneiloba	Multicellular teeth	Absent	5–13	30–180°	Southern part of Japanese archipelago: Okinawa, South Kyushu Chugoku and along the south coast of Honshu Island.	On soil near the anthropogenically modified areas, seldom on boulder near natural stream or river
M. radiata	Multicellular teeth	Absent	5–13	–	Same as above	Same as above
M. tosana	Uni or multicellular teeth	Present, discontinuous	5–8	Nearly 180 °	North Kyushu, Shikoku, Chugoku and along the shore of Honshu Island, never in Okinawa	Damp areas, such as on boulders near streams and on the walls of artificial waterways
M. tosayamensis	Unicellular teeth	Present, continuous	5–8	Nearly 180 °	Same as above	Same as above
M. papillata* subsp. *grossibarba	Unicellular teeth	Present, continuous	–	–	Same as above	Same as above

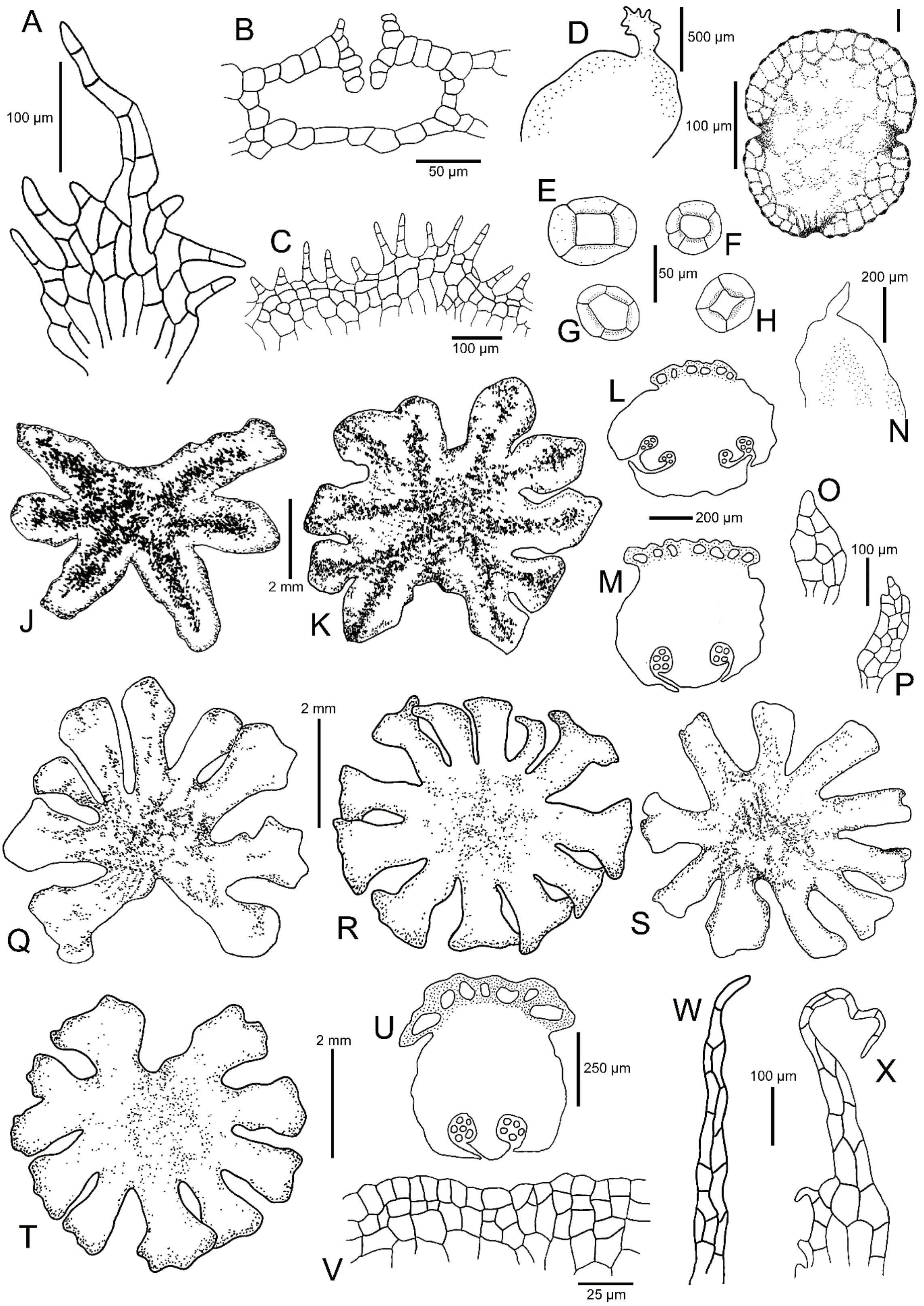


Fig. 3.1. *Marchantia emarginata* Reinw., Blume et Nees subsp. *cuneiloba* (Steph.) T.X.Zheng & M.Shimamura. **A.** appendages of ventral scales. **B.** cross section of air chamber. **C.** cupules. **D.** median ventral scales. **E–H.** inner opening of air pore. **I.** gemmae. **J, K.** male receptacles. **L, M.** section of antheridiophore stalk. **N.** median scales of male lobe. **O, P.** appendages of median scales of male lobe. **Q–T.** female receptacles. **U.** section of archegoniophore stalk. **V.** margin of involucre. **W, X.** scales of female receptacle, *T. Makino 201*, *T.-X. Zheng 1155*.

[**A, W.** *T. Makino 201*, holotype (G). **B.** *T.-X. Zheng 260*. **C, I.** *T.-X. Zheng 7*. **D.** *T.-X. Zheng 1536*. **E.** *T.-X. Zheng 1002*. **F.** *T.-X. Zheng 1019*. **G.** *T.-X. Zheng 1058*. **H.** *T.-X. Zheng 1547*. **J, M, N.** *T.-X. Zheng 1105*. **K, O, P.** *T.-X. Zheng 1075*. **L.** *T.-X. Zheng 205*. **Q.** *T.-X. Zheng 1029*.**R.** *T.-X. Zheng 1506*. **S.** *T.-X. Zheng 1028*. **T.** *T.-X. Zheng 1494*. **U, V.** *T.-X. Zheng 258*. **X.** *T.-X. Zheng 1155*.]

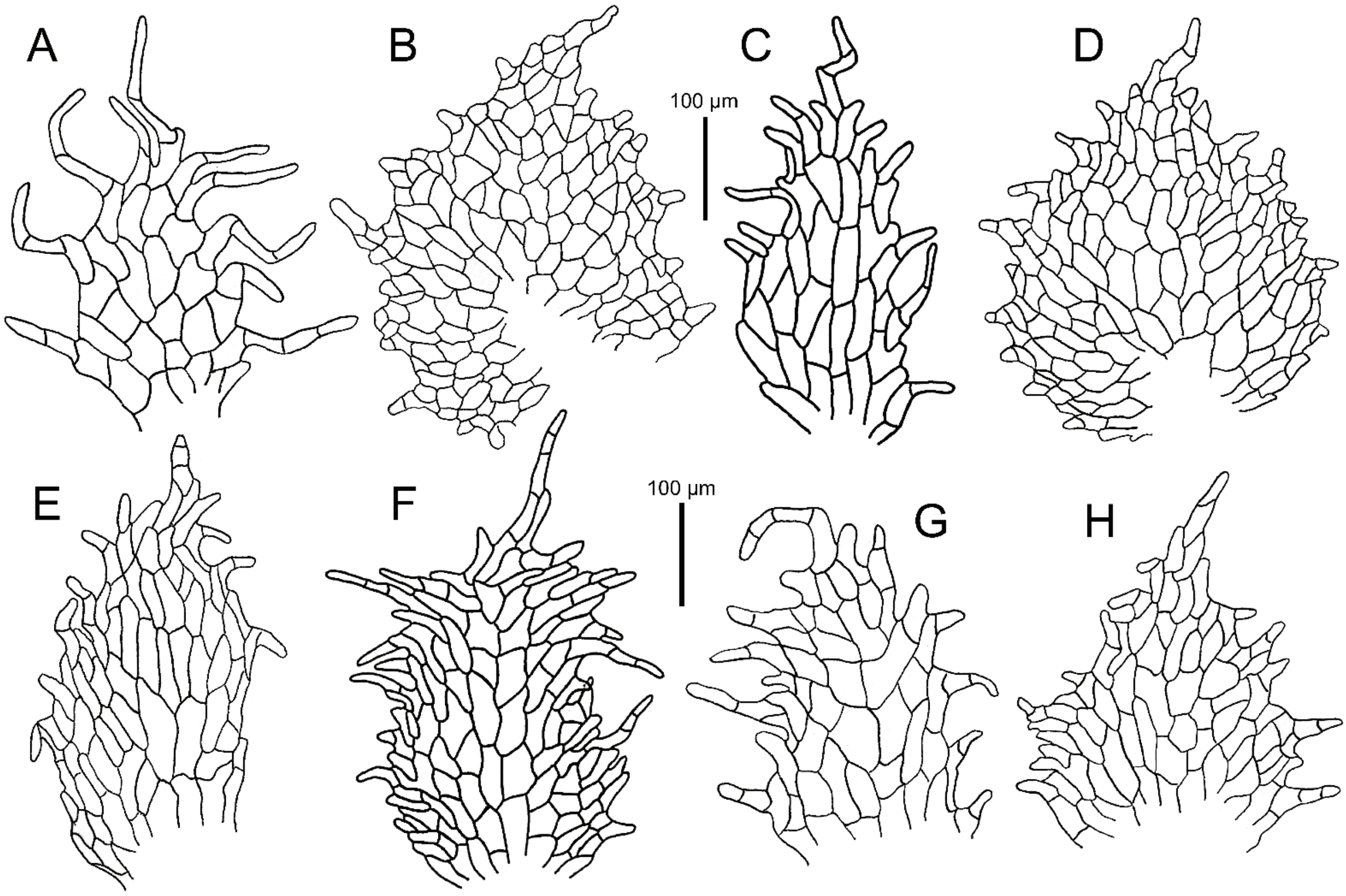


Fig. 3.2. Ventral scale appendages of *Marchantia emarginata* Reinw., Blume et Nees subsp. *cuneiloba* (Steph.) T.X.Zheng & M.Shimamura.

