広島大学学位請求論文

Systematics of the moss family Pottiaceae with special reference to the origin of sporophyte diversity in East Asian *Weissia*

（セン類センボンゴケ科の系統・分類学的研究：
東アジア産コゴケ属の胞子体多様化の起源に着目して）

2017 年

広島大学大学院理学研究科
生物科学専攻

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学位論文

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主論文

Systematics of the moss family Pottiaceae with special reference to the origin of sporophyte diversity in East Asian *Weissia*

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Summary

The family Pottiaceae (Dicranidae, Bryopsida) is the most generic and species rich family in mosses (Bryophyta), with around 1,400 species in 83 genera, comprising more than 10 % of extant moss species, and exhibit a entangled morphological diversification being associated with a wide range of habitat types, substrata and life strategies. This features made the phyletic assessment and classification of Pottiaceae based on morphological criteria very difficult and controversial at any taxonomic rank, even including the familial circumscription. From the early 19th century, variously attempts at a classification of the Pottiaceae and its related families have been proposed by many authors. Nevertheless their efforts, systematics of the family remains a challenge. The present dissertation provide a sound classifications at family and subfamily rank, and implications for sporophyte diversity within the genus *Weissia* which shows most complex and diverse sporophytes among the genera of Pottiaceae based on the molecular phylogenetic analyses.

Based on the molecular phylogenetic analysis of haplolepideous mosses (Dicranidae) with concatenated sequences of chloroplast *rbcL* and *rps4* genes, a new family Timmiellaceae is erected to accommodate the genera *Timmiella* and *Luisierella*, both of which have been formerly included in the family Pottiaceae. The family Timmiellaceae is resolved as a second branching clade together with *Distichium* (Distichiaceae) within the Dicranidae (haplolepideous moss) lineages and phylogenetically distinct from the Pottiaceae. Reassessment of morphological characters suggests that a combination of the characters: (1) adaxially bulging and abaxially flat leaf surfaces, (2) sinistrorse or straight peristomes, when present, and (3) sinistrorsely arranged operculum cells is unique to Timmiellaceae and discriminates it from other haplolepideous moss families.

Molecular phylogenetic inference based on a new approach using a codon substitution model is also undertaken to assess the subfamilial relationships within Pottiaceae and confirm four clades within the family, corresponding to Trichostomoideae, Pottioideae, Merceyoideae, and a newly proposed subfamily Streblotrichoideae. The combination of the characters: (1) strongly convolute perichaetial leaves, (2) yellow seta, (3) revoluble annulus, (4) well-developed twisted

peristome, and (5) brown, spherical, rhizoidal gemmae discriminates Streblotrichoideae from other subfamilies in Pottiaceae. Based on the results I propose a new circumscription of the family Pottiaceae comprising four subfamilies: Merceyoideae, Streblotrichoideae, Pottioideae and Trichostomoideae.

Four species including one new species of Japanese cleistocarpous species of *Weissia* (Pottiaceae): *W. exserta*, *W. japonica*, *W. kiiensis* and *W. parajaponica*, *sp. nov.* are recognized based on molecular phylogenetic inference and morphological reassessment. Rapid sporophyte modifications in *Weissia* and monophyletic positions of these four species are supported by the analysis with concatenated chloroplast *rbcL* and *rps4* gene sequences. This result suggests that sporophyte diversity of the genus has been maintained by morphological plasticity and reticulation between morphologically remote species.

General Introduction

Bryophytes are the oldest extant land plants comprising three major groups, Mosses (Bryophyta), Liverworts (Marchantiophyta), and Hornworts (Anthocerotophyta) and second divergent group in land plants (ca. 20,000 species: 12,500 spp. in mosses, 7,200 ssp. in liverworts, 200 ssp. in hornworts; Frey & Stech 2009, Söderström *et al.* 2016). Molecular dating and diversification analyses revealed that mosses and liverworts underwent bursts of diversification since the mid-Mesozoic and they still actively diversifying (Laenen *et al.* 2014). These results also hypothesized that the lower extant diversity of bryophytes in comparison with Angiosperms, comprising 80 % of all extant plant species (ca. 300,000 ssp.; Christenhusz & Byng 2016) results from massive extinctions, as in gymnosperms (Crips & Cook 2011).

Mosses, Liverworts and Hornworts are united by sharing unique life cycle featuring alternating haploid and diploid generations with a dominant gametophyte. Recent phylogenomic analysis have supported a paraphyletic bryophytes [(green algae,(liverworts,(mosses,(hornworts,vascular plants))))] (Ruhfel *et al.* 2014, chloroplast genome; Liu *et al.* 2014, mitochondrial genome), or a clade comprising mosses and liverworts and this clade is either sister to tracheophytes [(green algae,(hornworts,((mosses,liverworts),vascular plants)))], sister to a clade composed of hornworts and vascular plants [(green algae,(((mosses,liverworts),hornworts),vascular plants))] or included in a clade comprising all three bryophyte lineages [(green algae,((hornworts,(mosses,liverworts)),vascular plants))] (Nishiyama *et al.* 2004, Ruhfel *et al.* 2014, chloroplast genome; Wickett *et al.* 2014, nuclear genome).

The life cycle of bryophytes is divided into a dominant haploid gametophytic phase and a usually short-lived sessile diploid sporophytic phase. Both the gametophyte and sporophyte generations have sufficiently well developed to be taxonomically and phylogenetically informative. However, the morphological plasticity of bryophytes is uneven. Gametophytes often display a high degree of polymorphism while sporophytes remain less variable, especially liverworts and hornworts (e.g. Schuster 1966, Vanderpoorten & Goffinet 2009, Stanton & Reeb 2016), making it difficult to trace the origin and evolutionary history of sporophyte diversification in bryophytes. Mosses are most divergent group in bryophytes and

show the most complex and diverse sporophytes among bryophytes. The diversification of moss sporophytes can be explained in relation to their habitat preferences, and an understanding of the sporophyte modification will help to clarify ideas of evolutionary parallelisms and adaptive specialization in mosses (Vitt 1981).

Pottiaceae Hampe (Dicranidae, Bryopsida) is the most generic and species rich family in mosses, with around 1,400 species in 83 genera, comprising more than 10 % of extant moss species (Frey & Stech 2009), and exhibit a great variety of apparent morphological, physiological and genecological adaptations to their particular environments (Zander 1993). Geometric morphometric analyses with evolutionary hypothesis testing has revealed that the family is one of the lineages in which most shifts in sporangium shape have occurred, and the genus *Weissia* one of the most notable, where a shift in both habitat and also sporangium shape is seen (Rose *et al.* 2016). In addition to sporangium shape, the family shows a great range of variation in sporophytic structure, including length of the seta, capsule dehiscence, capsule ornamentation, and peristome teeth morphology. These features suggest that the family could be a model group for tracing the origin and evolutionary history of sporophyte diversification in bryophytes.

From the early 19th century, variously attempts at a classification of the Pottiaceae and its related families have been proposed by many authors. The name Pottiaceae was validly published by Hampe (1853) using the name at new rank for subtribe Pottiinae Müll.Hal. He recognized only six genera (*Pottia*, *Fiedleria*, *Anacalypta*, *Desmatodon*, *Trichostomum* and *Barbula*) in the family, but he treated other genera currently placed in Pottiaceae as a member of other families: *Acaulon*, *Astomum*, *Phascum* and *Ephemerum* in Phascaceae; *Hyophila* and *Leptodontium* in Hyophylaceae; *Gymnostomum*, *Hymenostomum* and *Weissia* in Weissiaceae; *Cinclidotus* in Grimmiaceae. Most other authors in the 19th Century divided the Pottiaceae into smaller families based mainly on sporophytic characters. Mitten (1859) merged Pottiaceae, Phascaceae, Ephemeraceae *ex parte* , Weissiaceae *ex parte* into Trichostomataceae based on the combination of sporophytic (peristome) and gametophytic (leaf cell) characters. Brotherus (1901–1902) also recognized only one family, the Pottiaceae, with 53 genera in four subfamilies [Trichostomoideae (32), Cinclidotoideae (1), Pottioideae (19) and Encalyptoideae (1)]. Later, Brotherus

(1924–1925) recognized 71 genera in five subfamilies [Pleuroweisioideae (3), Merceyoideae (2), Trichostomoideae (47), Pottioideae (18),Cinclidotoideae (1)]. His treatment remained as the standard compiliative work on the family to this date (Zander 1993). The use of Pottiaceae as a single family name is nomenclaturally appropriate since the name is the conserved one listed in App. IIB (ICN Art. 14.5, McNeill *et al.* 2012), as well as earliest legitimate one with the same rank (ICN Art. 11.3, McNeill *et al.* 2012). Many authors since Brotherus (1924–1925) have followed the single family concept of the Pottiaceae, while *Cinclidotus* is variously treated in the Pottiaceae or in its own family Cinclidotaceae. Historical development of family and supra-generic circumscriptions for the Pottiaceae has been discussed by several authors (Saito 1975, Zander 1993, Werner *et al.* 2004a).

Since Brotherus' (1924–1925) treatment, several comprehensive studies have been published (Hilpert 1933, Chen 1941, Saito 1975, Zander 1993). These studies contributed deep knowledge and extensive discussion to the systematics of the Pottiaceae. Hilpert (1933) separated Pottiaceae *sensu* Brotherus (1924–1925) into three families: Cinclidotaceae, Pottiaceae and Trichostomataceae, and placed the most genera in Trichostomataceae, which now corresponds to the subfamily Trichostomoideae in Pottiaceae. He recognized 39 genera in three subfamilies [Barbuloideae (22),Trichostomoideae (13) and Leptodontioideae (4)] in Trichostomataceae and discussed on morphology of each genus, while the rest of the genera in Pottiaceae and Cinclidotaceae were not studied. He also presented modern charts showing phylogenetic relationships among supra-specific taxa.

Chen (1941) followed the single family concept of Pottiaceae and recognized six subfamilies [Eucladioideae (8), Trichostomoideae (8), Barbuloideae (8), Pottioideae (8), Leptodontioideae (1) and Cinclidotoideae (2)] in East Asian taxa. He also discussed on phylogenetic relationships of intra-familial taxa with a chart of relationships.

Saito (1975) recognized two subfamilis [Trichostomoideae (6) and Pottioideae (14)] in Japanese taxa and *Cinclidotus* as the family of its own. He presented a generic and supra-generic classification based on several new characters such as axillary hairs, and thorough morphological and anatomical study. He also discussed on character evolution in the family such as reduction series in the peristome structure.

In the extensive monograph focusing on world genera of Pottiaceae, Zander (1993) conducted cladistic analysis based on 74 morphological characters and recognized seven subfamilies [Timmielloideae (1), Erythrophyllopsidoideae (2), Gertrudielloideae (1), Chionolomoideae (3), Trichostomoideae (8), Merceyoideae (20) and Pottioideae (39)]. He presented detailed descriptions and illustrations of all genera recognized in this study. The genus *Cinclidotus* was excluded from the Pottiaceae.

Nevertheless their efforts, systematics of the family remains a challenge. The phyletic assessment and classification of Pottiaceae based on morphological criteria is very difficult and controversial at any taxonomic rank, even including the familial circumscription, due to its entangled morphological diversification being associated with a wide range of habitat types, substrata and life strategies. A source of independent phyletic and taxonomic criteria is therefore needed for sound systematics and to trace the evolutionary history of diversification in this family. During the past 20 years a number of molecular phylogenetic analyses have been conducted to resolve the phylogenetic position of the family in Dicranidae (haplolepideous mosses) and inter- or intra- generic relationships within the family, and some taxonomic changes have been made. However, the limited number of morpho-molecular systematics at familial and subfamilial rank have been proposed (Werner *et al.* 2004a, Zander 2006, Frey & Stech 2009), and the systematic position of the genus *Timmiella* (Pottiaceae) remained to be fully resolved.

The aims of the present study are to (1) reconstruct a robust phylogeny of Pottiaceae and assess familial and subfamilial circumscriptions using comprehensive taxon sampling, and proper markers and analysis scheme, and (2) obtain a better knowledge of sporophyte evolution of this family through phylogenetic and taxonomic studies focused on the genus *Weissia*, which shows most complex and diverse sporophytes among the genera of Pottiaceae.

The present study consist of the following three chapters: (1) On the systematic position of the genus *Timmiella* and the circumscription of the family Pottiaceae, (2) Molecular phylogeny of the family Pottiaceae with special reference to the subfamilial circumscription, and (3) Molecular phylogeny and taxonomic revision of cleistocarpous species of *Weissia* in Japan.

In chapter 1, the systematic position of the genus *Timmiella* is reassessed based

on comprehensive taxon sampling of the Dicranidae and morphological assessment to provide a monophyletic circumscription of the family Pottiaceae. In chapter 2, Molecular phylogenetic inference based on a new approach using a codon substitution model is undertaken to reconstruct subfamilial relationships within the family Pottiaceae. In chapter 3, phylogenetic relationships and species circumscriptions of the cleistocarpous *Weissia* species in Japan are reassessed based on detailed morphological investigation and molecular phylogenetic inference, and the origin of sporophyte diversity within the genus is discussed.

Abbreviations and symbols in this dessertation are listed in Appendix A.

Chapter 1
On the systematic position of the genus *Timmiella* and the circumscription of the family Pottiaceae

Introduction

The genus *Timmiella* (De Not.) Limpr. is a haplolepideous moss which has been placed in the family Pottiaceae Hampe since it was first described as a section of the genus *Trichostomum* Bruch by De Notaris (1865). Although many authors have placed the genus in the subfamily Trichostomoideae Broth. of the Pottiaceae (e.g. Limpricht 1888; Brotherus 1902, 1924; Hilpert 1933; Chen 1941; Podpěra 1954; Saito 1975; Corley *et al.* 1981; Walther 1983), the systematic position of the genus has been questioned because of its unique morphological characters such as denticulate to dentate leaf margins, bistratose lamina, adaxially bulging and abaxially flat lamina, and sinistrorse peristomes (twisted to the left when viewed from the side). These characters indicate that it has a different evolutionary line from the other genera of Trichostomoideae as noted by Saito (1975). In the extensive monograph of Pottiaceae, Zander (1993) recognized seven subfamilies based on cladistic analysis using morphological characters, and established the subfamily Timmielloideae R.H.Zander with its sole genus *Timmiella*. Recent molecular phylogenetic studies have suggested the exclusion of *T. anomala* (Bruch & Schimp.) Limpr. or *T. crassinervis* (Hampe) L.F.Koch from the Pottiaceae and their repositioning as an early-diversing clade within the Dicranidae (haplolepideous mosses) (La Farge *et al.* 2000, 2002; Werner *et al.* 2004a; Hedderson *et al.* 2004; Tsubota *et al.* 2004; Wahrmund *et al.* 2009, 2010; Cox *et al.* 2010). However, *Timmiella* was retained as a member of the Pottiaceae because of its morphological affinity to the family, especially the distinctive twisted peristome (Zander 2006, 2007a). No taxonomic changes had been made based on the monophyletic groupings because the phylogenetic position of the genus in the early-diversing haplolepideous mosses remained to be fully resolved.

In this chapter, the phylogenetic position and taxonomic treatment of *Timmiella* and its allied genera are reassessed based on phylogenetic analysis with concatenated sequences of chloroplast ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) and ribosomal protein S4 (*rps4*) genes. I also discuss here morphological

characters that support the monophyly inferred from my analysis.

Materials and Methods

Taxon sampling

17 *rbcL* and 16 *rps4* gene sequences of the Dicranidae, including the type species of *Timmiella*, *T. anomala*, were newly obtained for the present study. A total of 85 concatenated *rbcL* and *rps4* gene sequences were examined in the present analysis, as shown in Appendix B. Taxa were selected to represent the haplolepideous moss families recognized by Frey & Stech (2009), as well as taxa placed in or near the Dicranidae by Cox *et al.* (2010). I also included representatives of peristomate moss orders as outgroup taxa and used *Buxbaumia aphylla* Hedw. and *Diphyscium fulvifolium* Mitt. as root of the tree following Tsubota *et al.* (2003, 2004) and Cox *et al.* (2010).

DNA extraction, PCR amplification and DNA sequencing

The protocol of the DNA extraction of total DNA followed Tsubota *et al.* (2009) and Suzuki *et al.* (2013). Condition of PCR amplification for both *rbcL* and *rps4* genes followed Tsubota *et al.* (1999, 2000) and Tsubota *et al.* (2013) with modifications: denaturation at 98 °C for 10 sec., annealing at 58 °C for 35 sec., and extention at 65 °C for 1–1.5 min. for total 45 cycles. Direct sequence analyses of the PCR products were performed following Inoue *et al.* (2012). The design of the PCR and DNA sequencing primers followed Nadot *et al.* (1994), Tsubota *et al.* (1999, 2001), Masuzaki *et al.* (2010), Inoue *et al.* (2011, 2012) and Inoue and Tsubota (2014) (see also Appendix C). Sequences obtained here have been submitted to DDBJ/EMBL/GenBank International Nucleotide Sequence Database Collaboration (INSDC).

Sequence alignment and phylogenetic analyses

The sequences were aligned using the program MAFFT ver. 7.027 (Katoh & Standley 2013) with some manual adjustment on the sequence editor of MEGA5.2 (Tamura *et al.* 2011). The indel confirmed in the *rps4* sequence of *Catoscopium nigritum* (Hedw.) Brid. was treated as missing data.

Phylogenetic analysis using concatenated *rbcL* and *rps4* gene sequences was performed based on maximum likelihood (ML) criteria (Felsenstein 1981) as previously described (Tsubota *et al.* 2003, Ozeki *et al.* 2007, Masuzaki *et al.* 2010) with some

differences as follows: Prior to the phylogenetic reconstruction, model testing was performed based on AICc (Sugiura 1978) using Kakusan4 (ver. 4.0.2012.12.14; Tanabe 2011) to make a rational decision regarding the partitioning scheme and nucleotide substitution model that best fitted my data, and AU test in the final stage of the analysis scheme. Phylogenetic trees were constructed using the following four program packages to obtain the candidate topologies: (1) RAxML ver. 8.0.0 (Stamatakis 2014) with ML method using codon-partitioned model (GTR + Γ for all codon positions); (2) Garli ver. 2.01 (Zwickl 2006) with ML method using codon partitioned model (GTR + Γ + Invariatn for all codon positions); (3) PAUPRat (Sikes & Lewis 2001) over PAUP* ver. 4.0b10 (Swofford 2002) with the maximum parsimony (MP) method (Fitch 1971) to implement Parsimony Ratchet searches (Nixon 1999) using the Parsimony Ratchet search strategy with random weighting of each character in fifty 200 iteration runs; (4) BEAST v1.8.0 (Drummond *et al.* 2012) with Bayesian inference (BI) method using codon-partitioned model (GTR + Γ for all codon positions) with 100,000,000 generations. Re-calculation of likelihood values for each tree topology was performed with the GTR (Yang 1994) + Γ + Invariant model which is the best fitted model for my data by PAUP. Alternative topology test and edge analysis were performed using the p-value of the approximate unbiased test (AU; Shimodaira 2002, 2004), bootstrap probability calculated through the same theory as AU (NP), and Bayesian posterior probability calculated by the BIC approximation (PP; Schwarz 1978, Hasegawa & Kishino 1989) as implemented in CONSEL ver. 0.20 (Shimodaira & Hasegawa 2001). A 50 % majority-rule condensed tree for the topologies passing both AU and PP tests was also computed by MEGA. Supporting values more than 50 % were overlaid to assess the robustness of each branch of the condensed topology: AU, NP and PP are shown on or near each branch.

Morphological investigation

Both fresh materials and dried specimens were used for light microscopic and scanning electron microscopic (SEM) observations. Preparation for SEM observation followed Inoue *et al.* (2011). Voucher specimen information is listed in Appendix D.

Results

A total of 1,595 distinct topologies were obtained in the ML, MP and BI analyses, of which 978 topologies passed the AU test and nine topologies passed the PP test. Fig. 1.1 shows the 50 % majority-rule condensed tree for the topologies passing both AU and PP tests. Five main clades are confirmed in the early-diversing haplolepideous moss lineages: Catoscopiaceae Boulay ex Broth., *Timmiella-Luisierella* Thér. & P. de la Varde-Distichiaceae Schimp., Drummondiaceae Goffinet-Scouleriaceae S.P.Churchill-*Hymenoloma brevipes* (Müll.Hal.) Ochyra-*Ditrichum flexicaule* (Schwägr.) Hampe, Bryoxiphiaceae Besch., and Eustichiaceae Broth. The clade consisting of *Timmiella*, *Luisierella* and *Distichium* Bruch & Schimp. is resolved as the second-branching clade in the haplolepideous moss lineages. In this clade, *Timmiella* is sister to *Luisierella* with moderate supporting values (AU/NP/PP = 75/61/1.00; Fig. 1.1).

Based on the phylogenetic tree, we reassessed the morphological characters shared with *Timmiella* and *Luisierella* which discriminate them from other haplolepideous moss families. In addition to gametophytic similarity: adaxially bulging and abaxially flat leaf surfaces, the sinistrorsely arranged operculum cells are unique to them. The operculum cells of *T. anomala* (type species) are sinistrorsely arranged and correlate with their sinistrorse peristome (Fig. 1.2: C, D). *T. acaulon* (Müll.Hal.) R.H.Zander, *T. barbuloides* (Brid.) Mönk., *T. crassinervis* and *T. diminuta* (Müll.Hal.) P.C.Chen, whose peristomes are apparently straight, have sinistrorsely arranged operculum cells (Fig. 1.2: A, B, E–J). *Luisierella barbula* (Schwägr.) Steere, also has sinistrorsely arranged operculum cells, although its peristome is delicate and sometimes absent (Fig. 1.2: K, L).

Discussion

In this chapter, we have shown the precise phylogenetic position of *Timmiella* by using all basal haplolepideous taxa suggested in previous studies (La Farge *et al.* 2000, 2002; Werner *et al.* 2004a, 2013; Hedderson *et al.* 2004; Tsubota *et al.* 2004; Wahrmund *et al.* 2009, 2010; Cox *et al.* 2010; Stech *et al.* 2012). The genus is distinct from the Pottiaceae-clade and resolved as the second-branching clade together with *Luisierella* and *Distichium* among the Dicranidae lineages.

Zander (1993) distinguished *Timmiella* from the other members of the Pottiacaeae and established a monogeneric subfamily Timmielloideae based on a combination of characters: very wide costa with multiple hydroid strands, epapillose leaf cells, adaxially bulging and abaxially nearly flat laminal cells, weakly sinistrorse (clockwise) or straight peristome. My study suggests that the direction of twist of the operculum cells, as well as the peristome, is a significant character that discriminates the genus from Pottiaceae and the other haplolepideous moss families. In *Timmiella* spp. with peristomes that are apparently straight, the operculum cells are sinistrorsely arranged. This suggests that the genus has a fundamentally sinistrorse amphithecium. Although its peristome is delicate and sometimes absent, *Luisierella*, which is a monotypic genus of Pottiaceae and phylogenetically sister to *Timmiella*, also has sinistrorsely arranged operculum cells, adaxially bulging and abaxially flat leaf cell surfaces. The close relationship between *Timmiella* and *Luisierella* is thus both morphologically and phylogenetically supported. *Luisierella* is much smaller than *Timmiella* in plant size, and often grows in association with cyanobacteria (blue-green algae) (Reese 1984, Deguchi 1987, Zander 1993). The genus *Seligeria* Bruch & Schimp. which is a very small moss and phylogenetically sister to Grimmiaceae Arn. (e.g. Tsubota *et al.* 2003) also grows in association with cyanobacteria (Longton 1988a). In the course of evolution, the association with cyanobacteria might have led these genera to reduced plant size.

The combination of characters: (1) adaxially bulging and abaxially flat leaf cell surfaces, (2) when present, sinistrorse or straight peristomes, and (3) sinistrorsely arranged operculum cells, supports the molecular groupings inferred from my analysis, and discriminates *Timmiella* and *Luisierella* from the other haplolepideous moss families. This study also provides the monophyletic circumscription of the family

Pottiaceae, which is characterized by dextrosely twisted peristome or dextrosely arranged operculum cells.

No significant characters that link *Distichium* and *Timmiella* + *Luisierella* are confirmed, although the two groups are phylogenetically sister to each other and both have the saxicolous habitat especially in limestone area (e.g. Tanaka 2012, Inoue *et al.* 2014). The genus *Distichium* has distinct sporophytic and gametophytic characters: peristome teeth with dextrorse spiral thickenings in the basal portion, the distichous leaf arrangement and the mammillose subula. Although the two groups share mammillose leaf surfaces, my observation proved that the mammillae are present in both adaxial and abaxial surfaces in *Distichium*, whereas in *Timmiella* + *Luisierella* they are restricted to adaxial surface. The Phylogenetic analysis using extensive taxon sampling of Dicranidae also supported the clade comprising *Distichium*, *Luisierella* and *Timmiella*, although *Luisierella* and *Timmiella* were paraphyletic (Fedosov *et al.* 2016).

The family Distichiaceae was originally proposed by Schimper (1860) to include *Distichium* and *Eustichium* Bruch & Schimp. (= *Bryoxiphium* Mitt.), and later Limpricht (1887) placed *Distichium* in Ditrichaceae Limpr. Due to its universal acceptance, Magill (1977) proposed Ditrichaceae as a conserved name against Distichiaceae and Ceratodontaceae Schimp., and this proposal was adopted in the Berlin Code (Greuter *et al.* 1988). From my study, the resultant tree suggests that *Distichium* should be treated as a distinct family from the other genera of Ditrichaceae. The family name Distichiaceae can be used to accommodate *Distichium*, because Distichiaceae and Ditrichaceae are heterotypic synonyms and either can be adopted as correct names when they are considered distinct from each other (ICN Art. 14.6, McNeill *et al.* 2012).

Taxonomy

Based on phylogenetic and morphological distinctions from the other haplolepideous moss families, I concluded that *Timmiella* and *Luisierella* are excluded from Pottiaceae and warrant accommodation within a new family. However, from the results no final decision regarding the order within which these families are accommodated can be made. Further analyses based on increased taxa, especially polyphyletic families such as Dicranaceae Schimp., Ditrichaceae and Oncophoraceae M.Stech, are necessary for further resolution.

Timmiellaceae Y.Inoue & H.Tsubota, Phytotaxa 181: 156. 2014.
Basionym: Timmielloideae R.H.Zander, Bull. Buffalo Soc. Nat. Sci. 32: 68. 1993.
Type: *Timmiella* (De Not.) Limpr., Laubm. Deutch. 1: 590. 1888. [based on *Trichostomum* sect. *Timmiella* De Not., Comment. Soc. Crittog. Ital. 2: 100. 1865.]
Included genera: *Timmiella* (De Not.) Limpr. and *Luisierella* Thér. & P.de la Varde
Diagnosis: Plants acrocarpous; leaves incurved and tubulose when dry, spreading when moist, leaf cell surfaces adaxially bulging and abaxially flat; peristomes straight to sinistrorse or absent, operculum cells sinistrorsely arranged.

Chapter 2
Molecular phylogeny of the family Pottiaceae with special reference to the subfamilial circumscription

Introduction

The family Pottiaceae Hampe is the most generic and species rich family of Bryophyta Schimp., with around 1,400 species in 83 genera, comprising more than 10 % of the extant moss species (Frey & Stech 2009). Widely distributed in the world, its species have adapted to a wide range of habitat types including xeric, mesic and hydric, growing on various substrata including saxicolous, tericolous and corticolous, and a possessing a variety of life strategies including perennial, annual and ephemeral. The family exhibits a great variety of apparent morphological, physiological and genecological adaptations to their particular environments (Zander 1993). Recent geometric morphometric analyses with evolutionary hypothesis testing revealed that the Pottiaceae was one of the lineages in which multiple evolutional changes of sporangium shape associated with the types of habitat have occurred (Rose *et al.* 2016).

Among the various types of habitat where they are found, most species exhibit a great tolerance of hot and dry environments, and show numerous adaptations to such harsh environments. The shoots of *Syntrichia caninervis* Mitt. remained viable after exposure to 120 °C for 30 min., which is a new upper thermo tolerance record for adult eukaryotic organisms for a minimum 30 min. exposure time (Stark *et al.* 2009), and dried herbarium specimen of *S. ruralis* (Hedw.) F.Weber & D.Mohr retained their viability for 20 years and 3 months, which is the longest record for a moss withstanding continuous desiccation (Stark *et al.* 2016). The Pottiaceae includes all three life strategies which dominate in hot desert bryofloras: the perennial stayer (most of the family), the annual shuttle (*Pottia* Ehrh. ex Fürnr. and *Phascum* Hedw.) and the perennial shuttle [*Tortula pagorum* (Milde) De Not. and *T. papillosa* Wilson ex Spruce] (Longton 1988b).

Adaptation to such harsh selective pressures often leads to the presence of parallel or convergent characters which develop in response to the same environmental stimuli, complicating phyletic assessment. Chen (1941) suggested that the lamellae of *Pterygoneurum* Jur. represented features of convergent evolution and phylogenetically

have nothing in common with filaments of *Aloina* Kindb. and *Crossidium* Jur. On the other hand, Delgadillo (1975) argued for the close relationship between *Pterygoneurum* and *Crossidium* since the abnormal filaments of *Crossidium* spp. resemble the lamellae of *Pterygoneurum* spp. Magill (1981) also demonstrated that specialized chlorophyllose marginal cells occur in *Tortula porphyreoneura* (Müll.Hal.) C.C.Towns. and *Barbula arcuata* Griff. growing in arid grasslands in southern Africa. He also suggested that the modification of marginal or costal cells into differentiated photosynthetic tissues is an adaptation to harsh environments, expressed through convergent evolution by several genera in the Pottiaceae: *Acaulon* Müll.Hal., *Aloina*, *Barbula* Hedw., *Crossidium*, *Pterygoneurum* and *Tortula* Hedw.

Mature sporophytes provide taxonomically important characters in mosses, but many species from xeric habitats produce no, or very few sporophytes, presumably because of the difficulty in effecting fertilization or allowing for the maturation of sporophytes under such xeric conditions. Stark (2002) and Stark *et al.* (2007) showed that in a desert climate, the massive sporophyte abortions seen in *Tortula inermis* (Brid.) Mont. are correlated with unusually heavy summer precipitation events followed by rapid drying, and that the sporophytes are more sensitive to rapid drying than are maternal gametophytes.

These environmental features have made the classification of Pottiaceae very difficult and controversial: the species concepts are often not well understood, and the family has been variously classified without an understanding of its phylogenetic relationships, leaving many ambiguous or poorly understood taxa unresolved (Satio 1975). A source of independent taxonomic evidence is therefore needed for the revision of this family (Spagnuolo *et al.* 1996, 1997), and during the past 20 years a number of molecular phylogenetic analyses have been conducted in an attempt to resolve relationships within the family (e.g. Spagnuolo *et al.* 1996, 1999; Werner *et al.* 2004a, 2005; Cano *et al.* 2010; Kučera *et al.* 2013; Alonso *et al.* 2016). From the early 19th century, variously attempts at a classification of the Pottiaceae and its related families have been proposed by many researchers as summarized in Table 2.1. The history of classification of the family based on morphological criteria has been overviewed by several authors (e.g. Saito 1975, Zander 1993, Werner *et al.* 2004a), with a limited number of reviews of recent progress in understanding the systematic

relationships based on integrated morphological and molecular data (Stech *et al.* 2012).

In this chapter, I review the current state of knowledge on phylogenetic relationships and classification at familial and subfamilial levels within the Pottiaceae. Previous studies are compared with a novel phylogenetic inference based on concatenated sequences of ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) and chloroplast ribosomal protein S4 (*rps4*) genes with codon substitution model. The codon substitution model is a statistically higher precision model than nucleotide and amino acid substitution models for the evolutionary analysis of protein-coding sequences (Seo & Kishino 2008, 2009; Miyazawa 2011).

Materials and Methods

Phylogenetic markers and taxon sampling

20 *rbcL* and 23 *rps4* gene sequences were newly obtained. The supposed ingroup species represent all the subfamilies of Pottiaceae recognized by Werner *et al.* (2004a): Trichostomoideae Broth., Pottioideae Broth., Merceyoideae Broth., as well as *Streblotrichum convolutum* (Hedw.) P.Beauv., the type species of the genus *Streblotrichum* P.Beauv., whose phylogenetic position has remained ambiguous (Köckinger & Kučera 2011, Kučera *et al.* 2013). Outgroup species [*Ditrichum heteromallum* (Hedw.) E.Britton and *Pseudephemerum nitidum* (Hedw.) Loeske] were selected based on the results of Inoue and Tsubota (2014), and Fedosov *et al.* (2016). List of investigated species was shown in Appendix E.

DNA extraction, PCR amplification and DNA sequencing

The protocol for total DNA extraction followed Tsubota *et al.* (1999) and Suzuki *et al.* (2013). Conditions for PCR amplifications for both *rbcL* and *rps4* genes followed Inoue and Tsubota (2014). Direct sequence analyses of the PCR products were performed following Tsubota *et al.* (1999, 2000, 2001) and Inoue *et al.* (2012). Primers used for PCR amplification and DNA sequencing followed Nadot *et al.* (1994), Souza-Chies *et al.* (1997), Tsubota *et al.* (1999, 2001), Masuzaki *et al.* (2010), Inoue *et al.* (2011, 2012), and Inoue and Tsubota (2014) (see also Appendix C). Sequences obtained here have been submitted to DDBJ/EMBL/GenBank International Nucleotide Sequence Database Collaboration (INSDC).

Phylogenetic analyses

Sequences of two genes were aligned separately by using the program MAFFT ver. 7.027 (Katoh & Standley 2013) with some manual adjustment on the sequence editor of MEGA ver. 5.2 (Tamura *et al.* 2011). Start and stop codons were removed, and the resulting total length was 2,025 bp. Phylogenetic analysis using the concatenated sequences of *rbcL* and *rps4* genes was performed based on the maximum likelihood (ML) method (Felsenstein 1981) and the approximate unbiased (AU) test (Shimodaira 2002, 2004) in the final stage of the analysis scheme. Prior to the phylogenetic reconstruction, Kakusan4 (ver. 4.0.2012.12.14; Tanabe 2011) was used to

determine the appropriate substitution model and partitioning scheme for my data based on corrected Akaike Information Criterion (AICc: Sugiura 1978). Since the codon substitution model is inappropriate for an heuristic search due to the huge computational burden, phylogenetic trees were constructed using the following three program packages to obtain the candidate topologies: (1) RAxML ver. 8.2.8 (Stamatakis 2014) with ML method using the equal mean rate model among codon positions (GTR + Γ for all codon positions of *rbcL* and *rps4*) with 1,000 heuristic searches; (2) PAUPRat (Sikes & Lewis 2001) over PAUP* ver. 4.0b10 (Swofford 2002) with the maximum parsimony (MP) method (Fitch 1971) to implement Parsimony Ratchet searches (Nixon 1999) using the Parsimony Ratchet search strategy with random weighting of each character in fifty 200 iteration runs; (3) MrBayes ver. 3.2.5 (Ronquist *et al.* 2012) with Bayesian inference (BI) method using the proportional model among codon positions (GTR + Γ for all codon positions of *rbcL*, HKY85 + Γ for first and second codon positions of *rps4*, GTR + Homogeneous for third codon position of *rps4*) with 10,000,000 generations, sampling trees every 1,000 generations. A 50 % majority-rule consensus tree was calculated after the convergence of the chains and discarding 25 % of the sampled trees as burn-in.

Based on the ML criteria, re-calculation of likelihood values for each tree topology was performed with the codon substitution model which was more or less equivalent to the GY94 model (Goldman & Yang 1994) implemented in Garli var. 2.01 (Zwickl 2006). The set of candidate topologies was evaluated by the AU test and Bayesian posterior probability (PP) calculated by the BIC approximation (Schwarz 1978, Hasegawa & Kishino 1989) using CONSEL ver. 0.20 (Shimodaira & Hasegawa 2001). A strict condensed tree for the topologies with high ranking log-likelihood values that passed both AU and PP tests was also computed by MEGA. Supporting values more than 50 % obtained by CONSEL were overlaid to assess the robustness of each branch of the highest likelihood and strict condensed topologies: AU test (AU), bootstrap probabilities (NP), and Bayesian posterior probabilities (PP) are shown on or near each branch (AU/NP/PP).

Results

The concatenated data matrix had a total length of 2,025 bp, of which 369 (18.2 %) were variable, and 209 (56.6 % of the variable sites) were parsimony-informative.

A total of 70 topologies were obtained from the three analyses: four ML topologies by RAxML; 65 MP by PAUPRat over PAUP*; and one BI by MrBayes. More detailed topologies were searched through the obtained trees using a loglikelihood measure. The best-supported tree with the highest likelihood value is shown in Fig. 2.1. The log-likelihood value for the tree was -7206.803252. One strict condensed tree was also obtained for the six topologies with high-ranking log-likelihood values that passed both AU and PP tests as shown in Fig. 2.2. Values for the percentage of supported topologies for each branch were superimposed in Figs. 2.1 and 2.2.

The best-supported tree with highest likelihood value confirmed the monophyly of the Pottiaceae with four major clades within the family, corresponding to Trichostomoideae (T), Pottioideae (P), Merceyoideae (M), and the newly proposed Streblotrichoideae (S) as shown in Fig. 2.1. The Merceyoideae was resolved as the most basal clade within the family with high supporting values (100/100/1.00). Pottioideae comprised the sister-group to Trichostomoideae and this clade was sister to Streblotrichoideae. Although the relationships among these three subfamilies were weakly supported (-/50/0.88), the strict condensed tree also supported this branching pattern as shown in Fig. 2.2.

Discussion

Phylogenetic position and circumscription of Pottiaceae

Earlier phylogenetic studies using molecular markers focused on the Pottiaceae were based on the nuclear internal transcribed spacer (nr ITS) region (Colacino & Mishler 1996; Spagnuolo *et al.* 1996, 1999). Spagnuolo *et al.* (1999) successfully aligned ITS1 sequences with a reduced number of taxa of Pottiaceae, and showed the usefulness of DNA sequences to clarify the phylogenetic relationships within this family. Their results suggested that the classification of the Pottiaceae based on morphological data did not depict the pattern of descent and therefore the systematics of this group needed to be revised.