[**A.** *T.-X. Zheng 792*. **B.** *T.-X. Zheng 226*. **C.** *T.-X. Zheng 899.* **D.** *T.-X. Zheng 226*. **E.** *T. Yamaguchi 39467*. **F.** *T.-X. Zheng 1536*. **G.** *T.-X. Zheng 1528*. **H.** *T. Amano 8112* (NICH)]

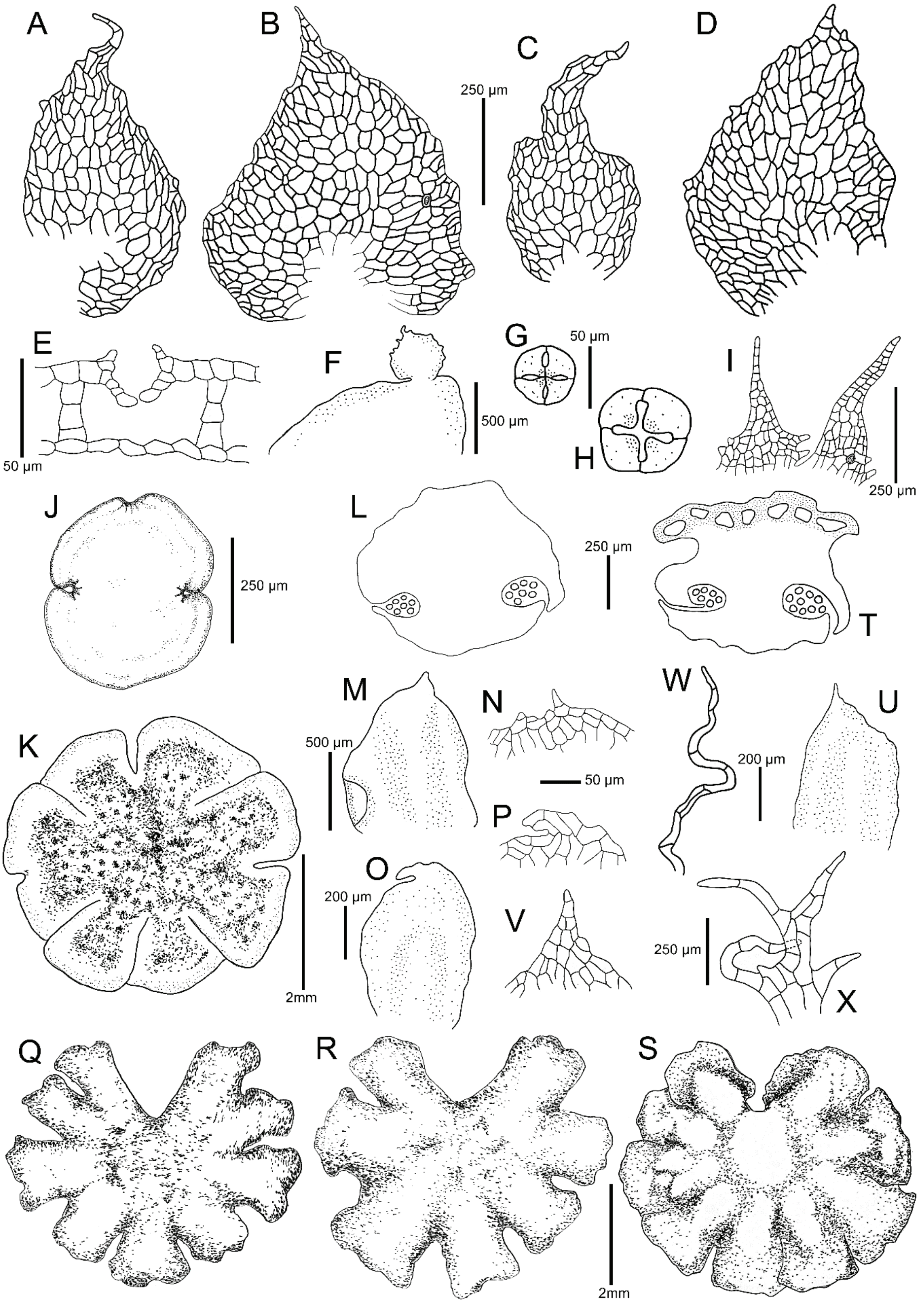


Fig. 3.3. *Marchantia paleacea* Bertol. subsp. *paleacea*. **A**–**D.** appendages of ventral scales. **E.** cross section of air chamber. **F.** median ventral scales. **G, H.** inner opening of air pore. **I.** cupules. **J.** gemmae. **K.** male receptacles. **L.** section of antheridiophore stalk. **M.** basal scales of antheridiophore stalk. **N.** apex of basal scales of antheridiophore stalk**. O.** median scales of male lobe. **P.** apex of median scales of male lobe. **Q**–**S.** female receptacles. **T.** section of archegoniophore stalk. **U.** basal scales of archegoniophore stalk. **V.** apex of basal scales of archegoniophore stalk. **W.** scales of female receptacle. **X.** margin of involucre.

[**A.** *T.-X. Zheng 1572*. **B.** *T.-X. Zheng 223*. **C.** leg. *M. Shimamura s.n.* **D.** *H. Ando 1396*. **E.** *T.-X. Zheng 484*. **F.** *T.-X. Zheng 1570*. **G, H.** *T.-X. Zheng 1601*. **I, J.** *T.-X. Zheng 223*. **K**–**P.** *H. Miyauchi 993*. **Q.** *T.-X. Zheng 1606*. **R.** *T.-X. Zheng 1607*. **S.** leg. *Inoue s.n.* **T.** *T. Sato 231*. **U, V.** *T. Katagiri 1645*. **W.** leg. *Inoue s.n*. **X.** *T. Sato 231*.]

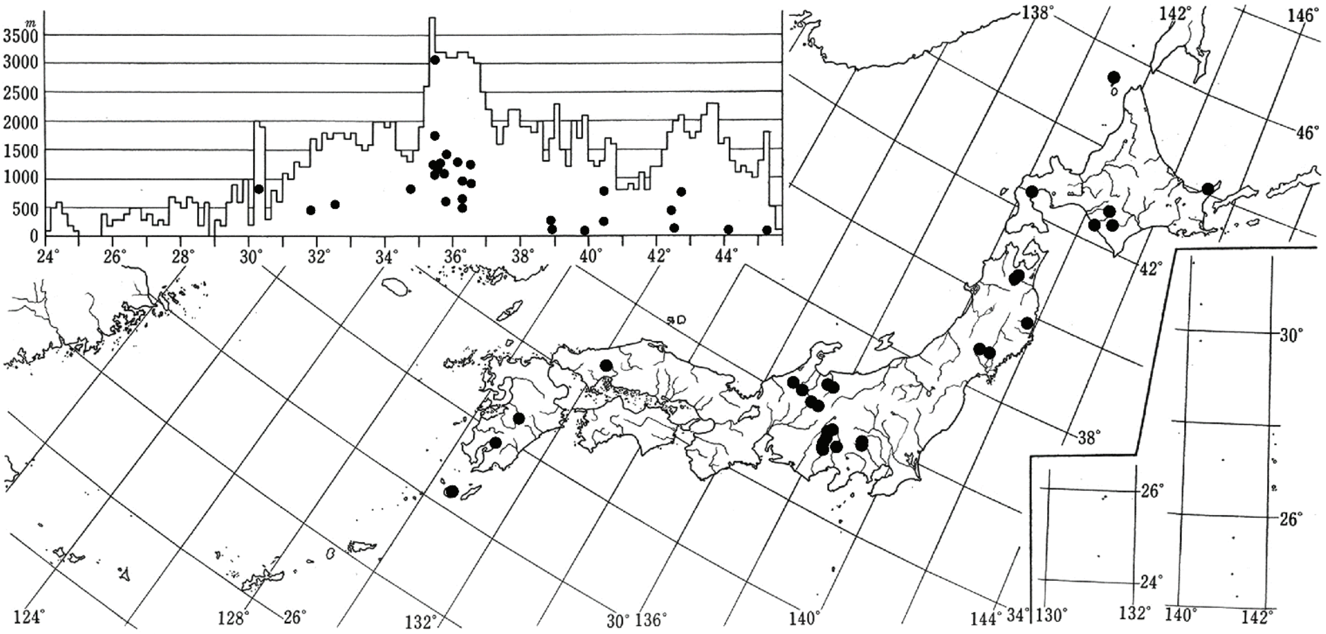


Fig. 3.4. Distribution map and vertical geographic ranges (inset) of *Marchantia paleacea* Bertol. subsp. *paleacea*. in Japan. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

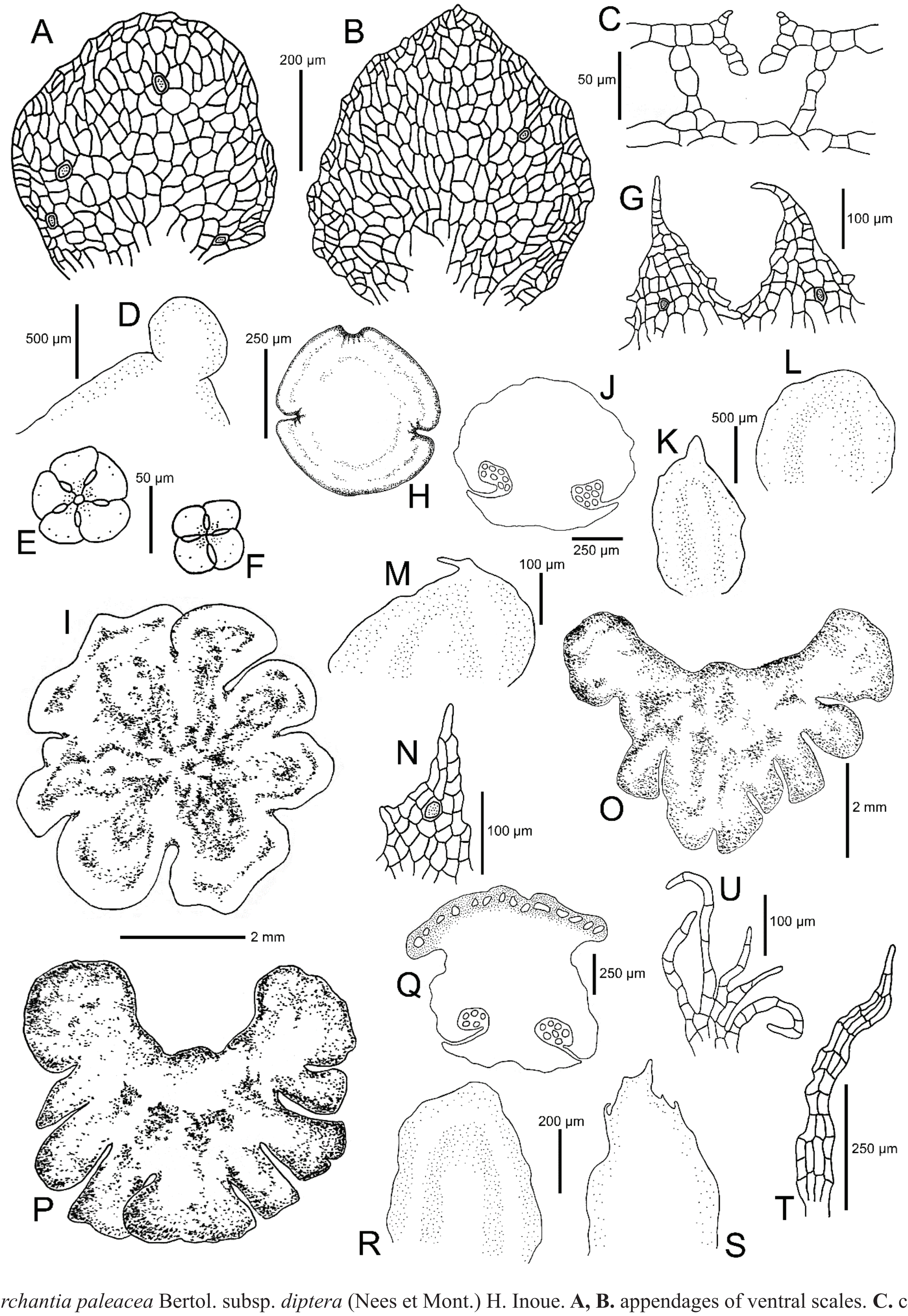


Fig. 3.5. *Marchantia paleacea* Bertol. subsp. *diptera* (Nees et Mont.) H. Inoue. **A, B.** appendages of ventral scales. **C.** cross section of air chamber. **D.** median ventral scales. **E, F.** inner opening of air pore. **G.** cupules. **H.** gemmae. **I.** male receptacles. **J.** section of antheridiophore stalk. **K, L.** basal scales of antheridiophore stalk. **M.** median scales of male lobe. **N.** apex of median scales of male lobe. **O, P.** female receptacles. **Q.** section of archegoniophore stalk. **R, S.** basal scales of archegoniophore stalk. **T.** scales of female receptacle. **U.** margin of involucre.