In molecular phylogenetic studies focusing on supra- familial relationships within mosses, the Pottiaceae was resolved in the clade of Dicranidae of the haplolepideous mosses (Cox & Hedderson 1999; Goffinet & Cox 2000; Goffinet *et al.* 2001; La Farge *et al.* 2000, 2002; Magombo 2003; Hedderson *et al.* 2004; Tsubota *et al.* 2004). However the number of genera and species included in these analyses was limited. Werner *et al.* (2004a) conducted the first comprehensive molecular phylogenetic analysis of the family using chloroplast *rps4* gene sequences which had been used successfully to resolve the phylogenetic relationships at species or generic level within the family (Werner *et al.* 2002, 2003). The Pottiaceae was almost monophyletic in its traditional circumscription, but with some exceptions as discussed below. Some genera, without general agreement on whether or not they belonged to Pottiaceae, were positioned in Pottiaceae (Werner *et al.* 2004a): *Cinclidotus* P.Beauv. (Cinclidotaceae Schimp.), *Ephemerum* Hampe (Ephemeraceae J.W.Griff. & Henfr.), *Goniomitrium* Hook. & Wilson (Funariaceae Schwägr.), *Kingiobryum* H.Rob. (Dicranaceae Schimp.) and *Splachnobryum* Müll.Hal. (Splachnobryaceae A.K.Kop.). The systematic position of *Cinclidotus*, *Ephemerum*, *Kingiobryum*, and *Splachnobryum* within Pottiaceae was also supported by other molecular phylogenetic studies (e.g. Goffinet *et al.* 2001; Sato *et al.* 2004, Werner *et al.* 2004b, 2007; Cox *et al.* 2010; Inoue *et al.* 2011, 2012). On the other hand, Werner *et al.* (2007) concluded that *Goniomitrium* should be excluded from Pottiaceae and placed again in Funariaceae, and they also showed that the name used in the previous studies resulted from misidentification. The inclusion of *Tridontium tasmanicum* Hook.f. (Grimmiaceae

Arn./Scouleriaceae S.P.Churchill) within Pottiaceae was also suggested by Cox *et al.* (2010) and Goffinet *et al.* (2011). *Hypodontium* Müll.Hal. and *Timmiella* (De Not.) Limpr. were resolved outside Pottiaceae (Werner *et al.* 2004a). Other molecular data also rejected the hypothesis of the taxonomic position of *Hypodontium* in Pottiaceae (Hedderson *et al.* 2004; Tsubota *et al.* 2004), and the family Hypodontiaceae M.Stech, as a distinct family, was segregated from Pottiaceae to accommodate *Hypodontium* (Stech & Frey 2008). In the most recent analysis (Fedosov *et al.* 2016) the Hypodontiaceae was included in the clade represented by Aongstroemiaceae De Not., Dicranaceae Schimp., Dicranellaceae M.Stech, Fissidentaceae Schimp. and Serpotortellaceae W.D.Reese & R.H.Zander. Although many molecular data rejected the hypothesis on the taxonomic position of *Timmiella* in Pottiaceae and supported its repositioning as an early diverging clade within the Dicranidae (La Farge *et al.* 2000, 2002; Hedderson *et al.* 2004; Tsubota *et al.* 2004; Wahrmund *et al.* 2009, 2010; Cox *et al.* 2010), it was retained as a member of the Pottiaceae because of its morphological affinity to the family, especially the presence of the characteristic twisted peristome. Zander (2006) argued that the complex twisted peristome was scattered among the lineages of the Pottiaceae *s. str.* and resulted from the re-activation of a silenced gene cluster involved in major organs that is highly adaptive, and that the same phenotype found in *Timmiella* and Pottiaceae *s. str.* was suggested to be homoiologous. Based on their comprehensive taxon sampling of basal haplolepideous taxa, Inoue and Tsubota (2014) showed the more sound phylogenetic position of *Timmiella* and showed its close relationship with *Luisierella* Thér. & P.de la Varde which had been placed in the Pottiaceae *s. str.* They further argued that the direction of twist of the operculum cells and of the peristome was a significant character that discriminated the genera from Pottiaceae and the other haplolepideous moss families, and proposed a new family Timmiellaceae Y.Inoue & H.Tsubota to accommodate the genera *Timmiella* and *Luisierella*. Their study also supported the monophyletic circumscription of the family Pottiaceae with a close relationship to Ditrichaceae Limpr. *p.p.* Phylogenetic trees using extensive taxon sampling of Dicranidae have showed that the Pottiaceae was resolved in the clade intermingled with genera of Bruchiaceae Schimp., Ditrichaceae *p.p.* and Erpodiaceae Broth. (Fedosov *et al.* 2015, 2016).

Subfamilial relationships within Pottiaceae

In his extensive revision of the family Pottiaceae, Zander (1993) recognized seven subfamilies based on phylogenetic analyses using morphological data as shown in Table 2.1. The molecular phylogenetic analyses by Werner *et al.* (2004a) based on cp *rps4* gene sequences included all the subfamilies recognized by Zander (1993), with the exception of Gertrudielloideae R.H.Zander. Based on the inferred trees they recognized three subfamilies: Trichostomoideae, Pottioideae and Merceyoideae. Their analyses supported the most basal position of Merceyoideae in the Pottiaceae. The remaining species of Pottiaceae formed the clade corresponding to Trichostomoideae and Pottioideae. The Trichostomoideae formed a paraphyletic group, and the Pottioideae was monophyletic. The genus *Eucladium* Bruch & Schimp. was placed in an intermediate position between these two subfamilies. The phylogenetic analysis by Werner *et al.* (2005) based on comprehensive taxon sampling of Trichostomoideae and nr ITS sequences supported the monophyly of the subfamily and *Eucladium* was resolved in the Trichostomoideae. Jiménez *et al.* (2012) first obtained DNA data for *Gertrudiella* Broth., and the genus was resolved in the Pottioideae *sensu* Werner *et al.* (2004a). Zander (2006) revised the classification of the family based on molecular and morphologically based phylogenies, and recognized five subfamilies [Timmielloideae R.H.Zander, Trichostomoideae (syn. Chionolomoideae R.H.Zander), Barbuloideae Hilp. (syn. Erythrophyllopsidoideae R.H.Zander, Gertrudielloideae R.H.Zander), Pottioideae and Merceyoideae]. The latest classification of subfamilies in Pottiaceae (Frey & Stech 2009) also adopted the five subfamilies recognized by Zander (2006). The present analyses also supported the most basal position of Merceyoideae within Pottiaceae, the monophyly of Trichostomoideae with inclusion of *Eucladium*, and the monophyly of Pottioideae (Figs. 2.1, 2.2).

Recent phylogenetic analyses (Köckinger & Kučera 2011, Kučera *et al.* 2013) have indicated the isolated position of some species traditionally assigned to the genus *Streblotrichum* P.Beauv. The phylogenetic position of this group is, however, ambiguous because it is: (1) sister to the clade Pottioideae-Trichostomoideae (cp *rps4*), (2) basal within the Trichostomoideae (cp *rps4* + *trnM-V*), or (3) even polyphyletic (nr ITS) with low support for any of these placements (Kučera *et al.* 2013). The sister position of *Streblotrichum* to the clade Trichostomoideae-Pottioideae was supported by

the ML tree inferred from the concatenated *rbcL* and *rps4* gene sequences with codon substitution model, and the strict condensed tree (Figs. 2.1, 2.2). *Streblotrichum* was originally established by Palisot de Beauvois (1804) and it has traditionally been recognized to be included in *Barbula s.l.* at generic, subgeneric or sectional rank (e.g. Limpricht 1888, Saito 1975). According to Kučera *et al.* (2013), the following combination of characters: (1) strongly differentiated convolute perichaetial leaves, (2) yellow seta, (3) revoluble annulus, (4) well-developed twisted peristome and (5) brown, spherical, rhizoidal gemmae, supports the molecular groupings and re-delimits Streblotrichum, with the acceptance of three species in the genus: *S. convolutum* (Hedw.) P.Beauv. (type species), *S. commutatum* (Jur.) Hilp. and *S. enderesii* (Garov.) Loeske. We conclude that the unique position of the genus *Steblotrichum* requires the recognition of a new subfamily, based on its morpho-molecular distinction.

As suggested by Stech *et al.* (2012), recent findings of several new species and genera based on morpho-molecular data indicate that the total diversity within the Pottiaceae remains insufficiently known or understood. In this chapter, we have succeeded in obtaining a more robust topology based on the codon substitution model. A more complete phylogenetic analysis could provide a better understanding of the diversity and evolutionary history of the family based on comprehensive taxon- and marker- samplings, as well as a proper analysis scheme.

Taxonomy

Subfamily Streblotrichoideae Y.Inoue & H.Tsubota, Hikobia 17: 124. 2016.

Basionym: *Streblotrichum* P.Beauv., Mag. Encycl. 9 (5): 317. 1804.

≡ *Tortula* subg. *Streblotrichum* (P.Beauv.) A.Chev., Fl. Gén. Env. Paris 2: 51. 1827.

≡ *Barbula* sect. *Streblotrichum* (P. Beauv.) Limpr., Laubm. Deutschl. 1: 626. 1888.

≡ *Barbula* subg. *Streblotrichum* (P.Beauv.) K.Saito, J. Hattori Bot. Lab. 39: 499. 1975.

= *Tortula* sect. *Convolutae* De Not., Mem. Reale Accad. Sci. Torino 40: 287. 1838. ≡ *Barbula* sect. *Convolutae* (De Not.) Bruch & Schimp., Bruch *et al.*, Bryol. Europ. 2: 91. 1842.

Type: *Streblotrichum* P.Beauv.

Included genus: *Streblotrichum* P.Beauv. [with *S. convolutum* (Hedw.) P.Beauv. as Type species]

Diagnosis: The subfamily Streblotrichoideae can be characterized by the combination of the following traits which discriminates it from the other subfamilies of Pottiaceae: Trichostomoideae, Pottioideae and Merceyoideae: (1) strongly convolute perichaetial leaves, (2) yellow seta, (3) revoluble annulus, (4) well-developed twisted peristome, and (5) brown, spherical, rhizoidal gemmae.

Chapter 3
Molecular phylogeny and taxonomic revision of cleistocarpous species of *Weissia* in Japan

Introduction

Among bryophytes, mosses show the most complex and diverse sporophytes. Sporophyte diversification can be explained in relation to their habitat preferences, and an understanding of sporophyte modification will help to clarify ideas of evolutionary parallelisms and adaptive specialization in mosses (Vitt 1981). The Pottiaceae Hampe is the most generic and species rich family of mosses, with around 1,400 species in 83 genera, comprising more than 10 % of the known extant moss species (Frey & Stech 2009), and exhibit a great variety of apparent morphological, physiological and genecological adaptations to their particular environments (Zander 1993). Geometric morphometric analyses together with evolutionary hypothesis testing have revealed that Pottiaceae is one of the lineages in which most shifts in sporangium shape have occurred, and the genus *Weissia* Hedw. one of the most notable where a shift in both sporangium shape and also habitat is seen (Rose *et al.* 2016). These results indicate the potential for the genus to be used as a model organism for investigating morphological diversification in moss sporophytes.

The genus *Weissia s.l.* grows mainly on arable land which is a transient habitat subject to regular disturbance such as by cultivation (Porley 2008). Sporophytes of the genus show a great range of variability, including having exserted stegocarpous capsules, immersed cleistocarpous capsules, and various combination of sporophyte characters, while the gametophytes are essentially identical and distinguishing species when sterile is difficult (Stoneburner 1985). These characteristics have caused incongruence between gametophyte based and sporophyte based classifications, and there has been no consensus on the species or even generic circumscriptions of this group (see review by Stoneburner 1985). *Weissia s.l.* is often divided into four genera: *Astomum* Hampe, *Hymenostomum* R.Br., *Phasconica* Müll.Hal. and *Weissia s. str.* *Astomum* is characterized by immersed cleistocarpous capsules, *Hymenostomum* by exserted stegocarpous, eperistomate capsules with hymenium, *Phasconica* is characterized by immersed stegocarpous (macrostomous), eperistomate capsules, and *Weissia s. str.* is

characterized by exserted stegocarpous, peristomate capsules. Morphological, cytological and molecular phylogenetic studies have shown close relationships among these genera and resulted in the subdivision of *Weissia* into several genera, and also lent support to the congeneric treatment of *Weissia* (*Weissia s.l.*). There have been many reports of morphologically intermediate or malformed sporophytes presumably caused by hybridization between the species of *Astomum* and *Weissia s. str.* or of *Astomum* and *Hymenostomum* in nature (Nicholson 1905, 1906; Smith 1964, Reese & Lemmon 1965, Crundwell & Nyholm 1972, Khanna 1960, Anderson & Lemmon 1972, Williams 1966), and cytological analysis has also provided circumstantial evidence of hybrid sporophytes (Khanna 1960, Anderson & Lemmon 1972). Superficial characters of spores in *Astomum*, *Hymenostomum* and *Weissia s. str.*, are very nearly the same, favoring a congeneric concept (Saito & Hirohama 1974). The phylogenetic tree based on nuclear ribosomal internal transcribed spacer (nr ITS) sequences has shown the independent origin (parallelism) of sporophyte structures and rapid diversification and radiation in this group (Werner *et al.* 2005). Based on this morphological and molecular evidence, I follow the congeneric concept of *Weissia* and include *Astomum*, *Hymenostomum* and *Phasconica* within the broader concept of the genus in this chapter.

In the Far East region, many species with different types of sporophytes have been described (e.g. Chen 1941, Saito 1975, Eddy 1990, Akiyama 1996). However, there are few DNA sequence data for species in this region, and a revisional study using integrated morphological and molecular data is necessary to clarify the evolutionary history and systematics of *Weissia* on a global scale. In this chapter I have focused on cleistocarpous species of the genus (traditionally treated as *Astomum*) which include many heterogeneous capsule taxa. In Japan, five cleistocarpous species of *Weissia* had been reported as *Astomum*: *A. acuminatum* Dixon & Thér., *A. crispum* (Hedw.) Hampe, *A. exsertum* Broth., *A. japonicum* G.Roth and *A. kiiense* S.Okamura. In a monograph of Japanese Pottiaceae, Saito (1975) recognized two cleistocarpous species under *Weissia* subg. *Astomum* (Hampe) Kindb.: *W. longifolia* Mitt. [as *W. crispa* (Hedw.) Mitt.] and *W. exserta* (Broth.) P.C.Chen, with *A. acuminatum* and *A. kiiense* synonymized in *W. longifolia*. The taxonomic status of *A. japonicum* was not discussed since the type material was not available. Based on a morphological study of the type specimens, Inoue and Tsubota (2017) recognized *A. japonicum* as a

well-established species and proposed a new combination, *W. japonica* (G.Roth) Y.Inoue & H.Tsubota for the species. In this chapter, phylogenetic relationships and species circumscriptions of the cleistocarpous species of *Weissia* in Japan were reassessed based on molecular phylogenetic inference and detailed morphological investigation.

Materials & Methods

Species delimitation

In this chapter I recognized species as the population which is morphologically homogeneous and phylogenetically monophyletic or paraphyletic on the DNA tree except for *W. controversa* Hedw. and *Trichostomum* Bruch which have been shown to be polyphyletic (Werner *et al.* 2005), but by accepting the current broad concept of these taxa I have avoided making any premature taxonomic changes.

Molecular phylogenetic analyses

Sampling for DNA was based mainly on material collected by field research on *Weissia* growing in Japan (Hokkaido, Honshu, Shikoku, Kyushu, and Ogasawara and Ryukyu Islands) during 2011–2016. Two phylogenetic markers were selected for the present analyses: chloroplast ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) and ribosomal protein S4 (*rps4*) genes. 33 *rbcL* and *rps4* gene sequences were newly obtained respectively. The supposed ingroup species represent species of Trichostomoideae *sensu* Werner *et al.* (2005). Outgroup species [*Barbula unguiculata* Hedw. and *Didymodon constrictus* (Mitt.) K.Saito var. *flexicuspis* (P.C.Chen) K.Saito] were selected based on Werner *et al.* (2005) and Inoue & Tsubota (2016). A total of 53 concatenated *rbcL* and *rps4* gene sequences were examined in the present analysis, as shown in Appendix F.

Genomic DNA was extracted from leaves of plants bearing sporophytes. The protocol for extraction of total DNA followed Suzuki *et al.* (2013). Conditions of PCR amplification for both *rbcL* and *rps4* genes followed Inoue and Tsubota (2014). Direct sequence analyses of the PCR products were performed following Inoue *et al.* (2012). Primers used for PCR amplification and DNA sequencing followed Souza-Chies *et al.* (1997), Tsubota *et al.* (1999, 2001), Masuzaki *et al.* (2010), Inoue *et al.* (2011, 2012) and Inoue and Tsubota (2014) (see also Appendix C). Sequences obtained here have been submitted to DDBJ/EMBL/GenBank International Nucleotide Sequence Database Collaboration (INSDC).

Sequences of two genes were aligned separately by using the program MAFFT ver. 7.027 (Katoh & Standley 2013) with some manual adjustment on the sequence editor of MEGA ver. 5.2 (Tamura *et al.* 2011). Start and stop codons were removed,

and the resulting total length was 2,025 bp. Duplicated sequences were eliminated using Phylogears2 (ver. 2.0.2013.10.22, Tanabe 2008).

Phylogenetic analysis using the concatenated sequences of *rbcL* and *rps4* genes was performed based on a maximum likelihood (ML) method (Felsenstein 1981) with a codon substitution model, and the approximate unbiased (AU) test (Shimodaira 2002, 2004) in the final stage of the analysis scheme.

Prior to the phylogenetic reconstruction, Kakusan4 (ver. 4.0.2015.01.23, Tanabe 2011) was used to determine the appropriate substitution model and partitioning scheme for my data based on corrected Akaike Information Criterion (AICc: Sugiura 1978). Since the codon substitution model is inappropriate for a heuristic search due to the huge computational burden, phylogenetic trees were constructed using the following three program packages to obtain the candidate topologies: (1) RAxML ver. 8.2.8 (Stamatakis 2014) with ML method using the equal mean rate model among codon positions (GTR + Γ for all codon positions of *rbcL* and *rps4*) with 1,000 heuristic searches; (2) PAUPRat (Sikes & Lewis 2001) over PAUP* ver. 4.0b10 (Swofford 2002) with the maximum parsimony (MP) method (Fitch 1971) to implement Parsimony Ratchet searches (Nixon 1999) using the Parsimony Ratchet search strategy with random weighting of each character in fifty 200 iteration runs; (3) MrBayes ver. 3.2.5 (Ronquist *et al.* 2012) with Bayesian inference (BI) method using the proportional model among codon positions (GTR + Γ + Invariant for first and second codon positions of *rbcL*, GTR + Γ for third codon position of *rbcL*, HKY85 + Γ for first and second codon positions of *rps4*, GTR + Homogeneous for third codon position of *rps4*) with 10,000,000 generations, sampling trees every 1,000 generations. A 50 % majority-rule consensus tree was calculated after the convergence of the chains and discarding 25 % of the sampled trees as burn-in.

Based on the ML criteria, re-calculation of likelihood values for each tree topology was performed with the codon substitution model which was more or less equivalent to the GY94 model (Goldman & Yang 1994) implemented in Garli var. 2.01 (Zwickl 2006). The set of candidate topologies was evaluated by the AU test and Bayesian posterior probability (PP) calculated by the BIC approximation (Schwarz 1978, Hasegawa & Kishino 1989) using CONSEL ver. 0.20 (Shimodaira & Hasegawa 2001). A strict condensed tree for the topologies with high ranking log-likelihood

values that passed both AU and PP tests was also computed by MEGA. Supporting values more than 50 % obtained by CONSEL were overlaid to assess the robustness of each branch of the highest likelihood topology: AU test (AU), bootstrap probabilities (NP), and Bayesian posterior probabilities (PP) are shown on or near each branch (AU/NP/PP).

Morphological investigation

The morphological investigation was made based on specimens included in the molecular phylogenetic analysis and additional specimens to assess whether each molecular grouping corresponds to species that could be recognized morphologically. Approximately 400 herbarium specimens of cleistocarpous species of *Weissia*, including several type specimens, were borrowed from BM, CBFS, H, HIRO, KOCH, MUB, NICH, NUM, NY, PC, S, SP, TNS and W were examined in this chapter. This study also includes new material collected by field research during 2011–2016 on *Weissia* growing in Japan and which have been deposited at HIRO. My morphological identification was made based only on the plants bearing sporophytes. Morphological characters were examined with a light microscope and scanning electron microscope (SEM). Preparation for SEM observation followed Inoue *et al.* (2011). To avoid developmental deviations, the descriptions and measurements were made only from plants with mature sporophytes. I defined mature sporophyte as the sporophyte which possesses mature spores that are a brownish color and are densely papillate.

Results

Molecular phylogenetic analysis

The concatenated data matrix had a total length of 2,025 bp, of which 269 (13.3 %) were variable, and 135 (50.2 % of the variable sites) were parsimony-informative.

A total of 291 topologies were obtained from the three analyses: 233 ML topologies by RAxML; 57 MP by PAUPRat over PAUP*; and one BI by MrBayes. More detailed topologies were searched through the obtained trees using a log-likelihood measure. Fig. 3.1 shows the best-supported tree with the highest likelihood value (ln L = -5770.556). The strict condensed tree was also obtained for the two topologies with high-ranking log-likelihood values that passed both AU and PP tests (not shown). These best-supported and strict condensed trees had identical topologies. Values for the percentage of supported topologies for each branch were superimposed in Fig. 3.1.

Weissia was resolved as monophyly with inclusion of *Trachycarpidium lonchophyllum* (G.Roth) R.H.Zander with high supporting values (100/100/1.00). The *Weissia* clade was sister to *Trichostomum brachydontium* Bruch. The exserted stegocarpous, peristomate species *W. controversa* is polyphyletic (*W. controversa* 1–3 vs. *W. controversa* 4). Four cleistocarpous clades were confirmed in Japanese *Weissia*, corresponding to *W. kiiensis*, *W. japonica*, *W. exserta* and a new species *W. parajaponica*. *W. exserta* was sister to *W. parajaponica*, and *W. kiiensis* was sister to *W. japonica* with high supporting values (both 100/100/1.00). The relationships among these cleistocarpous species and stegocarpous species (*W. controversa* 1–3) were ambiguous in the present analysis.

Morphology and ecology

My morphological investigations supported the molecular groupings of cleistocarpous species of *Weissia* in Japan, each circumscribed by a combination of sporophytic and perichaetial leaves characters. The most outstanding sporophytic feature shared by *W. exserta*, *W. japonica* and *W. parajaponica* is the presence of annulus (Fig. 3.2: A–C), which has been overlooked in Japanese species. The annulus consists of several rows of much smaller cells than adjacent exothecial cells of the beak

and urn. The deoperculation found in these species is nonfunctional, that is, spores are not released from the dehiscent part of the capsule. Thus, the capsules of these species are morphologically stegocarpous but functionally cleistocarpous, as shown in *Pleuridium japonicum* Deguchi, Matsui & Z.Iwats. (Deguchi *et al.* 1994). We also observed that capsules of all four species have a fragile, capsule-abscission tissue region located at the junction of the capsule and seta, where the mature capsules are easily detached from the seta.

All four species grow on ground in sunny places such as arable land, gardens, parks, temples, schools, shrines, and roadside cliffs covered with thin soil at low elevation as described by Saito (1975). In the Japanese archipelago, *W. exserta*, *W. japonica* and *W. kiiensis* are all distributed in Honshu, Shikoku and Kyushu. In Hokkaido, only *W. kiiensis* is known and in Ogasawara and Ryukyu Islands, only *W. parajaponica* is known.

Discussion

Implications for the evolutionary history of Weissia

My study has provided the first DNA sequences and phylogenetic relationships of the cleistocarpous *Weissia* species in Japan, and suggested monophyly of each species. The inferred length of the branches subtending nodes in Japanese *Weissia* is relatively short (< 0.0031), suggesting rapid and parallel sporophyte modifications (cleistocarpy) in this clade, as also shown in European and North American *Weissia* by Werner *et al.* (2005). Gametophytes often display a high degree of polymorphism while sporophytes remain less variable at intra- and inter-specific levels in bryophytes (Stanton & Reeb 2016). In the case of *Weissia*, however, my results suggest that sporophytes in *Weissia* species are more plastic than gametophytes, as also found in Funariaceae (Fife 1985). These groups usually occur in highly seasonal habitats, characterized by an alternation of moist and dry conditions over short periods and with bare soil not covered by larger plants, such as arable land. Vitt (1981) suggested that mosses occurring in highly seasonal habitat can be characterized by cleistocarpous, gymnostomous capsules that are often ovate and immersed. It appears as if selective pressures or relaxation in highly seasonal habitats are driving the diversification rather than the conservation of sporophytic architecture (Liu *et al.* 2012). The relatively short branch length in the Japanese *Weissia* clade also suggests reticulate evolution within the genus, as recently shown in the *Physcomitrium–Physcomitrella* species complex (McDaniel *et al.* 2010, Bike *et al.* 2014). The hybrids are usually found among weedy and semi-weedy species, that is species with potential life spans of a few years, and their highly seasonal habitats promote the growth of colonies of different species in close proximity, increasing the chance of intermixing and cross fertilization (Anderson 1980, Natcheva & Cronberg 2004). Rapidly rampant sporophyte diversification within *Weissia* might result in adaptation to highly seasonal habitats and the formation of a syngameon, which is the most inclusive unit of interbreeding in a hybridizing species group (Grant 1981).

In the Japanese cleistocarpous species, my DNA data showed that all four species are resolved in the monophyletic clade (Fig. 3.1). Morphologically, however, *W. japonica* and *W. parajaponica* are nearly the same and they cannot always be distinguished without DNA data. These two species partially share the sporophytic

characters with *W. exserta* (annulate capsules) and *W. kiiensis* (immersed capsules), and their urns show an intermediate shape between *W. exserta* and *W. kiiensis*. These results imply the following two hypotheses, as suggested in vascular plants (Kato *et al.* 1996). The first, that *W. japonica* and *W. parajaponica* originate from the hybrid-derived population: hybridization once occurred between *W. exserta* and *W. kiiensis*, and subsequent back-crosses repeatedly occurred with one of mother species. The second, that according to the morphological reduction series of the Pottiaceae (e.g. Saito 1975, Zander 1993), *W. japonica* and *W. parajaponica* (immersed capsules with annulus) originate from the ancient populations of *W. exserta* (exserted capsules with annulus), and rapidly diverged in Honshu, Shikoku and Kyushu (*W. japonica*), and Ogasawara and Ryukyu Islands (*W. parajaponica*). *W. kiiensis* (immersed capsules without annulus) originates from the ancient population of *W. japonica* and rapidly diverged in Hokkaido, Honshu, Shikoku and Kyushu. Formation of a hybrid sporophyte and the production of viable spores support the former hypothesis (Reese & Lemmon 1965). However, more solid evidence is necessary to untangle the evolutionary history among these species, provided by the comparison of chloroplast and nuclear DNA sequences, microsatellite analysis, or the comparison of genome size by flow cytometry based on broad geographical sampling.

Systematic position of Trachycarpidium lonchophyllum

The inferred tree supported monophyly of the genus *Weissia* with inclusion of a species of *Trachycarpidium* Broth. *Trachycarpidium* is characterized by long-lanceolate, plane-margined, entire leaves with a stout costa ending in a short awn, basal cells differentiated in a vee up the margins, and bulging, strongly protuberant cells of the body (not the apiculus) of the immersed, cleistocarpous capsule (Zander 1993). Its gametophytic similarity to *Weissia* and the possibility of it being included in the genus was suggested by Stone (1975). *T. lonchophyllum* was originally described as a species of *Astomum* from South America (Roth 1911). Later, Zander (1993) placed the species in *Trachycarpidium* due to its protuberant cells of the capsule. The present study supports the recognition of *Trachycarpidium* as a member of *Weissia*. According to my phylogenetic tree I concluded that *T. lonchophyllum* should be transferred to *Weissia*. However I retained *Trachycarpidium* as a genus because the phylogenetic

position of the type species *T. verrucosum* (Besch.) Broth. remains unclear.

Circumscriptions of Weissia controversa *and the genus* Trichostomum

The inferred tree suggested the current concept of *W. controversa* being polyphyletic, as shown by Werner *et al.* (2005) using nr ITS sequence data. A taxonomic revision of this species based on a broad geographical sampling is required for a comprehensive molecular phylogenetic analysis and reassessment of its defining morphological characters.

The type species of *Trichostomum* (*T. brachydontium*) was sister to the *Weissia* clade. Based on the analysis using ITS sequence data, this species was also resolved nested in *Weissia* and formed a subclade together with *T. brittonianum* R.H.Zander, *T. crispulum* Bruch, and *T. jamaicense* (Mitt.) A.Jaeger [as *W. jamaicensis* (Mitt.) Grout] (Werner *et al.* 2005). These results supports a broad circumscription of the genus *Weissia* including *Trichostomum* (e.g. Dixon 1913, Andrews 1945). However, other species belonging to *Trichostomum* are polyphyletic (Werner *et al.* 2005, and present study). The current taxon sampling of *Trichostomum* and other genera in the subfamily Trichostomoideae appears to be insufficient to make a final conclusion whether *Trichosomum* should be transferred to *Weissia*.

Taxonomy

Based on the present investigation, the following taxonomic treatment on the genus *Weissia* in Japan is presented. I follow the Melbourne Code of Nomenclature (McNeill *et al.* 2012) for nomenclatural elements.

Description of the genus

Weissia Hedw., Sp. Musc. Frond. 64. 1801. Lectotype:—*W. controversa* Hedw. *fide* Mitten (1856).

= *Cavanillea* Borkh., Tent. Disp. Pl. German., op. posth. 251. 1809, *nom. illeg.* [ICN Art. 53.1; later homonym (non Medik., non Desr.)].

= *Hymenostomum* R.Br., Trans. Linn. Soc. London 12: 572. 1819. Type:—*H. microstomum* (Hedw.) Nees & Hornsch.

= *Astomum* Hampe, Flora 20: 285, 1837. Lectotype:—*A. crispum* (Hedw.) Hampe *fide* Margadant (1959).

= *Systegium* Schimp., Syn. Musc. Eur. 30. 1860, *nom. illeg.* (ICN Art. 52.1; type of earlier name included).

= *Simophyllum* Lindb., Acta Soc. Sci. Fenn. 10: 74. 1871, *nom. illeg.* (ICN Art. 52.1; type of earlier name included).

= *Phasconica* Müll.Hal., Linnaea 43: 438. 1882. Lectotype:—*P. lorentzii* Müll.Hal. *fide* Zander (1993).

= *Rechingerella* J.Froehl., Ann. Naturhist. Mus. Wien 66: 36. 1963, *nom. illeg.* [ICN Art. 53.1; later homonym (non Petr.)]. Type:—*R. macedonica* J.Froehl.

Description:—*Plants* small, forming low cushions, turfs or loosely caespitose. *Stems* simple or branched, erect, smooth, rounded in cross section; central strand present; sclerodermis weakly differentiated; hyalodermis undifferentiated to well differentiated; axillary hairs hyaline throughout. *Rhizoids* sparse at base; rhizoidal tubers occasionally developed. *Leaves* strongly crisped when dry, spreading when moist, lanceolate to linear-lanceolate, tapering to an acute to acuminate apex from a broad to narrow oblong base; lamina unistratose; margins entire, incurved above the leaf base or plane throughout; costa single, stout, ending below apex to excurrent, papillose on adaxial surface, smooth or papillose on abaxial surface; cross section at midleaf ovate,

occasionally circular or semicircular; adaxial epidermis present; adaxial stereid band present; guide cells in a single row or seldom scattered bistratose pairs; hydroid strand absent or present, abaxial stereid band present, abaxial epidermis present or occasionally absent; upper laminal cells subquadrate to hexagonal, papillose on both surfaces; basal laminal cells irregularly oblong, smooth. *Laminal KOH color reaction* yellow. *Sexual condition* monoicous or dioicous. *Perichaetia* terminal; perichaetial leaves little different from vegetative leaves or somewhat larger. *Perigonia* appearing as stalked lateral buds on perichaetiate plants (but variably present) or terminal on usually smaller perigoniate plants; perigonial leaves much smaller than vagetative leaves, ovate. *Setae* dextrosely twisted throughout or straight. *Capsules* stegocarpous or cleistocarpous, spherical to cylindrical; exothecial cells irregularly quadrate to oblong, smooth or mamillose (except the apiculus); stomata phaneroporous at base of capsules; annulus absent or present, when present consisting of much smaller cells than adjacent exothecial cells of urn and operculum, or persistent thick-walled larger cells; peristome teeth absent or present, when present erect or weakly dextrosely twisted. *Operculum* undifferentiated or differentiated, when differentiated conic to rostrate; cells straight to weakly dextrosely arranged. *Calyptra* cucullate. *Spores* brown to yellowish brown, papillose.

Lectotypification of Weissia controversa

Towards a better circumscription of the genus *Weissia*, I designate here a lectotype for *W. controversa*, the type species of the genus.

Weissia controversa Hedw. Sp. Musc. Frond. 67. 1801.

Type:—Lipsiae ad rivulum post collem Bienitz. Humo theca loca, nec non sabulosa, uda, praeprimis regionum montosarum amat (lectotype designated here, Tab. 5. B. in Hedwig 1791–1792).

Typification notes:—The genus *Weissia* Hedw. was typified on *W. controversa* Hedw. by Mitten (1856). When *W. controversa* was proposed by Hedwig (1801), he used the validating descriptions and illustrations which he had previously given to the same species (Hedwig 1791–1792). Although there was no designation of the holotype in either publication (Hedwig 1791–1792, 1801), in the plotologue (Hedwig 1801) he

referred to a specimen from Leipzig. One specimen from Leipzig, named *W. controversa* in Hedwig's herbarium (G), is the best candidate for a lectotype (Fig. 3.3). In his taxonomic revision of *Weissia* for the Iberian Peninsula, Guerra (2002) selected this specimen as a lectotype for *W. controversa*. However, he did not include the phrase "designated here" or an equivalent, thus making this an ineffective typification (ICN Art. 7.10). This specimen has unfortunately been lost while on loan (Price 2005, p. 378). Hedwig's illustration (Hedwig 1971–1792, Tab. 5. B.) is from the original material and is considered to be the only element that certainly fits Hedwig's concept of the species, being the safest choice as lectotype. Hedwig (1791–1792, 1801) cited Vaillant's and Dillenius' pre-Linnean phrase-names with reference to their illustrations under *W. controversa* as synonyms. Vaillant (1727) and Dillenius (1742) did not refer to any particular specimen and made only general comment on habitat information. These two illustrations given by Vaillant and Dillenius can be considered parts of original material, but I believe that the Hedwig's illustration provides much more morphological information and is therefore better to select this as the lectotype.

To ensure nomenclatural stability a specimen from the type locality, Bienitz in Leipzig, with DNA information should be selected as the epitype supporting the lectotype illustration rather than selecting an old specimen without DNA information, because the modern concept of *W. controversa* is thought to be polyphyletic (Werner *et al.* 2005, and present study) and a morpho-molecular revision is necessary to provide a better circumscription of the species.

Key to the cleistocarpous species of Weissia *in Japan*

1. Perichaetial leaves little differentiated from vegetative leaves; capsules with functionally dehiscent operculum (spore release with opening of capsule mouth) .....Stegocarpous species
- Perichaetial leaves well differentiated and much larger than vegetative leaves; capsules without functionally dehiscent operculum (spore release with irregular dehiscence of capsule).....2
2. Annulus absent .....*W. kiiensis*
- Annulus present.....3
3. Seta 0.5–1.2 mm long; capsules exserted from perichaetial leaves; urn ellipsoidal

..... *W. exserta*

- Seta less than 0.4 mm long; capsules deeply immersed among perichaetial leaves; urn ovoid to subovoid.....4

4. Urn (550–)625–750(–840) × (450–)505–600(–720) μm; costa excurrent in a point reaching (80–)90–130(–160) μm.....*W. japonica*
- Urn (400–)500–660(–760) × (360–)415–515(–620) μm; costa excurrent in a point reaching (80–)100–250(–280) μm..... *W. parajaponica*

Notes:—Although *W. parajaponica* tends to have a smaller urn and longer excurrent costa than *W. japonica*, their dimensions sometimes show considerable overlap, and these two species cannot always be distinguished without phylogenetic analysis based on chloroplast DNA data.

Description of the species

1. ***Weissia exserta*** (Broth.) P.C.Chen, Hedwigia 80: 158. 1941.

Basionym:—*Astomum exsertum* Broth., Hedwigia 38: 212. 1899. Type:—JAPAN. Nagasaki Pref.: 20 January 1861, *Wichura 1379a* (lectotype designated here, H 190018!).

≡ *Systegium exsertum* (Broth.) Paris, Index Bryol. Suppl. 317. 1900.

≡ *Hymenostomum exsertum* (Broth.) Broth., Nat. Pflanzenfam. I (3): 386. 1902.

Description:—(Figs. 3.2: A, 3.4: A–J). *Plants* when moist ca. 5–10 mm high, including capsules. *Stems* simple or branched, erect; central strand present; sclerodermis weakly differentiated; hyalodermis undifferentiated. *Leaves* strongly crisped when dry, spreading when moist, gradually becoming larger toward shoot apex. *Autoicous*. *Perichaetial leaves* much larger than vegetative leaves, lanceolate to linear lanceolate, (2.3–)2.9–4.3(–4.7) mm long and 0.4–0.6(–0.75) mm wide at base, tapering to an acuminate apex from a broad oblong base; margins incurved in distal 1/2–2/3, plane in basal portion, smooth or nearly smooth with faint projections at shoulder part of leaf base; costa stout, excurrent in a point reaching (70–)80–115(–130) μm, papillose on adaxial surface and smooth on abaxial surface; guide cells 4 in a single row at midleaf; adaxial and abaxial stereids 2–4 stratose at midleaf; upper laminal cells

subquadrate, 6–9(–10) × 6–9 μm, papillose on both surfaces with bifid papillae; basal laminal cells enlarged, rectangular, (50–)65–85 × 8–10(–12) μm, smooth. *Perigonial leaves* much smaller than vegetative leaves, oval, acuminate, concave. *Asexual reproduction* unknown. *Setae* (450–)670–920(–1140) μm long; epidermal cells elongated, thick walled. *Capsules* cleistocarpous, exserted from perichaetial leaves; urn ellipsoidal, (690–)760–970(–1180) × (460–)570–625(–760) μm; exothecial cells irregularly quadrate, smooth; stomata phaneroporous, 4–6 at base of capsule; annulus present at the base of the apiculus, consisting of much smaller cells than adjacent exothecial cells of urn and operculum. *Operculum* differentiated as a slightly oblique finger-like beak, (280–)285–340(–385) μm long. *Calyptra* cucullate, (700–)905–1110(–1280) μm long. *Spores* (16–)18–20(–22) μm in diam., densely papillose.