[**A.** *T.-X. Zheng 255*. **B.** *T. Inouë 12* (G). **C.** *T.-X. Zheng 380*. **D.** *T.-X. Zheng 1515*. **E.** *T.-X. Zheng 202*. **F.** *T.-X. Zheng 1426*. **G, H.** *T.-X. Zheng 168*. **I, N.** *T.-X. Zheng 236*. **J.** *T.-X. Zheng 335*. **K, M.** *H. Ando 2127*. **L.** *H. Ando 13386.* **O, T.** *T.-X. Zheng 1223*. **P.** *T.-X. Zheng 394*. **Q.** *T.-X. Zheng 303*. **R.** *T.-X. Zheng 230*. **S.** *T.-X. Zheng 195*. **U.** *T.-X. Zheng 285*.]

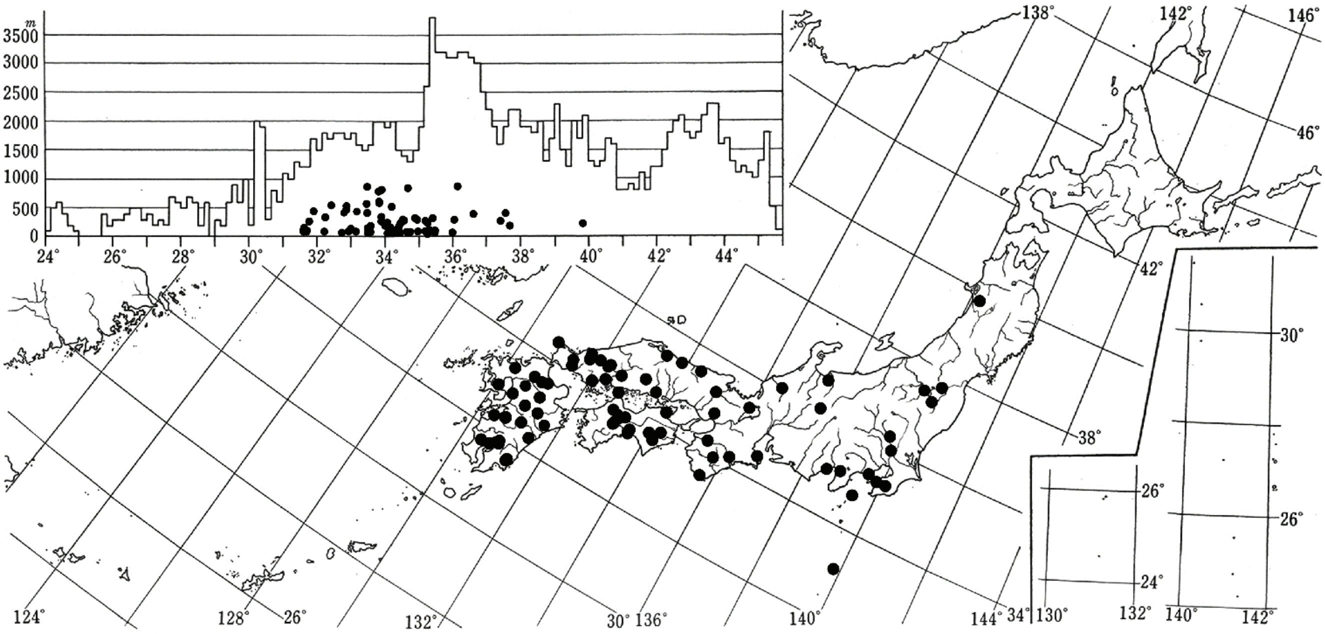


Fig. 3.6. Distribution map and vertical geographic ranges (inset) of *Marchantia paleacea* Bertol. subsp. *diptera* (Nees et Mont.) H. Inoue in Japan. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

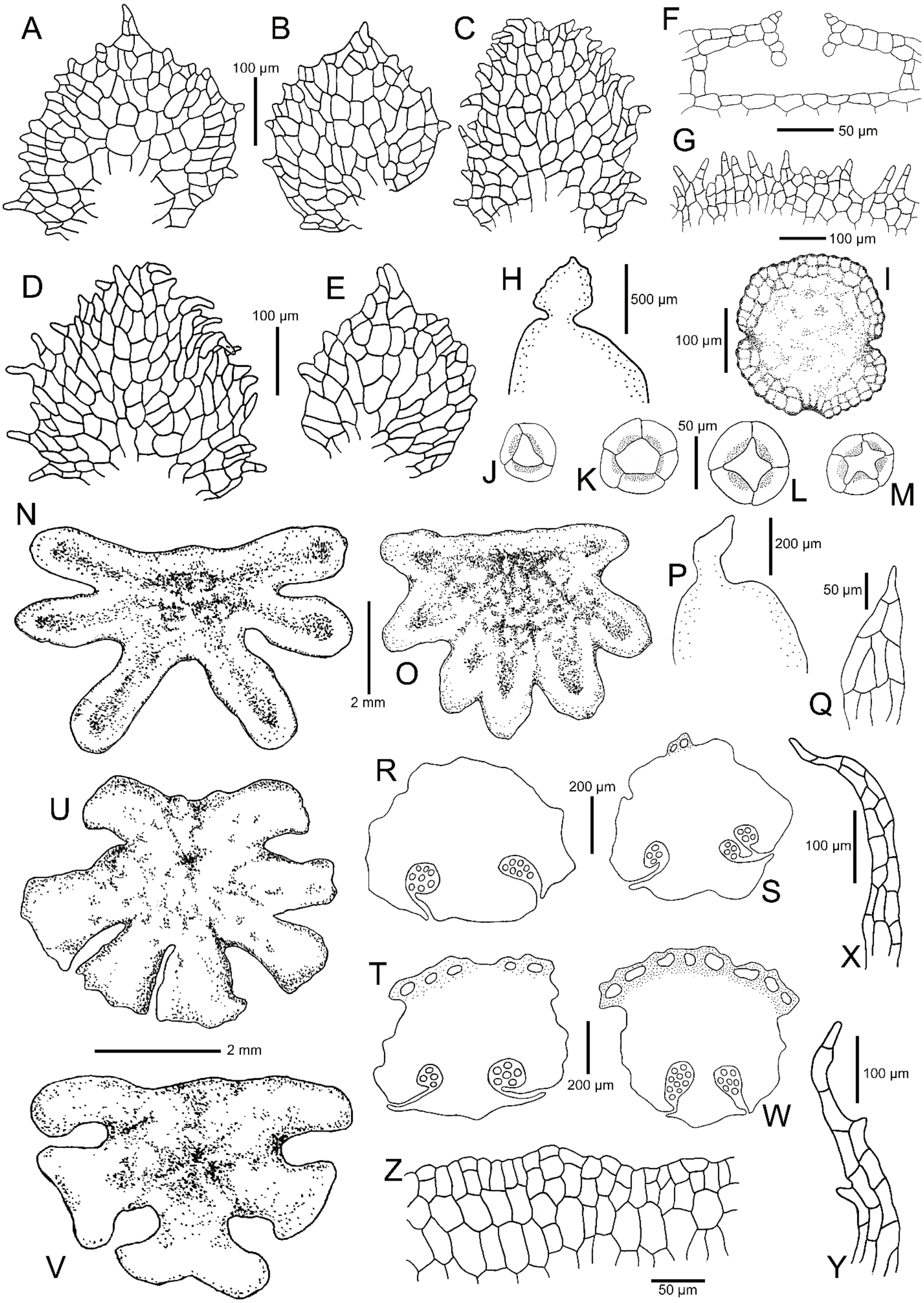


Fig. 3.7. *Marchantia papillata* Raddi. subsp. *grossibarba* (Steph.) Bischl. **A–E.** appendages of ventral scale. **F.** cross section of air chamber. **G.** cupules. **H.** median ventral scales. **I.** gemmae. **J–M.** inner opening of air pore. **N, O.** male receptacles. **P.** median scales of male lobe. **Q.** appendages of median scales of male lobe. **R–T.** section of antheridiophore stalk. **U, V.** female receptacles. **W.** section of archegoniophore stalk. **X, Y.** scales of female receptacle. **Z.** margin of involucre.
[**A.** *T.-X. Zheng 1157*. **B.** *T.-X. Zheng 1159*. **C.** *T.-X. Zheng 1228*. **D, U, W.** *T.-X. Zheng 1208*. **E, O.** *T. Inoue 5* (G). **F, S.** *T.-X. Zheng 992*. **G, I, R.** *T.-X. Zheng 993*. **H, L.** *T.-X. Zheng 1201*. **J.** *T.-X. Zheng 1190*. **K.** *T.-X. Zheng 1194*. **M.** *T.-X. Zheng 1202*. **N, P, Q, T.** *T.-X. Zheng 996*. **V.** *Y. Tokihisa 105* (G). **X.** *T.-X. Zheng 1251*. **Y.** leg. *Delavay s.n.*, holotype (G). **Z.** *T.-X. Zheng 1219*.]

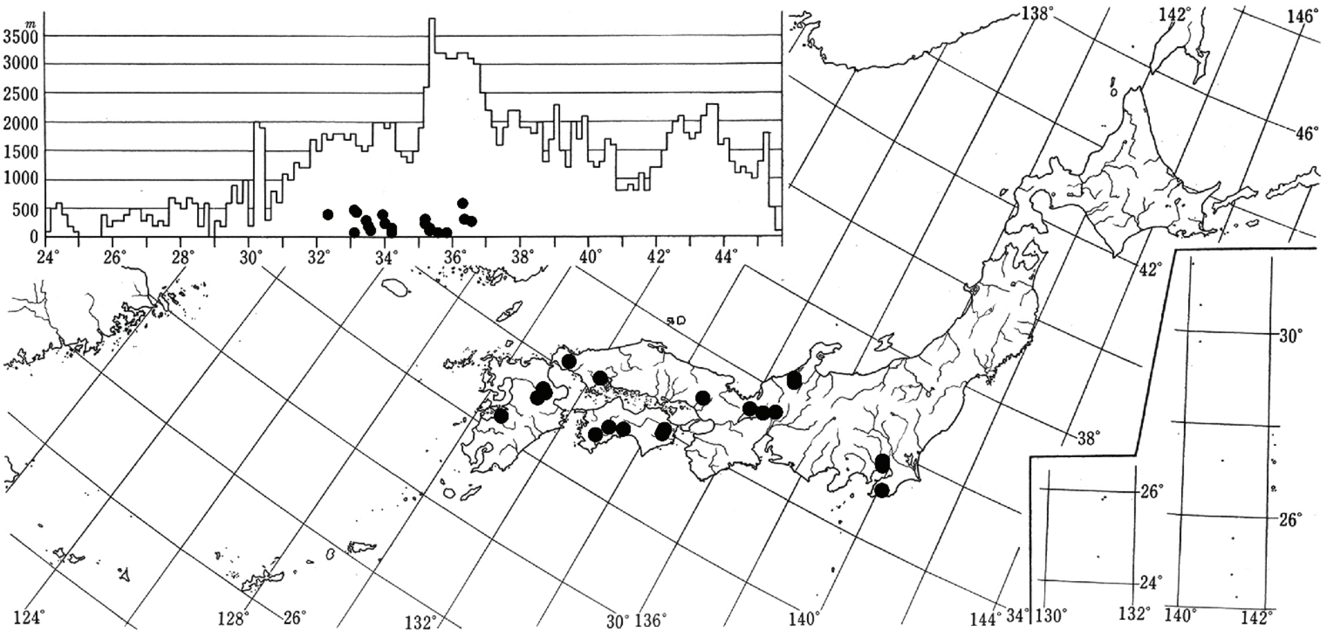


Fig. 3.8. Distribution map and vertical geographic ranges (inset) of *Marchantia papillata* Raddi. subsp. *grossibarba* (Steph.) Bischl. in Japan. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

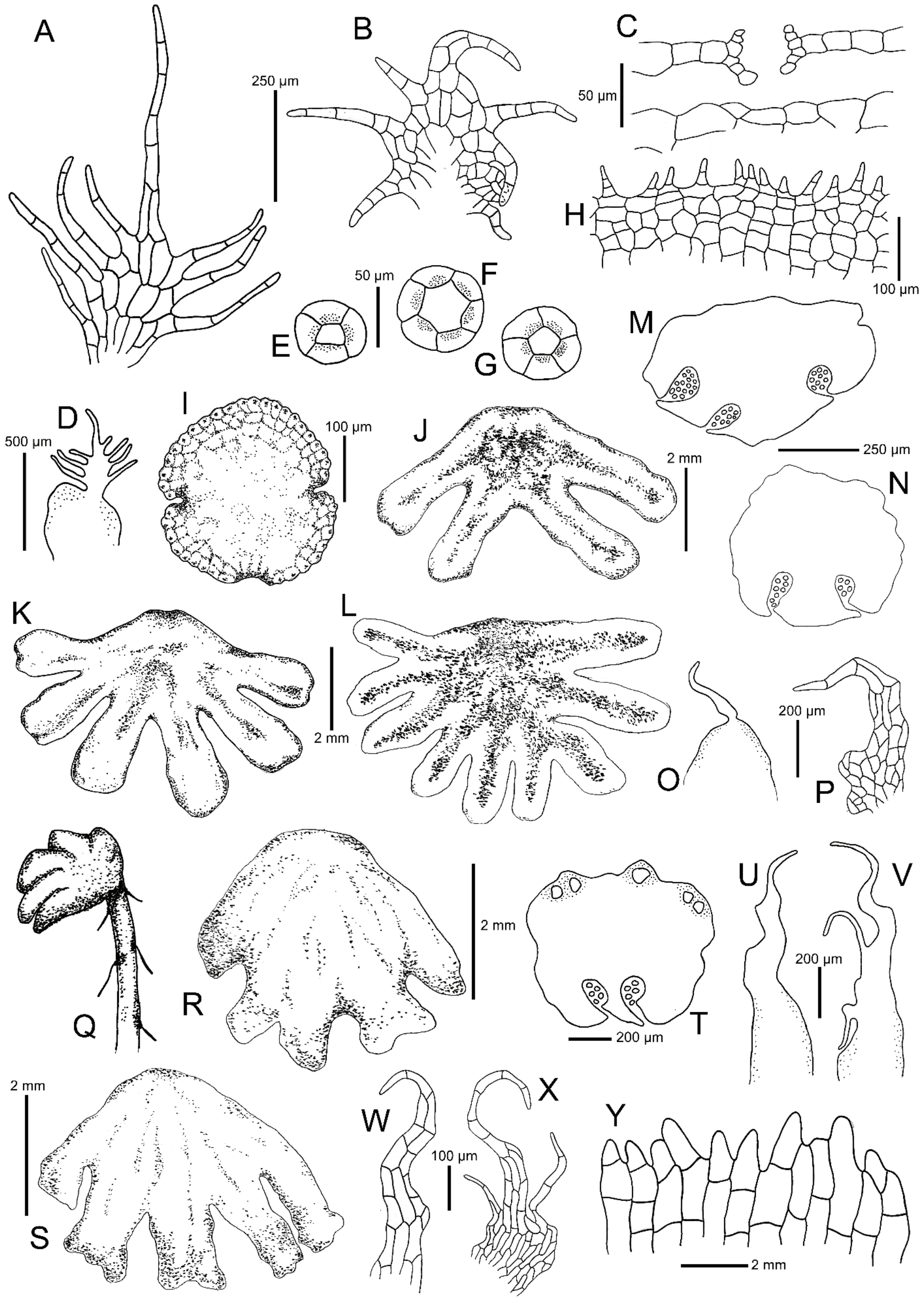


Fig. 3.9. *Marchantia pinnata* Steph. **A, B.** appendages of ventral scales. **C.** cross section of air chamber. **D.** median ventral scales. **E–G.** inner opening of air pore. **H.** cupules. **I.** gemmae. **J–L.** male receptacles. **M, N.** section of antheridiophore stalk. **O.** median scales of male lobe. **P.** appendages of median scales of male lobe. **Q.** archegoniophore. **R, S.** female receptacles **T.** section of archegoniophore stalk,. **U, V.** scales of female receptacle. **W, X.** apex of scales of female receptacle. **Y.** margin of involucre.
[**A.** *T.-X. Zheng 1072*. **B.** *T. Yamaguchi 1925*. **C.** *T.-X. Zheng 204*. **D.** *T.-X. Zheng 213*. **E.** *T.-X. Zheng 216*. **F.** *T.-X. Zheng 246*. **G.** *T.-X. Zheng 276*. **H, I.** *T.-X. Zheng 2*. **J, M.** *T.-X. Zheng 1471*. **K, N.** *T.-X. Zheng 1472*. **L, O, P.** *T.-X. Zheng 1475*. **Q.** *T.-X. Zheng 1470*. **R, U–X.** *T.-X. Zheng 1468*. **S, T, Y.** *T.-X. Zheng 1469*.]

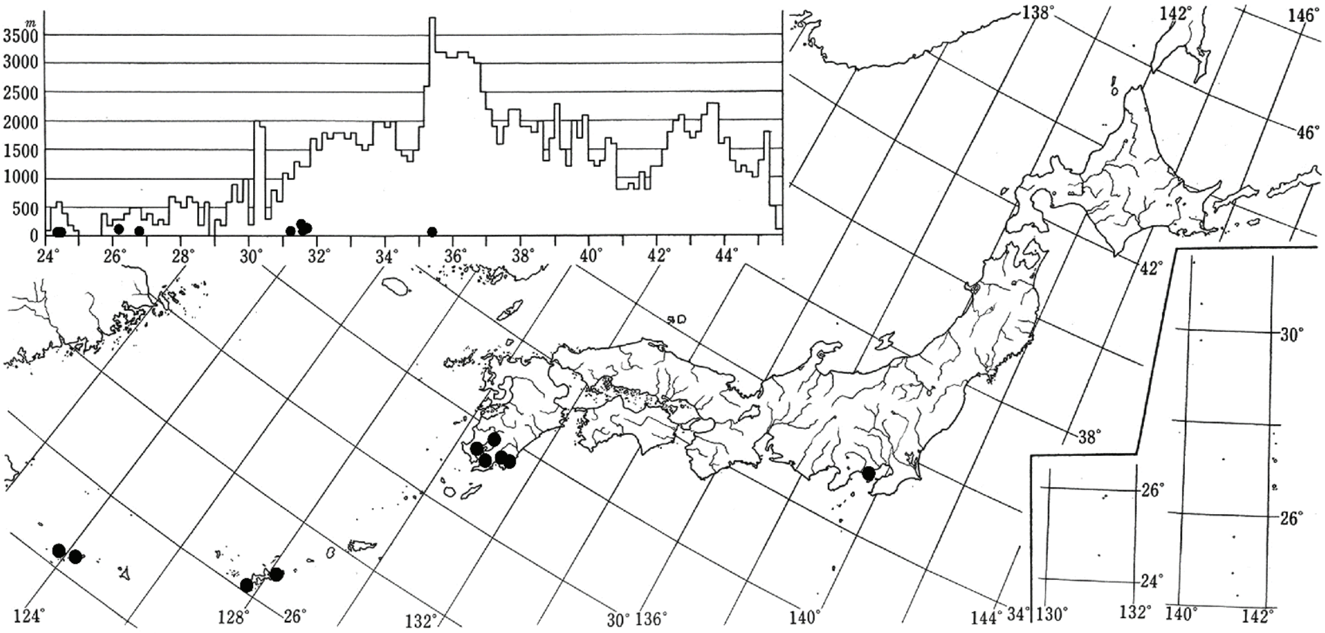


Fig. 3.10. Distribution map and vertical geographic ranges (inset) of *Marchantia pinnata* Steph. in Japan. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