Typification notes:—When Brotherus (1899) described *A. exsertum*, he cited two specimens: *Wichura 1379a* and *1379b*. However, he did not specify the holotype, so each of these specimens is a syntype (ICN Art. 9.5). Thus it is necessary to select the lectotype from these two specimens. Saito (1975) cited the specimen *Wichura 1396a* (H) as the holotype of *A. exsertum*. However, the specimen *Wichura 1396a* is the type for *Hyophila propagulifera* Broth. (Brotherus 1899). In a taxonomic account of Indian Pottiaceae, Aziz & Vohra (2008) cited the specimen *Wichura 1379a* (H) as the type of *A. exsertum*. However, they did not validly designate a lectotype for *A. exsertum*, because they did not include the phrase “designated here” (ICN Art. 7.10). I could confirm that the specimen *Wichura 1379a* agrees well with the original description of Brotherus (1899) and I designate it as the lectotype of *A. exsertum* (The specimen *Wichura 1379b* was not found in H: Curator, pers. comm., March 2015).

Distribution:—Japan (Honshu, Shikoku and Kyushu), China and India.

Representative specimens examined:—JAPAN. Honshu, Ibaraki Pref.: Nishi-ibaraki District, Iwase-cho, Ohta, 14 December 1981, *Z. Iwatsuki 9546* (NICH M185373); Kanagawa Pref.: Kamakura City, Imaizumidai, ca. 100 m elev., 35°20′05″N, 139°32′55″E, 9 March 2013, *Y. Inoue 1794* (HIRO, DNA voucher); Aichi Pref.: Toyokawa City, Solar-Terrestrial Environment Laboratory of Nagoya University, Toyokawa Branch, 7 January 1953, *N. Takaki s.n.* (NUM-BT 13762); Nara Pref.: Ikoma District, Tomio-mura, Hirano, ca. 100 m elev., 25 March 1949, *M. Mizutani 1487* (NICH

M31106); Hiroshima Pref.: Higashi-hiroshima City, Hiroshima University, ca. 220 m elev., 34°24′08″N, 132°42′42″E, 23 February 2012, *Y. Inoue 912* (HIRO, DNA voucher); Hatsukaichi City, Miyajima Isl., 10 m elev., 23 January 1969, coll. *T. Seki.* in hb. *Miyajima Natural Botanical Garden no. 798* (HIRO); Shikoku, Ehime Pref.: Imabari City, Ohshima Isl., ca. 100 m elev., 34°10′39″N, 133°03′59″E, 14 May 2011, *H. Tsubota 7699* (HIRO); Kyushu, Nagasaki Pref.: 20 January 1861, *Wichura 1379a* (holotype of *A. exsertum*, H 190018); Kumamoto Pref.: Hitoyoshi, Isshochi, ca. 100 m elev., 26 February 1971, *K. Saito 8546* (TNS 70370); Oita Pref.: Tsukumi City, Chinu, ca. 20 m elev., 33°04′29″N, 132°52′53″E, 2 March 2013, *Y. Inoue 1788a* (HIRO, DNA voucher).

2. ***Weissia japonica*** (G.Roth) Y.Inoue & H.Tsubota, Cryptog. Bryol. 38: 86. 2017.

Basionym:—*Astomum japonicum* G.Roth, Aussereur. Laubm. 187. 1911.
Type:—JAPAN. *s.loc.* & *s.d.*, *Siebold s.n.* [lectotype – (designated by Inoue & Tsubota 2017), PC 657676!; isolectotypes, BM 867124!, S B3524!].

= *Systegium crispum auct. non* (Hedw.) Schimp.: Sande Lacoste, Ann. Mus. Bot. Lugduno-Batavum 2: 292. 1866.

= *Astomum crispum auct. non* (Hedw.) Hampe: Sande Lacoste, Ann. Mus. Bot. Lugduno-Batavum 2: 292. 1866.

= *Systegium japonicum* Besch. in Paris, Index Bryol. ed. 2. 352. 1905, *nom. inval.* [ICN Art. 38.1; no description].

= *Astomum acuminatum* Dixon & Thér., Trav. Bryol. 1: 11. 1942. Type:—JAPAN. Hyogo Pref.: Awaji Island, Toshi-mura, 24 November 1917, *G. Takata s.n.* in hb. *H. Sasaoka 293* (holotype, BM 867097!), ***syn. nov.***

Description:—(Figs. 3.2: B, 3.4: K–T). *Plants* when moist ca. 5–10 mm high including capsules. *Stems* simple or branched, erect; central strand present; sclerodermis weakly differentiated; hyalodermis undifferentiated. *Leaves* strongly crisped when dry, spreading when moist, gradually becoming larger toward shoot apex. *Autoicous*. *Perichaetial leaves* much larger than vegetative leaves, lanceolate to linear lanceolate, (2.0–)2.6–4.2(–4.7) mm long and (0.4–)0.5–0.7(–0.9) mm wide at base, tapering to an acuminate apex from a broad oblong base; margins incurved in distal 1/3–1/2, plane in basal portion, smooth or nearly smooth with faint projections at

shoulder part of leaf base; costa stout, excurrent in a point reaching (70–)85–120(–125) μm, papillose on adaxial surface and smooth on abaxial surface; guide cells 4 in a single row at midleaf; adaxial and abaxial stereids 2–3 stratose at midleaf; upper laminal cells subquadrate, 6–9(–10) × 6–8 μm, papillose on both surfaces with bifid papillae; basal laminal cells enlarged, rectangular, (55–)60–90(–100) × 8–12(–15) μm, smooth. *Perigonial leaves* much smaller than vegetative leaves, oval, acuminate, concave. *Asexual reproduction* unknown. *Setae* (35–)120–190(–260) μm long; epidermal cells quadrate to subquadrate, thin walled. *Capsules* cleistocarpous, deeply immersed among perichaetial leaves; urn ovoid to subovoid, (550–)620–750(–840) × (445–)505–600 (–720) μm; exothecial cells irregularly quadrate, smooth; stomata phaneroporous, (3–)4–5 at base of capsule; annulus present at the base of the apiculus, consisting of much smaller cells than adjacent exothecial cells of urn and operculum. *Operculum* differentiated as a slightly oblique finger-like beak, (130–)185–240(–315) μm long. *Calyptra* cucullate, (520–)550–675(–715) μm long. *Spores* (17.5–)20–22.5(–26) μm in diam., densely papillose.

Typification notes:—*Astomum japonicum* G.Roth was originally reported from Japan as *Systegium crispum* (Hedw.) Schimp. (Sande Lacoste 1866) based on a collection of fruiting plants. In Paris' Index Bryologicus (1905), Bescherelle proposed a new species *S. japonicum* Besch. citing *S. crispum* (*sensu* Sande Lacoste 1866) as a synonym, although *S. japonicum* was a *nomen nudum* (ICN Art. 38.1). When Roth (1911) validly described *A. japonicum* based on the specimen collected by Siebold, he indirectly cited *S. japonicum* (*nom. nud.*), but the species name *A. japonicum* should correctly be ascribed to Roth. Roth (1911) also cited *S. crispum* (*sensu* Sande Lacoste 1866) as a synonym of *A. japonicum*; however the meaning of this synonymy was either "*S. crispum* (Hedw.) Schimp. *pro parte*" or "*S. crispum auct. non* (Hedw.) Schimp." because he recognized *A. crispum* (Hedw.) Hampe [≡ *S. crispum* (Hedw.) Schimp.] as a different species from *A. japonicum* in a species key of the same literature (ICN Art. 52.2).

I was able to examine type material of *A. japonicum* from three herbaria (PC, BM, and S). When Roth (1911) described this species, he did not specify the herbarium where the type was deposited, so each of these specimens is a syntype (ICN Art. 9.5). After detailed examination of these syntypes, we have selected the specimen (PC

657676) as the lectotype (Fig. 3.5). It corresponds to the original material of *Systegium japonicum* Besch. (*nom. nud.*). Among the three syntypes, only the specimen in PC contains fruiting plants which correspond well with the description provided by Roth (1911). The sporophytic characters were included in the original description by Roth (1911), although he apparently did not observe the sporophytes himself: "Kapsel nach Bescherelle ziemlich groß und schief geschnäbelt (non vidi)". The description of sporophyte was presumably based on the specimen in PC.

The isolectotype specimen (BM 867124 in the Bescherelle collection) does not contain fruiting plants, but information on Bescherelle's original label includes the sporophytic character of this species, suggesting that the specimen in BM is a duplicate of the specimen in PC.

The isolectotype specimen (S B3524 in the Roth collection), contains leaves from two different species (Fig. 3.6), placed on a pair of mica slides. The specimen label indicates that Roth observed the BM specimen and returned it, except for the two leaves in the mica slides, with a handwritten annotation "all returned". This suggests that the specimen in S is an unreturned portion of the BM specimen (kleptotype). My examination revealed the leaf (Fig. 3.6: B) belongs to *A. japonicum* and corresponds well with the description and illustration in Roth (1911). The other leaf (Fig. 3.6: C) probably belongs to a *Brachymenium* species mixed in the original collection.

Taxonomic notes:—*W. japonica* is similar to the European species *W. levieri* (Limpr.) Kindb. and *W. longifolia* Mitt. var. *angustifolia* (Baumgartner) Crundw. & Nyholm in having deeply immersed capsules which also have an annulus. However, the capsule mouth is much wider in latter two species (ca. 130–200 μm). As a consequence, the "opercula" on these two species look the normal shape (Fig. 3.6: D, E, G, H). In *W. japonica*, because the mouth of the capsule is much narrower (ca. 50–90 μm), there is no flaring of the base of the beak (Fig. 3.6: F, I).

W. japonica is very similar to *W. parajaponica*, and sometimes difficult to identify based only on morphological characters. However, *W. japonica* tends to have larger urns and shorter excurrent costae of perichaetial leaves. Separation of these species is also supported by their geographical distribution: *W. japonica* is distributed in Honshu, Shikoku and Kyushu, while *W. parajaponica* is distributed in Ryukyu and Ogasawara Islands.

Saito (1975) synonymized *A. acuminatum* with *W. longifolia* Mitt. [as *W. crispa* (Hedw.) Mitt.] due to gametophytic identity with *W. longifolia*. After detailed examination of the holotype, I concluded that *A. acuminatum* should instead be considered a synonym of *W. japonica* since the plants of holotype have immersed capsules with an annulus.

Distribution:—Japan (Honshu, Shikoku and Kyushu).

Representative specimens examined:—JAPAN. *s.l. & s.d.*, *Siebold s.n.* (lectotype of *A. japonicum*, PC 657676; isolectotypes of *A. japonicum*, BM 867124, S B3524); Honshu, Miyagi Pref.: Sendai City, Osaki-hachiman, 7 April 1907, *S. Okamura s.n.* (NICH M35935); Ibaragi Pref.: Mt. Mayumi, ca. 300 m elev., 17 February 1972, *K. Saito 10596* (TNS 72161); Shizuoka Pref.: Mikkabi, 21 February 1973, *K. Saito 13966* (TNS 72163); Hyogo Pref.: Awaji Island, Toshi-mura, 24 November 1917, *G. Takata s.n.* in hb. *H. Sasaoka 293* (holotype of *A. acuminatum*, BM 867097); Wakayama Pref.: Tanabe City, 25 March 1972, *H. Deguchi 9432* (KOCH); Hiroshima Pref.: Hiroshima City, Asakita-ku, Miiriminami, ca. 60 m elev., 33°32′18″N, 132°31′40″E, 18 March 2012, *Y. Inoue 914* (HIRO); ditto, 18 March 2012, *Y. Inoue 3830* (HIRO, DNA voucher); Shikoku, Ehime Pref.: Matsuyama City, Gogoshima Isl., ca. 50 m elev., 33°53′01″N, 132°40′24″E, 8 Februarly 2012, coll. *T. Seki* in hb. *Y. Inoue 4034* (HIRO); Kochi Pref.: Kochi City, Kochi University, ca. 5 m elev., 23 March 1986, *H. Hidaka 271* (KOCH, voucher specimen used for phenological study by Deguchi & Hidaka 1987, as *A. crispum*); Kyushu, Fukuoka Pref.: Fukuoka City, Fukuoka Castle, ca. 10 m elev., 33°35′01″N, 130°22′51″E, 13 March 2016, coll. *T. Katagiri* in hb. *Y. Inoue 3947* (HIRO, DNA voucher).

3. ***Weissia kiiensis*** (S.Okamura) Y.Inoue & H.Tsubota, ***comb. nov.***

Basionym:—*Astomum kiiense* S.Okamura, Bot. Mag. (Tokyo) 25: 140. 1911.

Type:—JAPAN. Wakayama Pref.: Wakanoura, the foot of Mt. Goboyama, 9 December 1900, *K. Minakata s.n.* (holotype, NICH M37518!).

Description:—(Figs. 3.2: D, 3.7: A–I). *Plants* when moist ca. 2–10 mm high including capsules. *Stems* simple or branched, erect; central strand present; sclerodermis weakly differentiated; hyalodermis undifferentiated. *Leaves* strongly crisped when dry, spreading when moist, gradually becoming larger toward shoot apex. *Autoicous*.

Perichaetial leaves much larger than vegetative leaves, lanceolate to linear lanceolate, (1.7–)2.3–3.1(–3.6) mm long and (0.45–)0.5–0.7(–0.8) mm wide at base, tapering to an acuminate apex from a broad oblong base; margins incurved in distal 1/2–2/3, plane in basal portion, smooth or nearly smooth with faint projections at shoulder part of leaf base; costa stout, excurrent in a point reaching (40–)70–115(–160) μm, papillose on adaxial surface and smooth on abaxial surface; guide cells 4 in a single row at midleaf; adaxial and abaxial stereids 2–3 stratose at midleaf; upper laminal cells subquadrate, 6–10 × 6–10 μm, papillose on both surfaces with bifid papillae; basal laminal cells enlarged, rectangular, 50–120 × 8–14 μm, smooth. *Perigonial leaves* much smaller than vegetative leaves, oval, acuminate, concave. *Asexual reproduction* unknown. *Setae* (70–)130–240(–350) μm long; epidermal cells quadrate to subquadrate, thin walled. *Capsules* cleistocarpous, deeply immersed among perichaetial leaves; urn spherical, (490–)645–770(–840) × (460–)580–700 (–800) μm, with a slightly oblique finger-like apiculus reaching (110–)150–205(–230) μm long; exothecial cells irregularly quadrate, smooth; stomata phaneroporous, (3–)4–6(–9) at base of capsule; annulus absent. *Operculum* undifferentiated. *Calyptra* cucullate, (510–)575–680(–775) μm long. *Spores* (16.25–)20–24(–30) μm in diam., densely papillose.

Taxonomic notes:—Saito (1975) synonymized *A. kiiense* with *W. longifolia* Mitt. [as *W. crispa* (Hedw.) Mitt.]. However, in their taxonomic revision of European *Weissia* subg. *Astomum*, Crundwell & Nyholm (1972) suggested that Japanese plants that had been named *W. crispa* belonged to a non-European species. After examination of the holotypes of *A. kiiense* (NICH M37518) and *W. longifolia* (NY 1408141), we conclude that *A. kiiense* should be resurrected and transferred to *Weissia*. *W. kiiensis* has a similar appearance to *W. longifolia* in having the deeply immersed capsules without an annulus, but the capsule shape of the former is spherical while that of the latter is ellipsoidal. *W. kiiensis* is also quite similar to the North American species *W. muhlenbergiana* (Sw.) W.D.Reese & B.A.E.Lemmon as suggested by Andrew (1922). Crum & Anderson (1981) shared Crundwell's opinion (*in litt.*) that Japanese plants referred to *A. crispum* were identical with the North American species *W. muhlenbergiana* [as *A. muhlenbergianum* (Sw.) Grout]. I examined some specimens identified as *W. muhlenbergiana* (Appendix G) and confirmed two morphological groups: (1) capsules without an annulus and (2) capsules with an annulus. No distinct

morphological differences are apparent between *W. kiiensis* and the former group identified as *W. muhlenbergiana*. In the plotologue of *Phascum muhlenbergianum* Swartz (1829) did not refer to whether the capsules have or lack an annulus. I have not been able to locate the type specimen of *P. muhlenbergianum*. Until additional morpho-molecular data are obtained to clarify the taxonomic identities of Japanese and North American plants, I consider these species best regarded as distinct.
Distribution:—Japan (Hokkaido, Honshu, Shikoku and Kyushu)
Representative specimens examined:—JAPAN. Hokkaido, Hokkaido Pref.: Obihiro City, Midorigaoka Park, ca. 50 m elev., 42°54′17″N, 143°11′17″E, 12 September 2012, *Y. Inoue 1493* (HIRO, DNA voucher); Honshu, Fukushima Pref.: Fukushima City, Mt. Shinobu, ca. 95 m elev., 37°46′18″N, 140°28′42″E, 9 March 2015, *Y. Inoue 3169* (HIRO, DNA voucher); Tokyo Pref.: Nishitokyo City, The University of Tokyo Tanashi Forest, ca. 90 m elev., 35°44′05″N, 139°32′28″E, 10 March 2015, *Y. Inoue 3183* (HIRO, DNA voucher); Niigata Pref.: Tsubame City, Shincho, ca. 10 m elev., 37°38′07″N, 138°49′48″E, 26 October 2015, *T. Sato 1430* (HIRO, DNA voucher); Shizuoka Pref.: Kakegawa City, Nagaya, ca. 55 m elev., 34°45′30″N, 137°59′40″E, 19 December 2015, *Y. Inoue 3816* (HIRO, DNA voucher); Aichi Pref.: Shinshiro City, Yanai, ca. 30 m elev., 34°51′52″N, 137°27′34″E, 18 March 2013, *Y. Inoue 1816* (HIRO, DNA voucher); Nara Pref.: Ikoma District, Ikaruga-cho, Horyuji Temple, ca. 60 m elev., 5 March 2010, *K. Une 10243* (TNS 211531); Wakayama Pref.: Wakanoura, the foot of Mt. Goboyama, 9 December 1900, *K. Minakata s.n.* (holotype of *Astomum kiiense*, NICH M37518); Hiroshima Pref.: Kure City, Kamikamagarijima Isl., ca. 25 m elev., 34°11′23″N, 132°43′09″E, 20 December 2015, *Y. Inoue 3826* (HIRO, DNA voucher); Shikoku, Kochi Pref.: Kochi City, Mononobe-cho, Odachi, ca. 200 m elev., 33°41′52″N, 133°52′25″E, 8 March 2014, *Y. Inoue 2606* (HIRO, DNA voucher); Kyushu, Oita Pref.: Tsukumi City, Chinu, ca. 20 m elev., 33°04′29″N, 132°52′53″E, 2 March 2013, *Y. Inoue 1788b* (HIRO, DNA voucher); Miyazaki Pref.: Nichinan City, Hoshikura, ca. 20 m elev., 31°37′29″N, 131°21′33″E, 28 November 2015, *Y. Inoue 3813* (HIRO, DNA voucher).

4. ***Weissia parajaponica*** Y.Inoue & H.Tsubota, ***sp. nov.***
Holotype:—JAPAN. Ryukyu Islands: Ishigakijima Isl., ca. 30 m elev., 24°29′25″N, 124°16′41″E, 18 January 2016, *Y. Inoue 3864* [HIRO, DNA voucher (*rbcL*/*rps4*:

LC183780/LC183813)].

Paratypes:—JAPAN. Ogasawara Islands: Mukojima Isl., ca. 15 m elev., 27°40′53″N, 142°07′47″E, 14 July 2008, *S. Uchida 10069* (HIRO, DNA voucher); Nakoudojima Isl., 12 July 2008, *T. Katagiri 409* (HIRO); Yomejima Isl., ca. 80 m elev., 27°29′47″N, 142°12′36″E, 11 July 2008, *S. Uchida 10008* (HIRO); Chichijima Isl., ca. 120 m elev., 27°05′39″N, 142°11′11″E, 12 June 2009, *T. Yamaguchi 30497* (HIRO); Hahajima Isl., ca. 30 m elev., 26°37′06″N, 142°10′47″E, 17 September 2008, *S. Uchida 10685* (HIRO, DNA voucher); Ryukyu Islands: Yakushima Isl., ca. 2 m elev., 30°27′02″N, 130°29′06″E, 3 January 2015, coll. *S. Uchida* in hb. *Y. Inoue 3143* (HIRO, DNA voucher); Amamioshima Isl., ca. 5 m elev., 28°22′53″N, 129°29′55″E, 25 February 2016, coll. *A. Ohno* in hb. *Y. Inoue 3951* (HIRO, DNA voucher); Okinoerabu Isl., 200–250 m elev., 30 March 1967, *N. Takaki & H. Katsurayama s.n.* (NUM-BT 38114); Yoron Isl., ca. 70 m elev., 28 March 1967, *N. Takaki & H. Katsurayama s.n.* (NUM-BT 38053); Izena Isl., ca. 80 m elev., 11 April 2004, *H. Sato 464* (HIRO); Okinawa Isl., ca. 70 m elev., 26°13′39″N, 127°42′58″E, 24 February 2016, *Y. Inoue 3912* (HIRO, DNA voucher); Kitadaitoshima Isl., 20–50 m elev., 25 March 2000, *T. Yamaguchi 18666* (HIRO); Minamidaitojima Isl., ca. 20 m elev., 25°49′38″N, 131°13′00″E, 25 February 2016, *Y. Inoue 3925* (HIRO, DNA voucher); Irabu Isl., ca. 80 m elev., 24°48′59″N, 125°12′58″E, 22 January 2016, *T. Yamaguchi 36877* (HIRO); Miyakojima Isl., ca. 10 m elev., 24°48′51″N, 125°16′58″E, 21 January 2016, *Y. Inoue 3910* (HIRO, DNA voucher); ditto, ca. 15 m elev., 24°48′51″N, 125°16′58″E, 25 March 2016, *T. Yamaguchi 36925* (HIRO); ditto, ca. 20 m elev., 24°48′56″N, 125°17′04″E, 25 March 2016, *T. Yamaguchi 36926* (HIRO); Hatomajima Isl., ca. 5 m elev., 17 March 1982, *T. Yamaguchi 2146* (HIRO); Ishigakijima Isl., ca. 30 m elev., 18 January 2016, *Y. Inoue 3884* (HIRO); Iriomotejima Isl., ca. 30 m elev., 24°26′01″N, 123°46′55″E, 16 January 2016, *Y. Inoue 3849* (HIRO, DNA voucher).

Description:—(Figs. 3.2: C, 3.7: J–W). *Plants* when moist ca. 5 mm high including capsules. *Stems* simple or branched, erect; central strand present; sclerodermis weakly differentiated; hyalodermis undifferentiated. *Leaves* strongly crisped when dry, spreading when moist, gradually becoming larger towards shoot apex. *Autoicous*. *Perichaetial leaves* much larger than vegetative leaves, lanceolate to linear lanceolate,

(2.1–)2.4–3.3(–4.2) mm long and (0.3–)0.4–0.55(–0.7) mm wide at base, tapering to an acuminate apex from a broad oblong base; margins incurved in distal 1/3–1/2, plane in basal portion, smooth; costa stout, excurrent in a point reaching (72–)105–160(–225) μm, papillose on adaxial surface and smooth on abaxial surface; guide cells 4 in a single row at midleaf; adaxial and abaxial stereids 2–3 stratose at midleaf; upper laminal cells subquadrate, 6–8 × 6–8 μm, papillose on both surfaces with bifid papillae; basal laminal cells enlarged, rectangular, (45–)60–100 × 10–15 μm, smooth. *Perigonial leaves* much smaller than vegetative leaves, oval, acuminate, concave. *Asexual reproduction* unknown. *Setae* (55–)125–185(–280) μm long; epidermal cells quadrate to subquadrate, thin walled. *Capsules* cleistocarpous, deeply immersed among perichaetial leaves; urn ovoid to subovoid, (400–)500–660(–760) × (360–)415–515(–620) μm; exothecial cells irregularly quadrate, smooth; stomata phaneroporous, (3–)4–5(–6) at base of capsule; annulus present at the base of the apiculus, consisting of much smaller cells than adjacent exothecial cells of urn and operculum. *Operculum* differentiated as a slightly oblique finger-like beak, (125–)165–225(–300) μm long. *Calyptra* cucullate, (390–)520–645(–680) μm long. *Spores* (15–)19–22(–25) μm in diam., densely papillose.
Taxonomic notes:—This species is very similar to *W. japonica*, and sometimes difficult to identify based only on morphological characters. However, *W. parajaponica* tends to have smaller urns and longer excurrent costae of the perichaetial leaves.
Distribution:—Japan (Ogasawara and Ryukyu Islands).

Taxonomic status of Trachycarpidium lonchophyllum

When Roth (1911) described *Trachycarpidium lonchophyllum* he did not specify the herbarium where the holotype was deposited. A number of duplicates were distributed. Costa (2016) cited the original materials of *A. lonchophyllum* as isotypes. However, each of these duplicates constitutes a syntype (ICN Art. 9.5).

Based on my molecular phylogenetic analysis, I consider that *T. lonchophyllum* is better placed in *Weissia* and I here propose the transfer of *Trachycarpidium lonchophyllum* to the genus *Weissia* as follows:

Weissia lonchophylla (G.Roth) Y.Inoue & H.Tsubota, ***comb. nov.***

Basionym:—*Astomum lonchophyllum* G.Roth, Aussereur. Laubm. 182. 1911.

Type:—BRASIL. Santa Catarina: Tubarão, July 1889, *E. Ule 7* [holotype: herbarium not cited in the protologue; syntypes: G, GOET, JE, LE, MICH, PC, R, *fide* Costa (2016); *non vidi*].

≡ *Trachycarpidium lonchophyllum* (G.Roth) R.H.Zander, Bull. Buffalo Soc. Nat. Sci. 32: 213. 1993.

Specimen examined:—BRAZIL. São Paulo: Pirassununga, Cerrado de Emas, 27 March 2006, *O. Yano & B.L. Morretes 28820* (SP 382923, DNA voucher).

General Discussion

Phylogenetic position and circumscription of the family Pottiaceae

Historically, peristomial characters have been emphasized in classification of mosses (e.g. Philibert 1884–1902, Brotherus 1924–1925), and their phylogenetic signal at supra- subclass rank has also been proved by molecular phylogenetic analyses (e.g. Goffinet *et al.* 2001, Magombo 2003, Tsubota *et al.* 2004, Cox *et al.* 2010, Chang & Graham 2013). In molecular phylogenetic studies focusing on supra- familial relationships within mosses, the Pottiaceae was resolved in the clade of haplolepideous mosses, characterized by a single row of arthrodontous peristome teeth (Dicranidae) (Cox & Hedderson 1999; Goffinet & Cox 2000; Goffinet *et al.* 2001; La Farge *et al.* 2000, 2002; Magombo 2003; Hedderson *et al.* 2004; Tsubota *et al.* 2004). Phylogenetic trees using extensive taxon sampling of Dicranidae have showed that the Pottiaceae was resolved in the clade intermingled with genera of Bruchiaceae, Ditrichaceae *p.p.* and Erpodiaceae (Fedosov *et al.* 2015, 2016). However the closest relative of Pottiaceae is ambiguous. Further analysis based on broad taxon and marker sampling is necessary to assess the sound phylogenetic position of the family.

Present study excluded *Timmiella* and *Lusiserella* from Pottiaceae and accommodated these genera in a newly proposed family Timmiellaceae. This taxonomic treatment also provided the monophyletic circumscription of the family Pottiaceae. Zander (2007b) discussed that a twisted peristome, strongly differentiated costal anatomy, and the complexly papillose distal laminal cells are characteristic of this mostly acrocarpous family, commonly found in harsh environments. In the present study the Pottiaceae is recircumscribed by monophyletic clade comprising taxa which is characterized by dextrosely twisted peristome or dextrosely arranged operculum cells, strongly differentiated costal anatomy (double stereid in costal cross section), and the complexly papillose distal laminal cells. These complex characters are repeatedly lost and recurrent in the Pottiaceae lineages. This phenotypic plasticity may aid the family in adaptation to various environment and diversification. The taxa in Merceyoideae which is the most basal clade in the family share so reduced morphological characters: absent or reduced peristome, single stereid in costal cross section, and smooth or low-verrucose lamina. Although I retain Merceyoideae as a subfamily in Pottiaceae,

these features support the recognition of this subfamily as its own family as discussed by Zander (2006).

The characteristic twisted peristome of the Pottiaceae (present sense) is also found in Timmiellaceae which is placed in basal haplolepideous lineages, but the twist direction of peristome in Pottiaceae is reverse to that in Timmiellaceae. Zander (2006) argued that the twisted peristome of the Pottiaceae *s. str.* resulted from the re-activation of a gene cluster which silenced in lineages after *Timmiella*. He called the Pottiaceae *s. str.* a evolutionary "Lazarous taxon", not in the geologic sense as a group that has skipped a long fossil epoch (Wignall & Benton 1999) but as a resurfacing in evolutionary time of a major developmental adaptive complex contrary to Dollo's Law (Hall 2003). As suggested by Stech *et al.* (2012), further investigation is necessary to test whether the development of the twisted peristome in Timmiellaceae is in fact developmentally homologous to that in Pottiaceae and whether they share same developmental pathways.

Phylogeny and subfamilial classification of Pottiaceae

According to the present phylogenetic analysis I recognized four subfamilies in the Pottiaceae: Merceyoideae, Streblotrichoideae, Pottioideae and Trichostomoideae. Following rearrangement of the familial and subfamilial names is proposed with newly synonymization based on the present study and other phylogenetic studies cited in Chapter 2. For nomenclatural elements I follow the Melbourne Code of Nomenclature (McNeill *et al.* 2012).

Family **Pottiaceae** Hampe, Bot. Zeitung (Berlin) 11: 329. 1853, *nom. cons.* (Basionym: Pottiinae Müll.Hal., Syn. Musc. Frond. 1: 546. 1849, 'Pottiaceae') Type: *Pottia* Ehrh. ex Fürnr.

= Barbulaceae [unranked] Rabenh., Linnaea 9: 553. 1835, *nom. inval.* (ICN Art 38.1; no description).

= Hyophilaceae Hampe, Linnaea 20: 68. 1847, *nom. inval.* (ICN Art 38.1; no description, see Zander 1993, p. 52).

= Ephemeraceae J.W.Griff. & Henfr., Microgr. Dict. 235. 1855, *nom. cons.*, ***syn. nov.*** Type: *Ephemerum* Hampe

= Anoectangiaceae Schimp., Coroll. Bryol. Eur. 11. 1856. Type: *Anoectangium* Schwägr.

= Astomataceae Schimp. Coroll. Bryol. Eur. 7. 1856, ‘Astomaceae’. Type: *Astomum* Hampe

= Phascaceae Schimp., Coroll. Bryol. Eur. 4. 1856. Type: *Phascum* Hedw.

= Ripariaceae Schimp., Coroll. Bryol. Eur. 53. 1856, *nom. illeg.* (ICN Art. 18.1; based on *Cinclidotus* P.Beauv.).

= Weissiaceae Schimp., Coroll. Bryol. Eur. 7. 1856, ‘Weisiaceae’. Type: *Weissia* Hedw.

= Trichostomataceae Schimp., Syn. Musc. Eur. 141. 1860, ‘Trichostomaceae’. Type: *Trichostomum* Bruch.

= Cinclidotaceae Schimp., Syn. Musc. Eur. 193. 1860. Type: *Cinclidotus* P.Beauv., *orth. cons.,* ‘*Cicclidotus*’.

= Eupottiaceae [unranked] Hampe, Flora 50: 67. 1867, *nom. illeg.* (ICN Art. 10.6; the name not based on generic name)

= Euweisiaceae [unranked] Hampe, Flora 50: 67. 1867, *nom. illeg.* (ICN Art. 10.6; the name not based on generic name)

= Systegiaceae De Not., Atti Reale Univ. Genova 1: 33. 1869, *nom. illeg.* (ICN Art. 18.3; based on illegitimate generic name). Type: *Systegium* Schimp.

= Tortulaceae Lindb., Utkast Eur. Bladmoss. 25. 1878, *nom. inval.* (Art. 38.1; no description). Type: *Tortula* Hedw.

= Merceyaceae Casares-Gil, Fl. Ibér. Brióf., Musg. 247. 1932. Type: *Merceya* Schimp.

= Splachnobryaceae A.K.Kop., Ann. Bot. Fenn.18: 128. 1981. Type: *Splachnobryum* Müll.Hal.

1. Subfamily **Merceyoideae** Broth., Nat. Pflanzenfam. ed. 2, 10: 246. 1924. Type: *Merceya* Schimp.

≡ Merceyaceae Casares-Gil, Fl. Ibér. Brióf., Musg. 247. 1932.

2. Subfamily **Streblotrichoideae** Y.Inoue & H.Tsubota, Hikobia 17: 124. 2016. Type: *Streblotrichum* P.Beauv.

3. Subfamily **Pottioideae** Broth., Nat. Pflanzenfam. 1 (3): 381. 1901. Type: *Pottia* Ehrh. ex Fürnr.

= Ripariaceae Schimp., Coroll. Bryol. Eur. 53. 1856, *nom. illeg.* (ICN Art. 18.1; based on *Cinclidotus* P.Beauv.).

= Cinclidotaceae Schimp., Syn. Musc. Eur. 193. 1860, ***syn. nov.*** ≡ Cinclidotoideae Broth., Nat. Pflanzenfam. 1 (3): 381. 1901, ‘Cinclidoteae’, ***syn. nov.*** Type:

Cinclidotus P.Beauv., *orth. cons.,* '*Cicclidotus*'.

= Barbuloideae Hilp., Beih. Bot. Centralbl. 20: 612. 1933. Type: *Barbula* Hedw.

= Phascaceae Schimp., Coroll. Bryol. Eur. 4. 1856. Type: *Phascum* Hedw.

= Tortulaceae Lindb., Utkast Eur. Bladmoss. 25. 1878, *nom. inval.* (ICN Art. 38.1; no description). ≡ Tortuloideae Visotska, Citol. Genet. (Kiev) 1(4): 38. 1963, *nom. inval.* (Art. 39.1; no Latin description). Type: *Tortula* Hedw.

= Leptodontioideae Hilp., Beih. Bot. Centralbl. 50: 679. 1933. Type: *Leptodontium* (Müll.Hal.) Hampe ex Lindb.

= Erythrophyllopsidoideae R.H.Zander, Bull. Buffalo Soc. Nat. Sci. 32: 71. 1993, 'Erythrophyllopsoideae', ***syn. nov.*** Type: *Erythrophyllopsis* Broth.

= Gertrudielloideae R.H.Zander, Bull. Buffalo Soc. Nat. Sci. 32: 74. 1993, ***syn. nov.*** Type: *Gertrudiella* Broth.

4. Subfamily **Trichostomoideae** Broth., Nat. Pflanzenfam. 1 (3): 381. 1901, 'Trichostomeae'. Type: *Trichostomum* Bruch.

≡ Trichostomataceae Schimp., Syn. Musc. Eur. 141. 1860, 'Trichostomaceae'.

= Hyophilaceae Hampe, Linnaea 20: 68. 1847, *nom. inval.* (ICN Art 38.1; no description).

= Ephemeraceae J.W.Griff. & Henfr., Microgr. Dict. 235. 1855, *nom. cons.*, ***syn. nov.*** Type: *Ephemerum* Hampe

= Astomataceae Schimp. Coroll. Bryol. Eur. 7. 1856, 'Astomaceae'. Type: *Astomum* Hampe

= Weissiaceae Schimp., Coroll. Bryol. Eur. 7. 1856, 'Weisiaceae'. Type: *Weissia* Hedw.

= Anoectangiaceae Schimp., Coroll. Bryol. Eur. 11. 1856. Type: *Anoectangium* Schwägr.

= Systegiaceae De Not., Atti Reale Univ. Genova 1: 33. 1869, *nom. illeg.* (ICN Art. 18.3; based on illegitimate generic name). Type: *Systegium* Schimp.

= Pleuroweisioideae Broth., Nat. Pfl. (ed. 2), 10: 243. 1924, *nom. illeg.* (ICN Art. 18.3; based on illegitimate generic name), ***syn. nov.*** Type: *Pleuroweisia* Limpr. ex Schlieph.

= Eucladioideae P.C.Chen, Hedwigia 80: 40. 1941. Type: *Eucladium* Bruch & Schimp.

= Splachnobryaceae A.K.Kop., Ann. Bot. Fenn. 18: 128. 1981, ***syn. nov.*** Type: *Splachnobryum* Müll.Hal.

= Chionolomoideae R.H.Zander, Bull. Buffalo Soc. Nat. Sci. 32: 76. 1993. Type: *Chionoloma* Dixon.

Evolutionary trends in sporophytes of Weissia

Among the genera of Pottiaceae, *Weissia* exhibits a highest degree of variation in sporophyte structure along the reduction series. Eperistomate immersed capsules may be neotenous sporophytes that skipped seta elongation and peristome development to proceed directly to sporogenesis (Shaw *et al.* 2000). This structural reduction in the sporophytes has independently occurred in several lineages of Pottiaceae (e.g. *Ephemerum* and *Tortula*) and also in other distantly related moss families: Funariaceae (Fife 1985), Orthotrichaceae Arn. (Vitt 1981) and Neckeraceae Schimp. (Olsson *et al.* 2009, Huttunen *et al.* 2012). These reduction is often observed among taxa in xeric or highly seasonal habitats (Vitt 1981). As discussed by Huttunen *et al.* (2012), in these habitat where resources are limited the small reduced sporophytes may cost less than the large complex ones and be more advantageous.