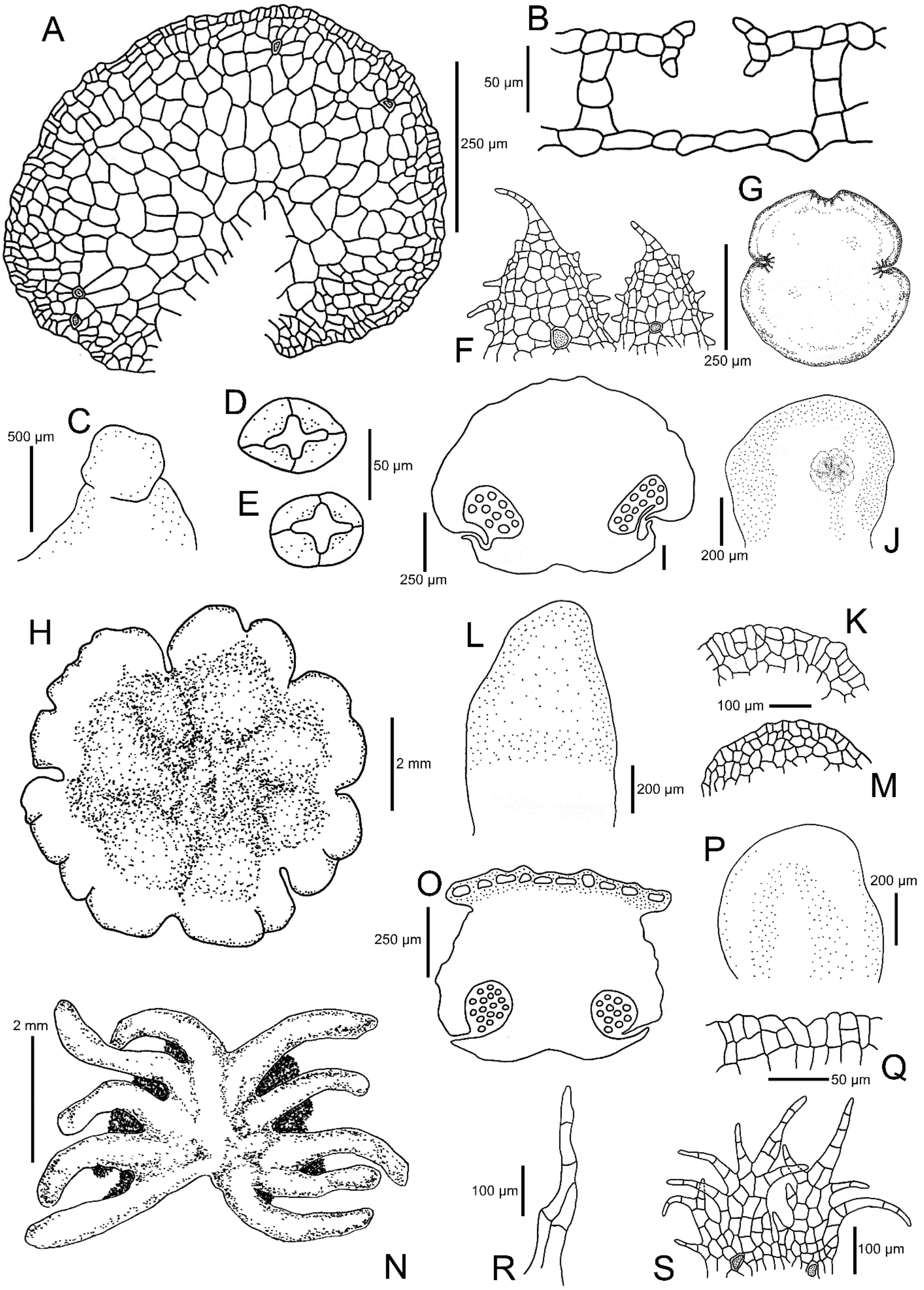


Fig. 3.11. *Marchantia polymorpha* L. subsp. *polymorpha*. **A.** appendages of ventral scale. **B.** cross section of air chamber. **C.** median ventral scales. **D, E.** inner opening of air pore. **F.** cupules. **G.** gemmae. **H.** male receptacles. **I.** section of antheridiophore stalk. **J.** basal scales of antheridiophore stalk. **K.** apex of basal scales of antheridiophore stalk. **L.** median scales of male lobe. **M.** apex of median scales of male lobe. **N.** female receptacles. **O.** section of archegoniophore stalk. **P.** basal scales of archegoniophore stalk. **Q.** apex of basal scales of archegoniophore stalk. **R.** scales of female receptacle. **S.** margin of involucre.
[**A.** *T.-X. Zheng 1564*. **B.** *T.-X. Zheng 434*. **C.** *T.-X. Zheng 1577*. **D, E.** *T.-X. Zheng 1309*. **F, O, S.** *S. Nemoto 970*. **G.** *T.-X. Zheng 435*. **H–M.** *T.-X. Zheng 1308*. **N, R.** *T.-X. Zheng 433*. **P, Q.** *H. Ando 9142*.]

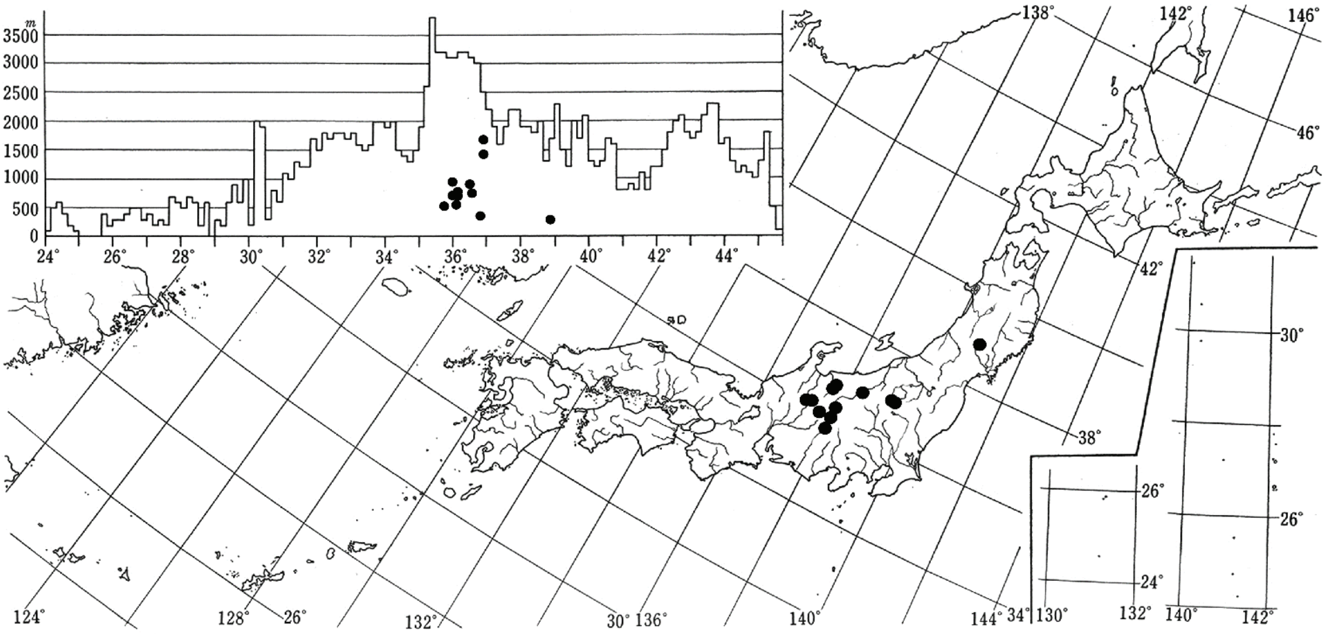


Fig. 3.12. Distribution map and vertical geographic ranges (inset) of *Marchantia polymorpha* L. subsp. *polymorpha*. in Japan. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

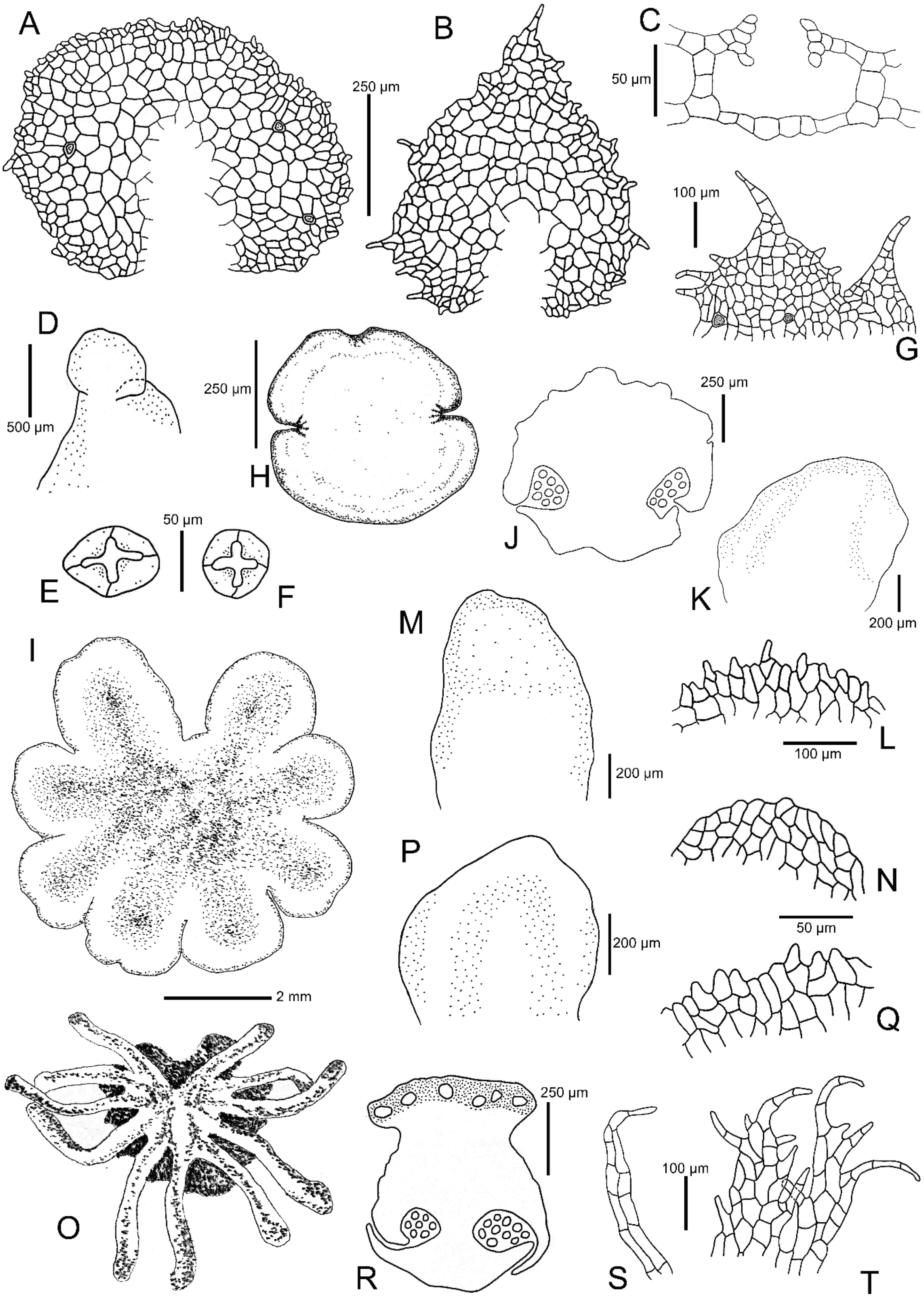


Figure 3.13. *Marchantia polymorpha* L. subsp. *ruderalis* Bischl. et Boisselier. **A, B.** appendages of ventral scale. **C.** cross section of air chamber. **D.** median ventral scales. **E, F.** inner opening of air pore. **G.** cupules. **H.** gemmae. **I.** male receptacles. **J.** section of antheridiophore stalk. **K.** basal scales of antheridiophore stalk. **L.** apex of basal scales of antheridiophore stalk. **M.** median scales of male lobe. **N.** apex of median scales of male lobe. **O.** female receptacles. **P.** basal scales of archegoniophore stalk. **Q.** apex of basal scales of archegoniophore stalk. **R.** section of archegoniophore stalk. **S.** scales of female receptacle. **T.** margin of involucre. [**A.** *T.-X. Zheng 1420*. **B.** *M. Nakao 6*. **C.** *T.-X. Zheng 1616*. **D.** *T.-X. Zheng 1604*. **E, F.** *T.-X. Zheng 1209*. **G.** *T.-X. Zheng 207*. **H.** *T.-X. Zheng 423*. **I, J.** *T.-X. Zheng 1619*. **K, L.** from *T.-X. Zheng 1178*. **M, N.** *T.-X. Zheng 1300*. **O.** *T.-X. Zheng 386*. **P, Q.** *T.-X. Zheng 1407*. **R, S.** *T.-X. Zheng 314*. **T.** *T.-X. Zheng 253*.]