Acknowledgements

I would like to thank my supervisor Associated Professor Dr. Hiromi Tsubota for his invaluable guidance, discussion, continuous encouragement, and immense support given through my dissertation. I am highly grateful and indebted to my co-supervisor Dr. Tomio Yamaguchi for his invaluable support, encouragement, great kindness, and generous guidance for field work. I would also like to extend my sincere thanks to Drs. Hironori Deguchi, Tomoyuki Katagiri, Miho Nakahara-Tsubota, Tarow Seki and Masaki Shimamura for their encouragement and making time to discuss my ideas and queries, and to Drs. Katsunori Suzuki and Yousuke Takahashi (Former directors of Miyajima Natural Botanical Garden) for various assistance. Special thanks to all members of the Laboratory of Island Biology (Miyajima Natural Botanical Garden) and the Laboratory of Plant Taxonomy and Ecology, for their assistance in the laboratory experiment, especially to Mr. Seiji Mukai, Ms. Mieko Mukai and Mr. Shinji Uchida for their supporting my research life. I am indebted to the curators and staff of the herbaria at BM, CBFS, H, KOCH, MUB, NICH, NUM, NY, PC, S, SP, TNS and W for loan of the specimens including types. I also thank Mr. T. Nasu (President of Hattori Botanical Laboratory) for financial assistance to enable field research in Ryukyu Islands; Dr. K. Saito for giving valuable information on Japanese *Weissia*; Drs. M. J. Cano and M. J. Price for their valuable suggestions on the lectotypification of *Weissia controversa*; Dr. C. La Farge for giving information on the voucher specimen of *Stegonia latifolia* in ALTA; The staff at The University of Tokyo Tanashi Forest, Ms. M. Chishiki, Dr. B. Estébanez, Mr. M. Hayashi, Dr. J. A. Jiménez, Mr. T. Kamiyama, Dr. J. Kučera, Ms. M. Matsumoto, Mr. S. Nagatani, Dr. J. D. Orgaz, Mr. H. Sato, Dr. T. Suzuki, Mr. Y. Tateishi and Ms. K. Uemura for study material. I also thank Dr. Rod Seppelt for checking the English text and his valuable suggestions. I would also like to extend my deepest gratitude to my family for their mental, motivational, and financial support to enable me to achieve this work.

Sequencing for this study was carried out at the Analysis Center of Life Science, Natural Science Center for Basic Research and Development, Hiroshima University. This study was partly supported by JSPS KAKENHI for HT (Grant Number 16K07481).

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Tables & Figures

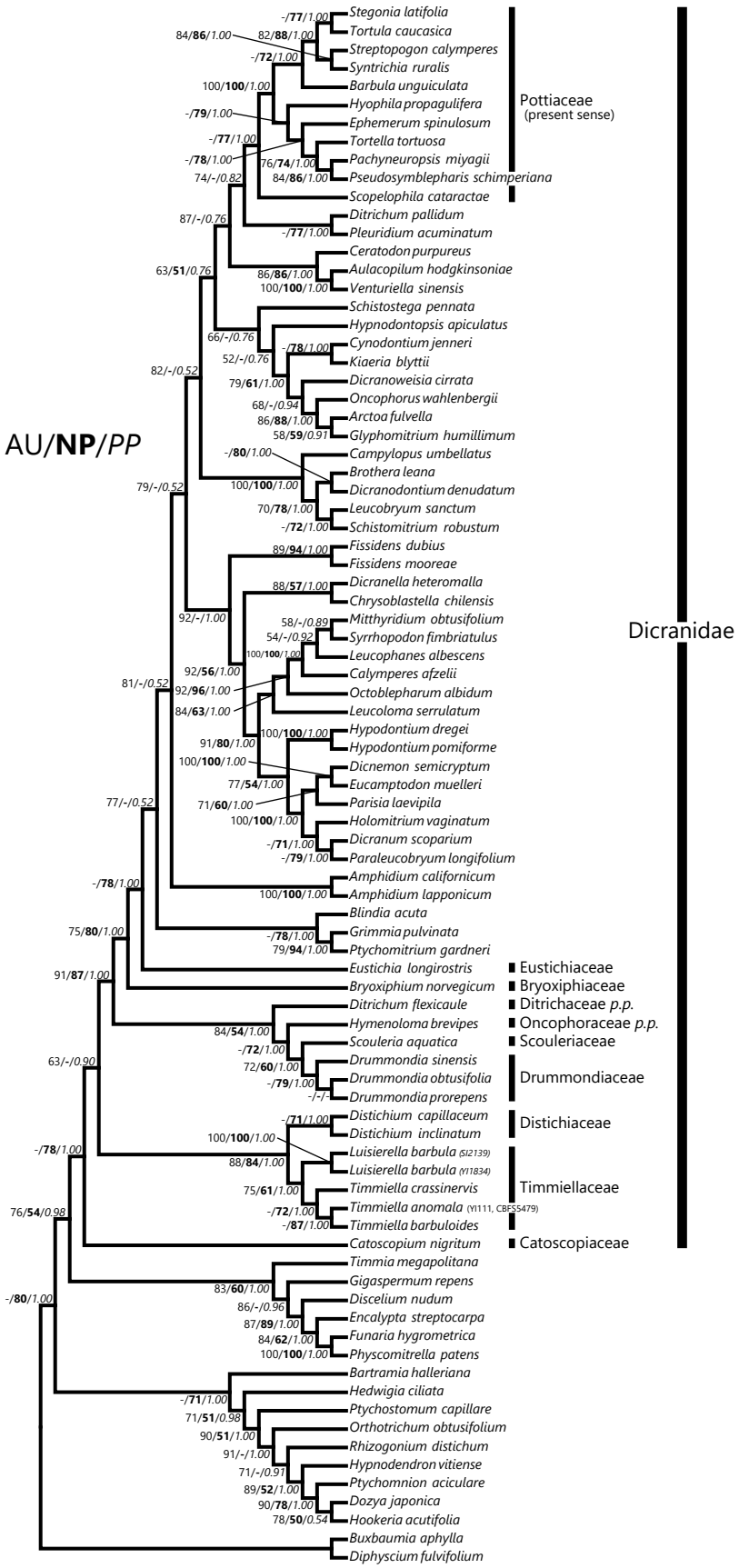

Fig. 1.1. Phylogenetic tree based on analysis with the concatenated sequences of chloroplast *rbcL* and *rps4* genes, depicted by a 50 % majority-rule condensed tree for the nine topologies passing both AU and PP tests. Supporting values more than 50 % obtained by the program CONSEL were overlaid: the values by the AU test (AU), bootstrap probabilities calculated through the same theory as AU (NP), and Bayesian posterior probabilities (PP) are shown on or near each branch (AU/NP/PP). The root is arbitrarily placed on the branch leading to the clade which includes members of the genera *Buxbaumia* and *Diphyscium* following Tsubota *et al.* (2003, 2004) and Cox *et al.* (2010).

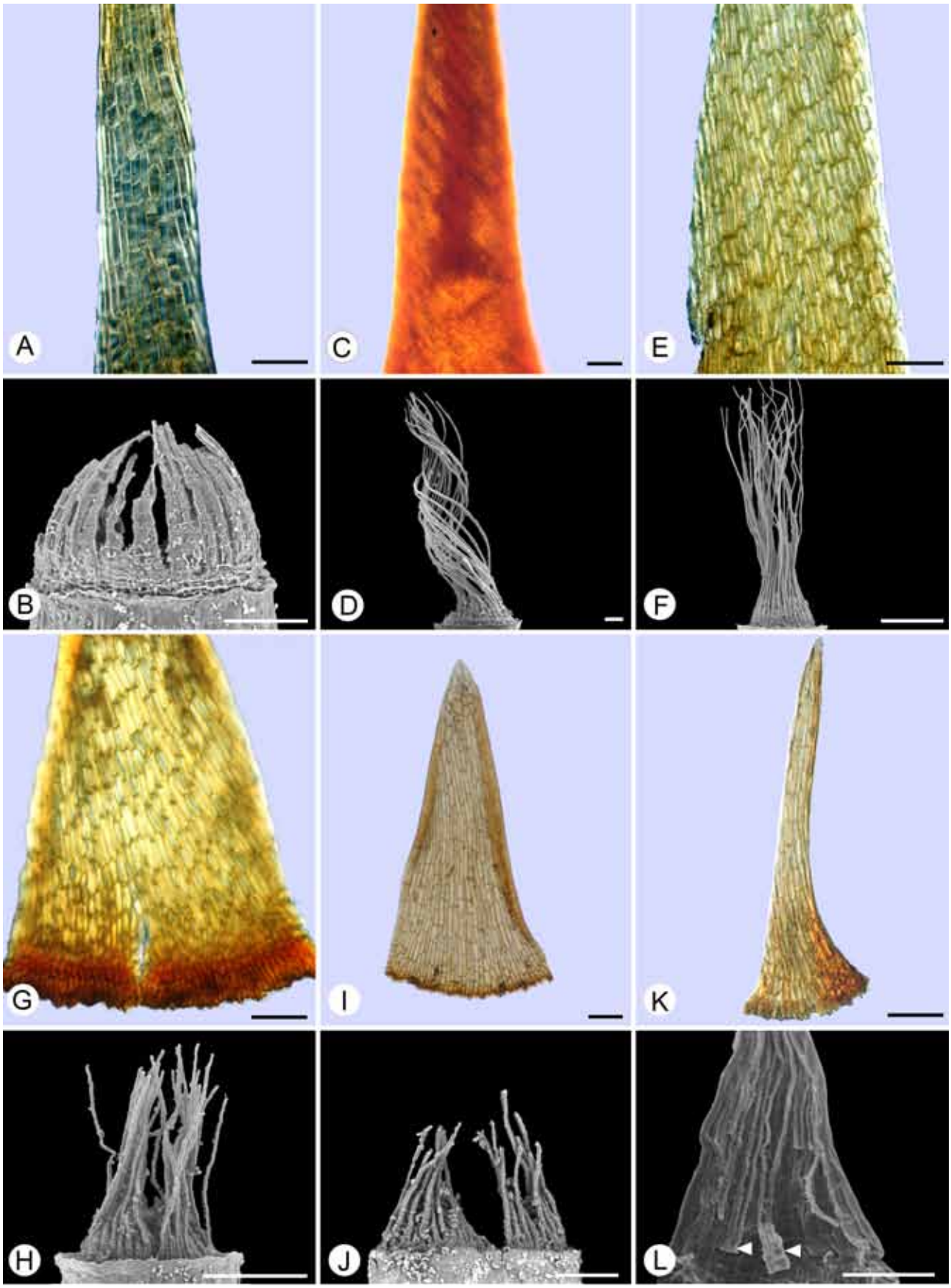

Fig. 1.2. Opercula (A, C, E, G, I, K) and peristomes (B, D, F, H, J, L) of *Timmiella* and *Luisierella*. A & B, *Timmiella acaulon*. C & D, *T. anomala*. E & F, *T. barbuloides*. G & H, *T. crassinervis*. I & J, *T. diminuta*. K & L, *Luisierella barbula* (Peristome teeth indicated by arrowheads). A & B from *C. C. Hosseus 396* (HIRO). C & D from *Y. Inoue 1910* (HIRO). E & F from *C. C. Townsend s.n.* (HIRO). G & H from *W. B. Schofield 14404* (HIRO). I & J from *C. Y. Chang s.n.* (TNS). K from *R. A. Pursell 632* (HIRO). L from *R. L. Redfearn Jr. 73–55* (HIRO). Scale bars = 100 μm.

Table 2.1. History of classification of Pottiaceae and its related families modified from the tables after Saito (1975) and Werner *et al.* (2004a).

Schimper (1856)	Limpricht (1888)	Brotherus (1902)	Brotherus (1924)	Hilpert (1933)
PHASCACEAE	PHASCACEAE	POTTIACEAE	POTTIACEAE	TRICHOSTOMATACEAE
		Trichostomoideae	Pleuroweisioideae	Trichostomoideae
ASTOMATACEAE	WEISSIACEAE	Pottioideae	Merceyoideae	Leptodontioideae
	Gymnoweisieae	Encalyptoideae	Trichostomoideae	Barbuloideae
WEISSIACEAE	Pleuroweisieae	Cinclidotoideae	Pottioideae	
			Cinclidotoideae	POTTIACEAE
ANOECTANGIACEAE	POTTIACEAE			
	Trichostomeae			CINCLIDOTACEAE
POTTIACEAE	Pottieae			

Chen (1941)	Podpěra (1954)	Saito (1975)	Corley *et al.* (1981)	Walther (1983)
POTTIACEAE	POTTIACEAE	POTTIACEAE	POTTIACEAE	POTTIACEAE
Trichostomoideae	Trichostomoideae	Trichostomoideae	Trichostomoideae	Trichostomoideae
Eucladioideae	Eucladioideae	Pottioideae	Pottioideae	Pottioideae
Leptodontioideae	Leptodontioideae		Cinclidotoideae	Cinclidotoideae
Barbuloideae	Pottioideae	CINCLIDOTACEAE		Leptodontioideae
Pottioideae				
Cinclidotoideae	CINCLIDOTACEAE			

Zander (1993)	Werner *et al.* (2004a)	Zander (2006)	Frey & Stech (2009)	Present study
POTTIACEAE	POTTIACEAE	POTTIACEAE	POTTIACEAE	POTTIACEAE
Timmielloideae	Trichostomoideae	Timmielloideae	Timmielloideae	Trichostomoideae
Erythrophyllopsidoideae	Pottioideae	Trichostomoideae	Trichostomoideae	Pottioideae
Gertrudielloideae	Merceyoideae	Barbuloideae	Barbuloideae	Streblotrichoideae
Chionolomoideae	Gertrudielloideae?	Pottioideae	Pottioideae	Merceyoideae
Trichostomoideae		Merceyoideae	Merceyoideae	
Merceyoideae				HYPODONTIACEAE
Pottioideae			HYPODONTIACEAE	
				TIMMIELLACEAE
CINCLIDOTACEAE				

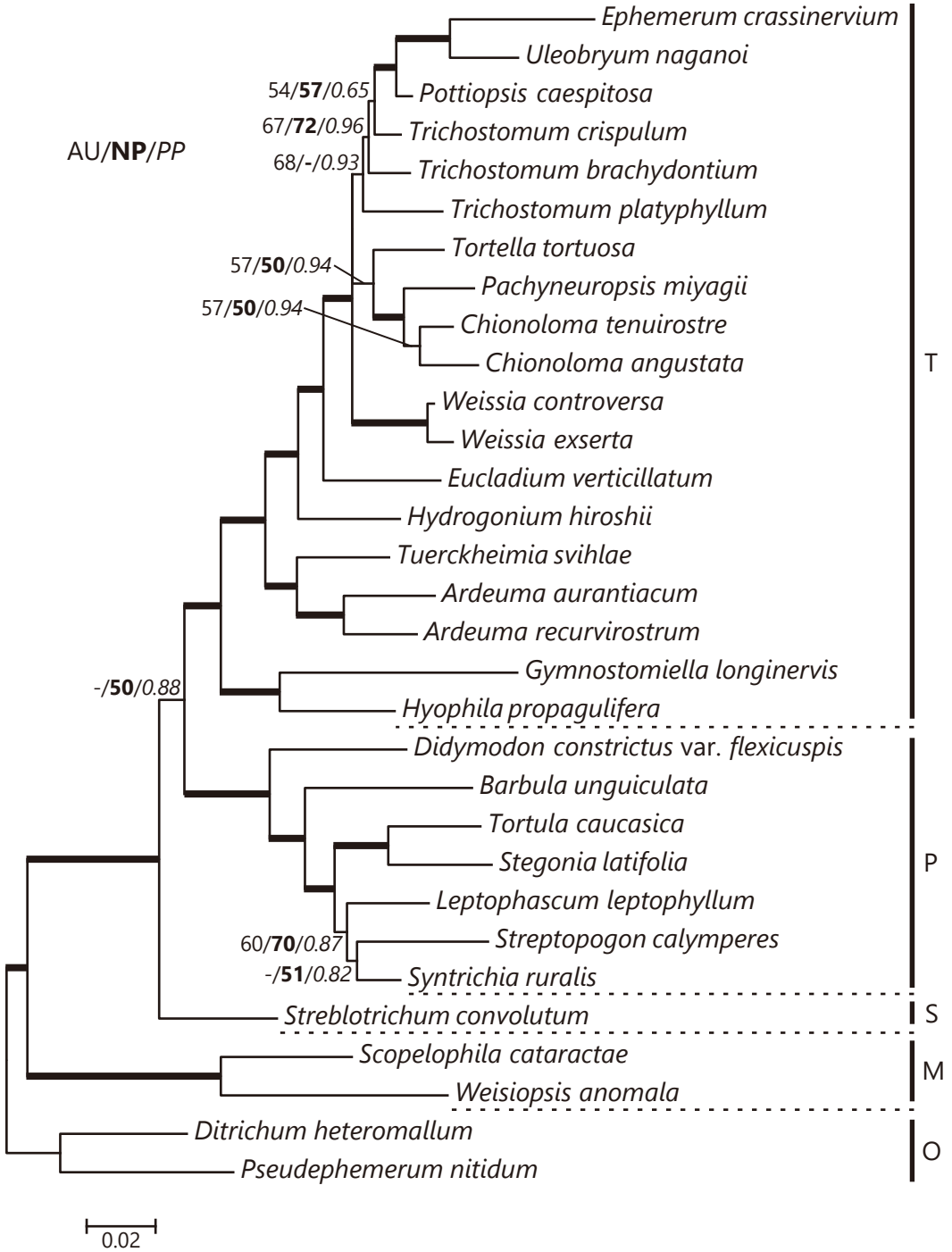

Fig. 2.1. Phylogenetic tree based on analysis with the concatenated sequences of chloroplast *rbcL* and *rps4* genes, depicted by the best-supported tree with highest likelihood value (ln *L* = -7206.803252 by Garli). Supporting values more than 50 % obtained by the program CONSEL were overlaid: AU test (AU), bootstrap probabilities (NP), and Bayesian posterior probabilities (PP) are shown on or near each branch (AU/NP/PP). Thickened branches indicate that all three supporting values are 100 %. The Roman characters correspond to the outgroup species and the subfamilial classification (T = Trichostomoideae, P = Pottioideae, S = Streblotrichoideae, M = Merceyoideae, O = outgroup).