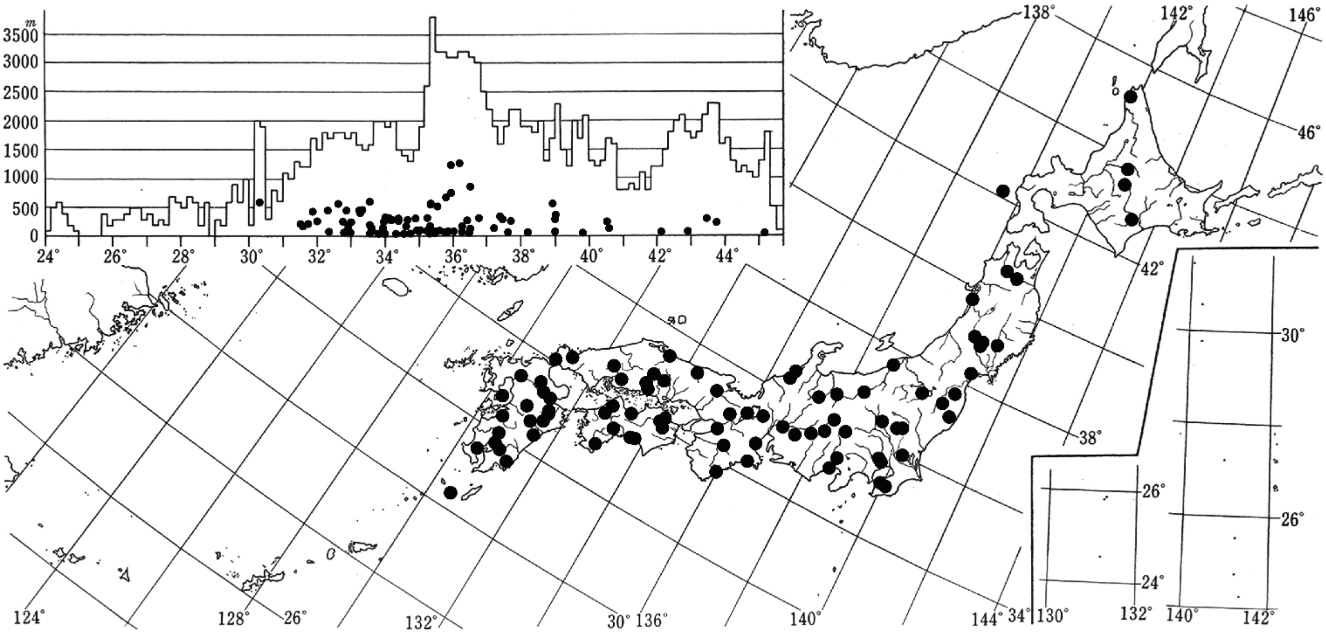


Fig. 3.14. Distribution map and vertical geographic ranges (inset) of *Marchantia polymorpha* L. subsp. *ruderalis* Bischl. et Boisselier. in Japan. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

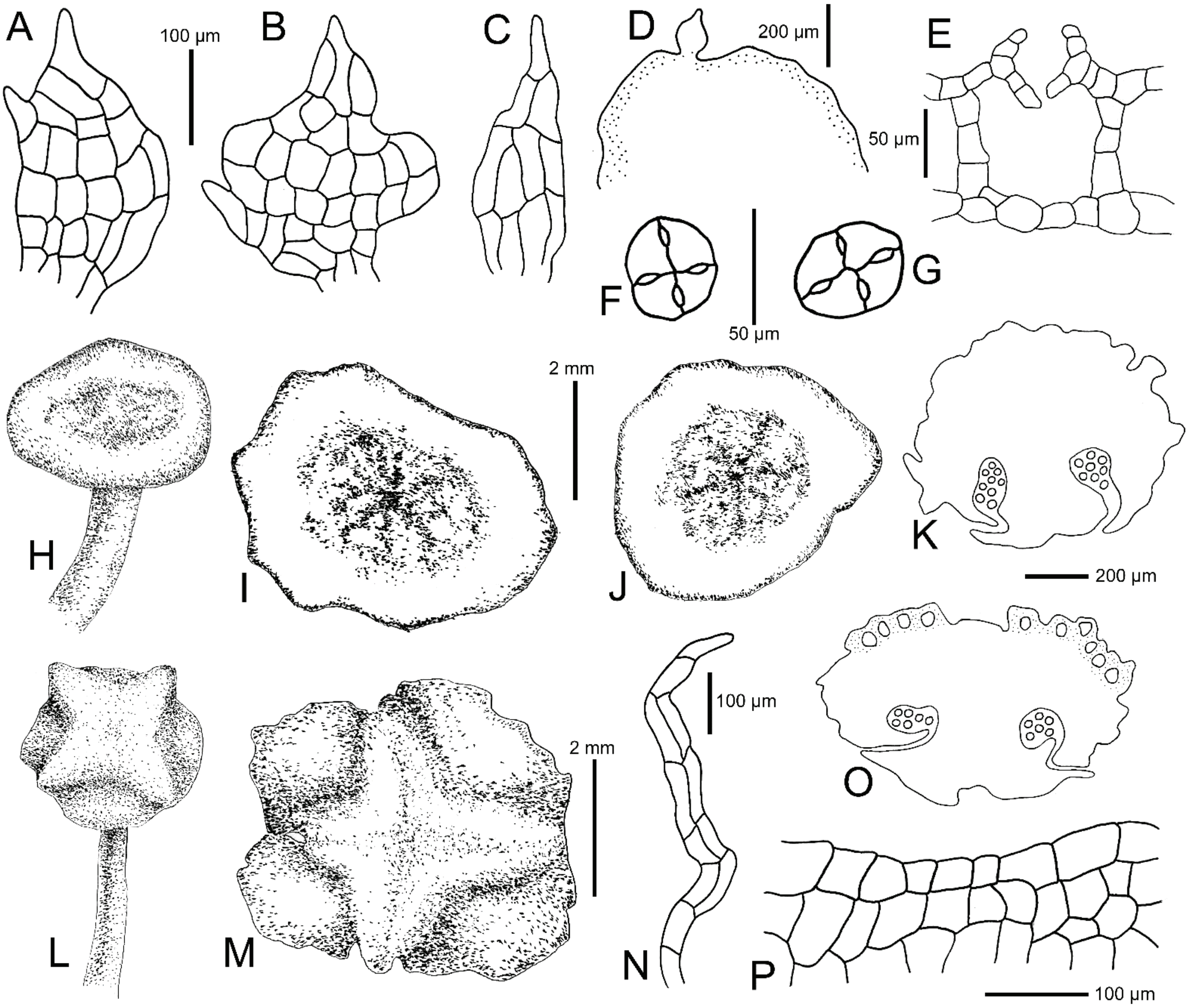


Figure. 3.15. *Marchantia quadrata* Scop. **A–C.** appendages of ventral scale. **D.** median ventral scales. **E.** cross section of air chamber. **F, G.** inner opening of air pore. **H.** antheridiophore. **I, J.** male receptacles. **K.** section of antheridiophore stalk. **L.** archegoniophore. **M.** female receptacles. **N.** scales of female receptacle. **O.** section of archegoniophore stalk. **P.** margin of involucre. [**A, H.** *T.-X. Zheng 1553*. **B, I.** *T.-X. Zheng 1555*. **C, J, K.** *T.-X. Zheng 1556*. **D, N, O.** *T.-X. Zheng 1560*. **E.** *T.-X. Zheng 1558*. **F, G.** *H. Deguchi 39122*. **L, P.** *T. Sato 755*. **M.** *T. Sato 1761*.]

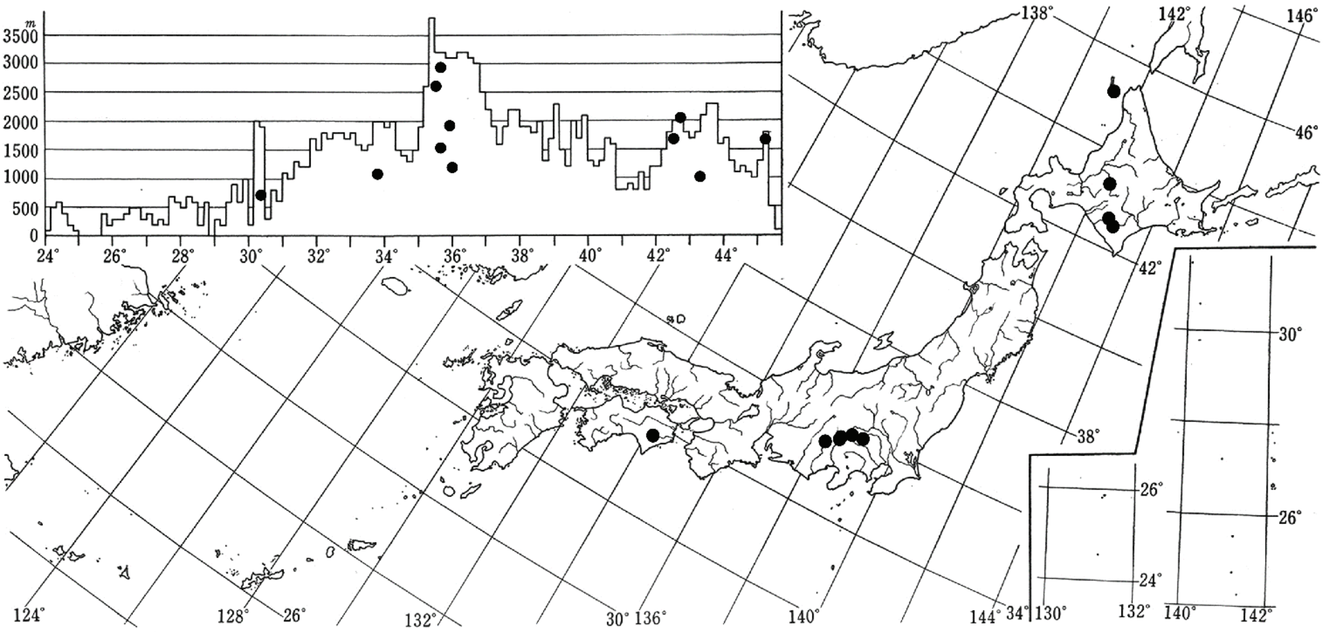


Fig. 3.16. Distribution map and vertical geographic ranges (inset) of *Marchantia quadrata* Scop. in Japan. For the insets, X axis and Y axis indicated the latitude and altitude, respectively.

Tabl. 3.1. Morphological differences between taxa of subg. *Preissia* and those of residual *Marchantia*

	Subg. *Preissia* taxa	Residual *Marchantia* taxa
Habitat	Alpine of sub-alpine	Anthropogenic
Sexual condition	Monoicous	Dioicous
Asexual propagules	Absent	Present
Branching pattern	Dichotomous and apically ventral innovative	Dichotomous
Female receptacle	Terminal conical and shallowly lobed	Planar and deeply lobed
Number of female receptacle lobe	Same with number of fertilized sporophytes	Uncorrelated with number of fertilized sporophytes
Elongation of female receptacle stalk	After the maturity of sporophyte	Before the maturity of sporophyte
Number of capsule for each involucre	1	1 to multiple
Male receptacle	Unlobed	Lobed

Appendices

Appendix A List of voucher specimens for morphological comparison and molecular phylogenetic analysis for chapter 1, with locality, specimen number and accession numbers if necessary (rbcL/rps4/trnL-F/ITS). All specimens are deposited in Herbarium of Hiroshima University (HIRO).

Marchantia polymorpha L. subsp. ***polymorpha***
JAPAN. Miyagi Pref., Kurihara City, *T.-X. Zheng 490*, *492* (**LC536759/LC536778/LC536797/LC536816**); Fukushima Pref., Hinoemata Village, *T.-X. Zheng 435*.
Gemmae/Specimens examined: 119/3;

M. polymorpha L. subsp. ***ruderalis*** Bischl. et Boissel.-Dub.
JAPAN. Hokkaido, Obihiro City, *T.-X. Zheng 321*; Okushiri Isl., *T.-X. Zheng 451*, *452*; Iwate Pref., Ichinoseki City, *T.-X. Zheng 500*, *501*; Miyagi Pref., Sendai City, *T.-X. Zheng 454*, *455*, *502*, *503*, *512*; Fukushima Pref., Miharu Town, *T.-X. Zheng 13*; Bandai Town, *T.-X. Zheng 438*, *440*; Chiba Pref., Futtsu City, *T.-X. Zheng 59*; Kamogawa City, *T.-X. Zheng 55, 169*; Osaka Pref., Osaka City, *T.-X. Zheng 400* (**LC536760/LC536779/LC536798/LC536817**); Hiroshima Pref., Higashi-hiroshima City, *T.-X. Zheng 6*; Sera Town, *T.-X. Zheng 115*; Shobara City, *T.-X. Zheng 137*, *138*; Yamaguchi Pref., Mine City, *T.-X. Zheng 423* (**LC536761/LC536780/LC536799/LC536818**); Tokushima Pref., Yoshinogawa City, *T.-X. Zheng 385* (**LC536762/LC536781/LC536800/LC536819**); Ehime Pref., Niihama City, *T.-X. Zheng 333*, *334*; Kochi Pref., Niyodogawa Town, *T.-X. Zheng 342*; Oita Pref., Tsukumi City, *T.-X. Zheng 287*; Miyazaki Pref., Nichinan City, *T.-X. Zheng 251*, *282*; Tsuno Town, *T.-X. Zheng 262*; Kagoshima Pref., Soo City, *T.-X. Zheng 207*; Kirishima City, *T.-X. Zheng 221*.
Gemmae/ Specimens examined: 844/32;

M. paleacea Bertol. subsp. ***paleacea***
JAPAN. Miyagi Pref., Kurihara City, *T.-X. Zheng 474, 477*; Sendai CIty, *T.-X. Zheng 510*; Toyama Pref., Tateyama Town, *T.-X. Zheng 515, 529*; Nagano Pref., Ina City, *T. Sato s.n.* (HIRO-1038712, **LC536763/LC536782/LC536801/LC536820**); Kagoshima Pref., Kirishima City, *T.-X. Zheng 223* (**LC536764/LC536783/LC536802/LC536821**).
Gemmae/ Specimens examined: 266/7;

M. paleacea Bertol. subsp. ***diptera*** (Nees et Mont.) Inoue

JAPAN. Akita Pref., Akita City, *T.-X. Zheng 425*; Chiba Pref., Futtsu City, *T.-X. Zheng 51*, *53*; Kamogawa City, *T.-X. Zheng 56* (**LC536765/LC536784/LC536803/LC536822**); Tokyo Met., Hachioji City, *T.-X. Zheng 168*; Toyama Pref., Tateyama Town, *T.-X. Zheng 514*; Mie Pref., Matsusaka City, *T.-X. Zheng 413*; Shimane Pref., Tsuwano City, *T.-X. Zheng 299*; Hiroshima Pref., Kita-hiroshima Town, *T.-X. Zheng 171*; Yamaguchi Pref., Yamaguchi City, *T.-X. Zheng 420*; Mine City, *T.-X. Zheng 421* (**LC536767/LC536786/LC536805/LC536824**); Ehime Pref., Toon City, *T.-X. Zheng 39* (**LC536766/LC536785/LC536804/LC536823**)*, 44*; Niihama City, *T.-X. Zheng 335*, *336*; Kochi Pref., Niyodogawa Town, *T.-X. Zheng 343*; Kochi City, *T.-X. Zheng 363* (**LC536768/LC536787/LC536806/LC536825**); Oita Pref., Bungo-ohno City, *T.-X. Zheng 236*; Tsukumi City, coll. *Y. Inoue* in hb. *T.-X. Zheng 285*; Miyazaki Pref., Tsuno Town, *T.-X. Zheng 16*; Nichinan City, *T.-X. Zheng 261*; Kagoshima Pref., Kirishima City, *T.-X. Zheng 3* (**LC536769/LC536788/LC536807/LC536826**); Aira City, *T.-X. Zheng 199*; Soo City, *T.-X. Zheng 219*.

Gemmae/ Specimens examined: 724/24;

M. emarginata Reinw., Blume et Nees subsp. ***tosana*** (Steph.) Bischl.

JAPAN. Hiroshima Pref., Akiota Town, *T.-X. Zheng 403*; Yamaguchi Pref., Mine City, *T.-X. Zheng 422*; Kochi Pref., Niyodogawa Town, *T.-X. Zheng 341* (**LC536770/LC536789/LC536808/LC536827**); Miyazaki Pref., Nichinan City, *T.-X. Zheng 245, 330, 258*; Kagoshima Pref., Kirishima City, *T.-X. Zheng 1* (**LC536771/LC536790/LC536809/LC536828**), *T.-X. Zheng 211*; Okinawa Pref., Ishigakijima Isl., *T.-X. Zheng 7* (**LC536772/LC536791/LC536810/LC536829**); Okinawa Isl., *T. Yamaguchi 39439*.

Gemmae/ Specimens examined: 246/9;

M. pinnata Steph.

JAPAN. Miyazaki Pref., Nichinan City, *T.-X. Zheng 242*, *T.-X. Zheng 281* (**LC536773/LC536792/LC536811/LC536830**); Kagoshima Pref., Kirishima City, *T.-X. Zheng 2* (**LC536774/LC536793/LC536812/LC536831**), *T.-X. Zheng 214*; Soo City, *T.-X. Zheng 203* (**LC536775/LC536794/LC536813/LC536832**), *204*; Okinawa Pref., Okinawa Isl., *T. Yamaguchi 39500*.

Gemmae/ Specimens examined: 225/7;

M. quadrata Scop.

JAPAN. Yamanashi Pref., Minami Alps City, *T.-X. Zheng 8* (**LC536776**/**LC536795**/**LC536814**/**LC536833**).

Lunularia cruciata (L.) Dumort. Ex Lindb.

JAPAN. Shimane Pref., Tsuwano City, *T.-X. Zheng 302* (**LC536777**/**LC536796**/**LC536815**/**LC536834**); Hiroshima Pref., Higashi-hiroshima, *T.-X. Zheng 921*.

Gemmae/ Specimens examined: 29/1.

Appendix B. List of voucher specimens for morphological examination and molecular phylogenetic analysis for chapter-2, with locality, specimen number and accession numbers if necessary (*rbc*L/*rps*4/*trn*T-L-F/ITS). Bold accession numbers indicated newly obtained sequences for present study. All specimens are deposited in Herbarium of Hiroshima University (HIRO) unless otherwise indicated.

M. cuneiloba Steph.

JAPAN. Shizuoka Pref., Shizuoka City, *T.-X. Zheng 1543*, *1547*, *1548*. Hiroshima Pref., Higashi-Hiroshima City, *T.-X. Zheng 1505*, *1506*, *1507*. Shobara City, *T.-X. Zheng 315* (**LC629648**/**LC630843**/**LC631256**/**LC631302**); Wakayama Pref., Higashimuro Co., Matsune, *T.-X. Zheng 1536*, *1538*, *1539*, Nabera, *T.-X. Zheng 1524*, *1525*, *1526*, *1527*, *1528*, *1529*, Nishikawa, *T.-X. Zheng 1530*, *1531*. Saga Pref., Karatsu City, *T.-X. Zheng 1145* (**LC629644**/**LC630839**/**LC631252**/**LC631298**); Nagasaki Pref., Minamishimabara City, *T.-X. Zheng 1147* (**LC629654**/**LC630849**/**LC631262**/**LC631308**). Unzen City, *T.-X. Zheng 1155* (**LC629643**/ **LC630838**/**LC631251**/**LC631297**); Kumamoto Pref., Hitoyoshi City, *T.-X. Zheng 1105* (**LC636439**/**LC636442**/**LC636446**/**LC636449**)*, 1108* (**LC629653**/**LC630848**/**LC631261**/**LC631307**). Kikuchi City, *T.-X. Zheng 1126* (**LC629647**/**LC630842**/**LC631255**/**LC631301**). Kuma Co., *Horikawa 16557*; Oita Pref., Tsukumi City, *T.-X. Zheng 516* (**LC629646**/**LC630841**/**LC631254**/**LC631300**); Miyazaki Pref., Ebino City, *T.-X. Zheng 1099*, *1101*. Kushima City, *T.-X. Zheng 1042*, *1043*, *1044*. Miyazaki City, Imaizumi, *T.-X. Zheng 1018*. Tano *T.-X. Zheng 1022*, *1023* (**LC636440**/**LC636443**/**LC636447**/**LC636450**). Nichinan City, Hoshikura, *T.-X. Zheng 1053*, *1054*. Kitagawachi, *T.-X. Zheng 1028*, *1029*. Kusubara, *T.-X. Zheng 275*, *278*, *1055*, *1056*. Nishiusuki Co., *T.-X. Zheng 1002*, *1003*, *1004*, *1005*. Nobeoka City, *T.-X. Zheng 1009*, *1010*, *1011*. Obi, *T.-X. Zheng 331* (**LC629645**/**LC630840**/**LC631253**/**LC631299**), *1058*, *1059*, *1062* (-/**LC636444**/-/**LC636451**). Sakatani *T.-X. Zheng 250*, *256*; Kagoshima Pref., Aira City, Hiramatsu, *T.-X. Zheng 197*, *198*. Kajiki, *T.-X. Zheng 226* (**LC629649**/**LC630844**/**LC631257**/**LC631303**), *1494* (**LC636438**/**LC636441**/**LC636445**/**LC636448**). Hioki City, Nakahara, *T.-X. Zheng 1081*, *1082*, *1083*. Koinohara, *T.-X. Zheng 1086*. Kanoya City, *T.-X. Zheng 1073*, *1074*, *1075*. Kimotsuki Co., Nejimeyokobeppu, *T.-X. Zheng 1079*, *1080*. Kirishima City, Kareigawa, *T.-X. Zheng 210*, *211*, *212*. Kumage Co., *Y. Sakamoto 566*. Oshima Co., *M. Higuchi 7706*. Sataizashiki, *T.-X. Zheng 1084*, *1085*, *1094*, *1095*. Shibushi City, *T.-X. Zheng 1032*, *1035*, *1036*, *1037*. Shiromoto, *T.-X. Zheng 1077*. Tarumizu City, *Horikawa 4673*; Okinawa Pref., Ginowan City, *T. Yamaguchi 39421* (**LC629651**/**LC630846**/**LC631259**/**LC631305**), *39467*. Iriomotejima Isl, *T.-X. Zheng 848* (**LC629642**/**LC630837**/**LC631250**/**LC631296**), *K. Nishihata 634*, *670*, *834*, *878*, *1163*, *1247*, *1252*, *T. Yamaguchi 346*, *852*, *869*, *2097*. Ishigakijima Isl, *T. Yamaguchi 2668, 3033*, *3034*, *3118*. Fukai, *801*. Maezato, *T.-X. Zheng 780*, *781*, *782*, *783*, *784*. Nagura, *T.-X. Zheng 819* (**LC629652**/**LC630847**/**LC631260**/**LC631306**). Tonoshiro, *T.-X. Zheng 795*, *796*, *797*, *798*. Kunigami Co., *Y. Horikawa 13126*, *T. Yamaguchi 12929*, *13166*, *T.-X. Zheng 886*, *887*, *888*, *889*. Nago City, *T.-X. Zheng 893*, *894*, *895*, *896*. Naha City, *T. Amano 8112* (NICH). Nakagami Co., *T.-X. Zheng 904*, *905*. Okinawa City, *T.-X. Zheng 867* (**LC629650**/**LC630845**/**LC631258**/**LC631304**). Yonagunijima Isl., *T. Yamaguchi* & *T. Seki 4893*.

M. emarginata Reinw. Blume et Nees subsp. ***emarginata***
INDONESIA: Sumatra, Karbau-canyon, *W. Meijer 6428* (NICH); PAPUA NEW GUINEA: Star Mts., Sibil-vally, *B. O. van Zanten 875* (NICH); PHILIPPINES. Luzon, *M. Jacobs B798* (NICH);

M. emarginata Reinw. Blume et Nees subsp. ***lecordiana*** (Steph.) Bischl.
NER CALEDONIA: Ouraï, *Lecord s. n.* (G 43729), *Lecord s. n.* (G 43730); VANUATU: Efate, Pang Pang, *K. Sugimura 1418* (TNS). Espiritu Santo, Butmas, *K. Sugimura 1741* (TNS);

M. paleacea Bertol. subsp. ***paleacea***
JAPAN. Kagoshima Pref., Kirishima City, *T.-X. Zheng 223* (LC536764/LC536783/LC536802/LC536821); Kumage County, leg. *M. Shimamura s.n.* (**LC629641**/**LC630836**/**LC629687**/**LC631295**).

M. paleacea Bertol. subsp. ***diptera*** (Nees et Mont.) Inoue
JAPAN. Chiba Pref., Futtsu City, *T.-X. Zheng 56* (LC536765/LC536784/LC536803/LC536822); Yamaguchi Pref., Mine City, *T.-X. Zheng 421* (LC536767/LC536786/LC536805/LC536824); Ehime Pref., Toon City, *T.-X. Zheng 39* (LC536766/LC536785/LC536804/LC536823).
M. papillata Raddi. subsp. ***grossibarba*** (Steph.) Bischl.
CHINA. Sichuan Province, Yanbian Co., *M.-Z. Wang 20126* & *20128* (PE); Yunnan Prov., Mengla Co., *P.-C. Wu 21708* (PE). Ruili City, *Wang et al. 20150419-40* (HSNU) (KX792416/-/KX792402/KX792429); INDIA. Pubjab, *W. Koelz 4420* (NICH). Utta Pradesh, *W. Gollan 4585* (G). West Bengal, *A. C. Hartless 3324* (G); JAPAN. Yamaguchi Pref., Mine City, *T. Shiomi 19*, *T.-X. Zheng 966*

(**LC629659/LC630854/LC631267/LC631977**), *967*, *1157* (**LC629658/LC630853/LC631266/ LC631976**), *1158*. Iwakuni City, *S. Katsui 444*; Kagoshima Pref., Aira City, *T.-X. Zheng 1092* (**LC629660/LC630855/LC631268/LC631978**); MYANMAR. Falam, *F. G. Dickason 7325* (NICH).

Marchantia polymorpha L. subsp. ***polymorpha***
JAPAN. Miyagi Prefecture, Kurihara City, *T.-X. Zheng 492*
(LC536759/LC536778/LC536797/LC536816)

M. polymorpha L. subsp. ***ruderalis*** Bischl. et Boissel.-Dub.
JAPAN. Osaka Pref., Osaka City, *T.-X. Zheng 400* (LC536760/LC536779/LC536798/LC536817); Yamaguchi Pref., Mine City, *T.-X. Zheng 423* (LC536761/LC536780/LC536799/LC536818); Tokushima Pref., Yoshinogawa City, *T.-X. Zheng 385* (LC536762/LC536781/LC536800/LC536819);

M. pinnata Steph.
JAPAN. Miyazaki Pref., Nichinan City, *T.-X. Zheng 281* (LC536773/LC536792/LC536811/LC536830); Kagoshima Pref., Kirishima City, *T.-X. Zheng 2* (LC536774/LC536793/LC536812/LC536831); Soo City, *T.-X. Zheng 203* (LC536775/LC536794/LC536813/LC536832).

M. quadrata Scop.
JAPAN. Yamanashi Pref., Minami Alps City, *T.-X. Zheng 8* (LC536776/LC536795/LC536814/LC536833).

M. radiata Horik.
JAPAN. Nagasaki Pref., Sasebo City, *Horikawa 4776*. Kagoshima Pref., Kumage Co., *Y. Horikawa 11873*; Okinawa Pref., Nago City, *Y. Horikawa 2945*.

M. tosana Steph.
JAPAN. Saitama Pref., Saitama City, *T.-X. Zheng 1480*, *1481*, *1482*, *1483*, *1484*. Tokyo, Ota Dist., *T.-X. Zheng 1491*, *1492*, *1493*, Shibuya Dist., *M. Uazawa 2336*, *5639*. Ishikawa Pref., Hakusan City, Chuugu, *T.-X. Zheng 1610*, *1611*, *1612*, *1613*, *1614*, *1615*, Senami, *T.-X. Zheng 1617*, *1618*. Shiga Pref., Maibara City, *T.-X. Zheng 1519*, *1520*, *1521*, *1522*, *1523*, Takashima City, *T.-X. Zheng 1509*, *1510*, *1511*, *1512*. Hyogo Pref., Asago City, *T.-*

X. Zheng 1497, *1498*. Hiroshima Pref., Higashi-hiroshima City, *T.-X. Zheng 923, 924, 1167* (**LC629668/LC630863/LC631276/LC631986**), *1172* (**LC629670/LC630865/LC631278/LC631988**); Tokushima Pref., Myouzai Co., *T.-X. Zheng 398* (**LC629661/LC630856/LC631269/LC631979**), *1238* (**LC629662/LC630857/LC631270/LC631980**), *1246* (**LC629664/LC630859/LC631272/LC631982**), *1251* (**LC629663/LC630858/LC631271/LC631981**), *1260* (**LC629667/LC630862/LC631275/LC631985**); Kochi Pref., Agawa Co., Nanokawa, *T.-X. Zheng 350* (**LC629672/LC630867/LC631280/LC631990**). Kochi City, *T.-X. Zheng 368* (**LC629686/LC630880/LC631294/LC632004**), *1200* (**LC629669/LC630864/LC631277/LC631987**), *1208* (**LC629676/LC630871/LC631284/LC631994**), *1214* (**LC629673/LC630868/LC631281/LC631991**), *1228* (**LC629685/LC630879/LC631293/LC632003**); Kumamoto Pref., Kuma Co., *T.-X. Zheng 417* (**LC629671/LC630866/LC631279/LC631989**); Miyazaki Pref., Nishiusuki Co., *T.-X. Zheng 1014* (**LC629656/LC630851/LC631264/LC631974**).

M. tosayamensis Steph.

JAPAN. Chiba Pref., Kamogawa City, *T.-X. Zheng 328* (**LC629665/LC630860/LC631273/LC631983**); Gifu Pref., Yamagata City, *T.-X. Zheng 411*, *412*. Shimane Pref., Kanoashi Co., *T.-X. Zheng 305* (**LC629657/LC630852/LC631265/LC631975**); Tokushima Pref., Naka Co., *T.-X. Zheng 1202* (**LC629684/-/LC631292/LC632002**); Kochi Pref., Kochi City, Tosayama, Hirose, *T.-X. Zheng 1201* (**LC629675/LC630870/LC631283/LC631993**). Kajitani, *T.-X. Zheng 380* (**LC629666/LC630861/LC631274/LC631984**), *1217* (**LC629677/LC630872/LC631285/LC631995**). Kuwao, *T.-X. Zheng 1232* (**LC629674/LC630869/LC631282/LC631992**), *1234* (**LC629679/LC630874/LC631287/LC631997**). Shimanto City, *T.-X. Zheng 1192* (**LC629678/LC630873/LC631286/LC631996**); Saga Pref., Kanzaki Co., *T.-X. Zheng 1136* (**LC629655/LC630850/LC631263/LC631973**); Oita Pref., Nakatsu City, *T.-X. Zheng 539* (**LC629683/LC630878/LC631291/LC632001**), *992* (**LC629682/LC630877/LC631290/LC632000**), *993* (**LC629681/LC630876/LC631289/LC631999**). Kusu Co., *T.-X. Zheng 996* (**LC629680/LC630875/LC631288/LC631998**);

Mannia fragrans (Balbis) Frye & L. Clark

SWITZRLAND. *Schill 34* (E) (DQ286013/DQ220687/-/-).

Plagiochasma appendiculatum Lehm. & Lindenb.
NEPAL. Long 28934 (E) (KT356976/KT356986/-/-).

Reboulia hemisphaerica (L.) Raddi
U.S.A., Illinois, *Forrest 531* (ABSH) (AY688788/AY688801/-/-).