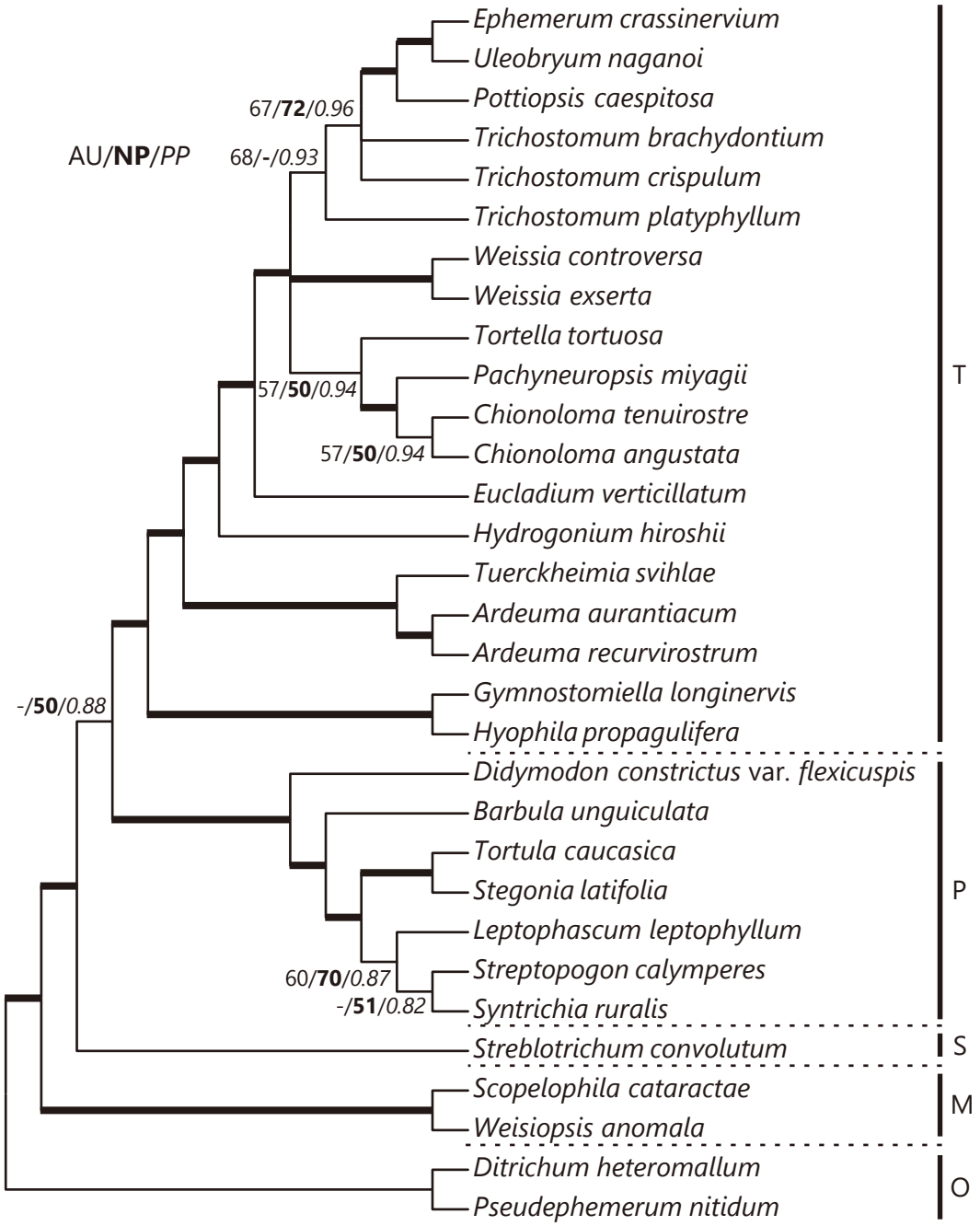

Fig. 2.2. Phylogenetic tree based on analysis with the concatenated sequences of chloroplast *rbcL* and *rps4* genes, depicted by the strict condensed tree for six topologies passing both AU and PP tests. Supporting values more than 50 % obtained by the program CONSEL were overlaid: AU test (AU), bootstrap probabilities (NP), and Bayesian posterior probabilities (PP) are shown on or near each branch (AU/NP/PP). Thickened branches indicate that all three supporting values are 100 %. The Roman characters correspond to the outgroup species and the subfamilial classification (T = Trichostomoideae, P = Pottioideae, S = Streblotrichoideae, M = Merceyoideae, O = outgroup).

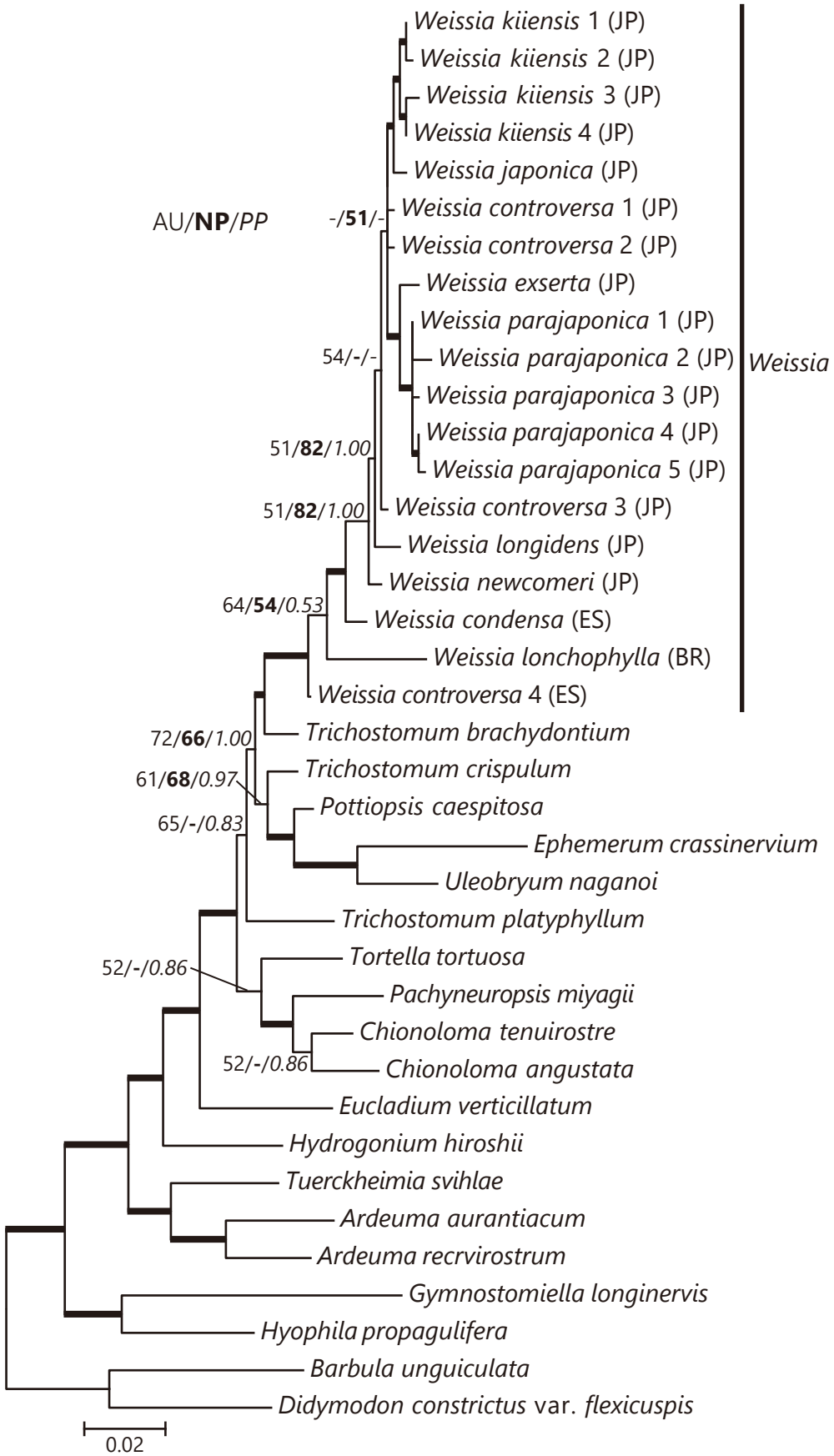

Fig. 3.1. Phylogenetic tree based on analysis with the concatenated sequences of chloroplast *rbcL* and *rps4* genes, depicted by the best-supported tree with highest likelihood value (ln *L* = -5770.556 by Garli). Supporting values more than 50 % obtained by the program CONSEL were overlaid: AU test (AU), bootstrap probabilities (NP), and Bayesian posterior probabilities (PP) are shown on or near each branch (AU/NP/PP). Thickened branches indicate that all three supporting values are 100 %.

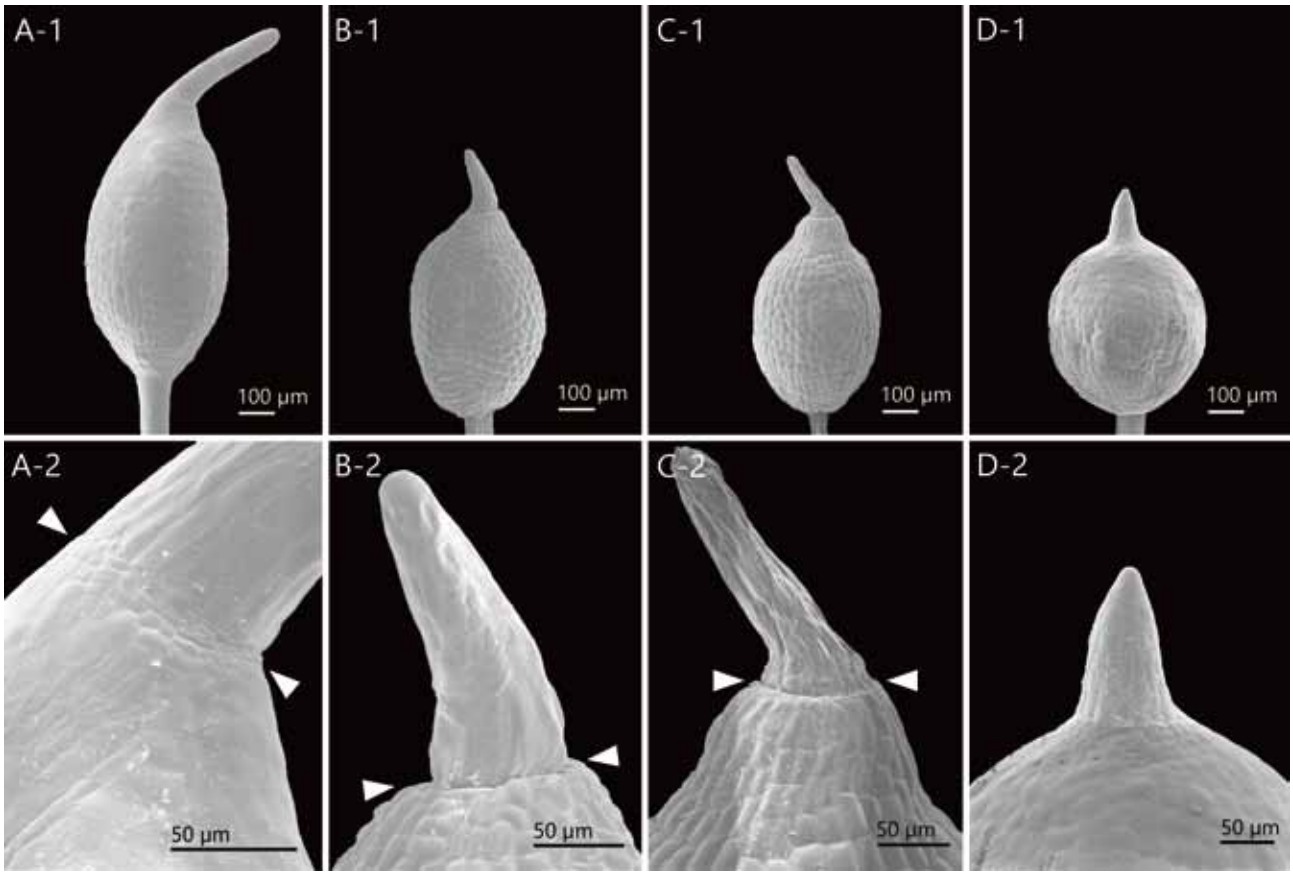

Fig. 3.2. Scanning electron microscope (SEM) images of cleistocarpous capsules of *Weissia* in Japan. A, *W. exserta* (*Y. Inoue 3828* in HIRO); B, *W. japonica* (*Y. Inoue 3830* in HIRO); C, *W. parajaponica* (*T. Yamaguchi 36925* in HIRO); D, *W. kiiensis* (*Y. Inoue 3813* in HIRO). 1, Capsule overviews; 2, Close up of upper portion of capsules (Arrowheads indicate dehiscence line).

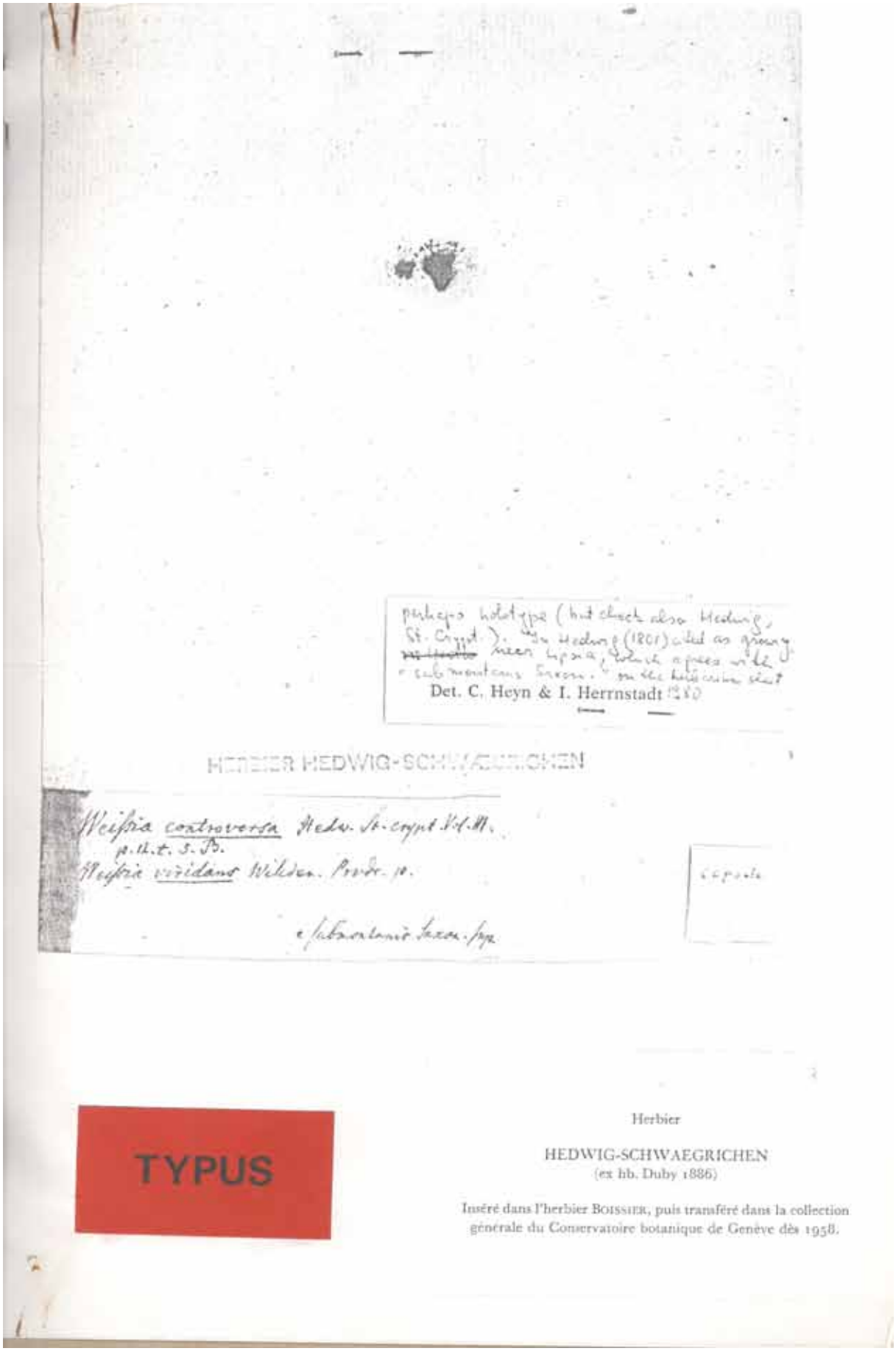

Fig. 3.3. A photocopy of the lost herbarium sheet of the specimen from Leipzig, named *Weissia controversa* in Hedwig's herbarium (G), which was the best candidate for a lectotype (used with permission of the Conservatory and Botanical Garden of the City of Geneva).

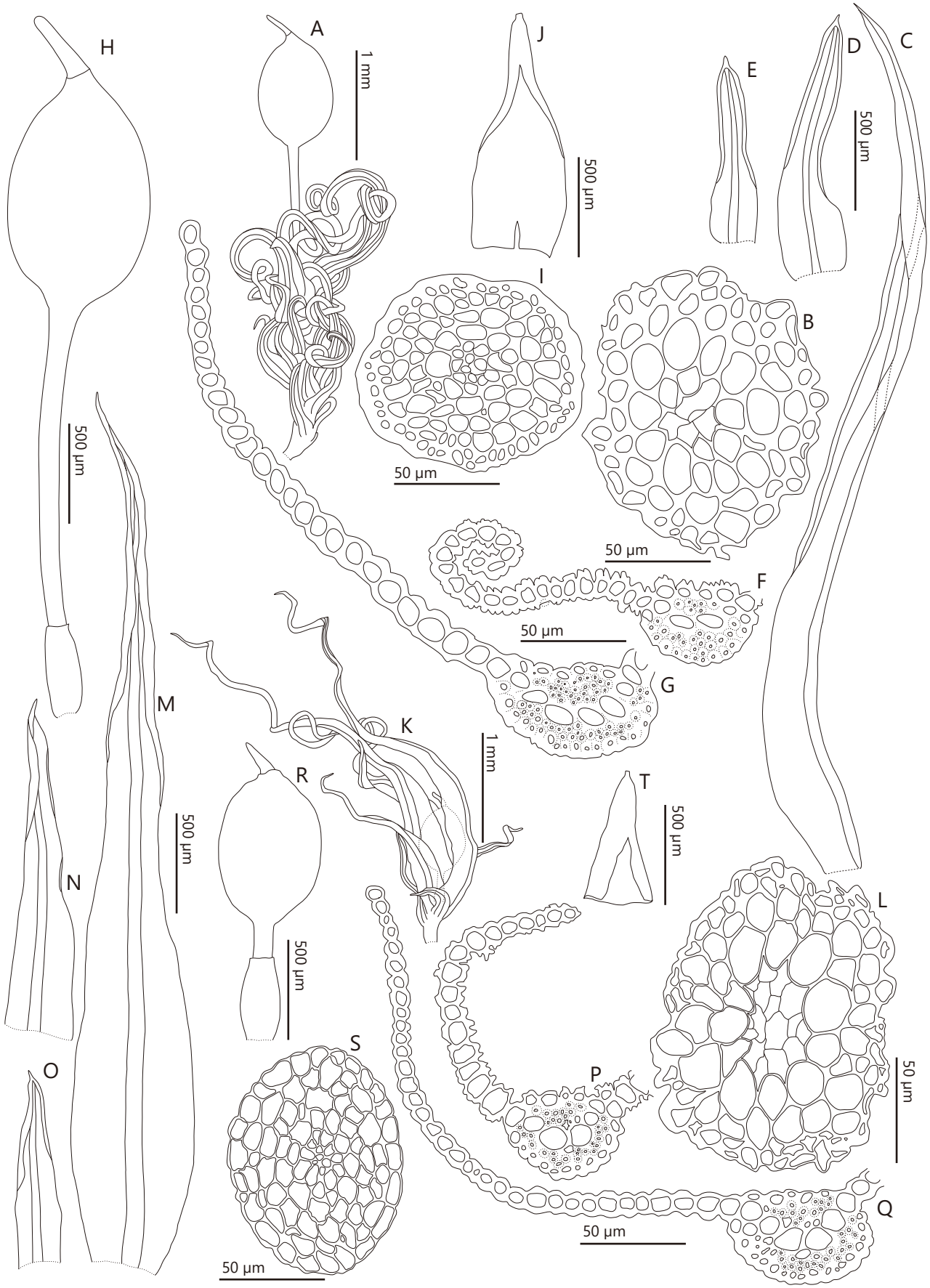

Fig. 3.4. *Weissia exserta* (A–J) and *W. japonica* (K–M). A, Habit (dry); B, Cross section of stem; C, Perichaetial leaf; D & E, Vegetative leaves; F & G, Cross sections of perichaetial leaf; H, Sporophyte; I, Cross section of seta; J, Calyptra; K, Habit (dry); L, Cross section of stem; M, Perichaetial leaf; N & O, Vegetative leaves; P & Q, Cross sections of perichaetial leaf; R, Sporophyte; S, Cross section of seta; T, Calyptra. A–J drawn from *Wichura 1379a* (H 190018, lectotype of *Astomum exsertum*); K–T from *Y. Inoue 914* (HIRO).

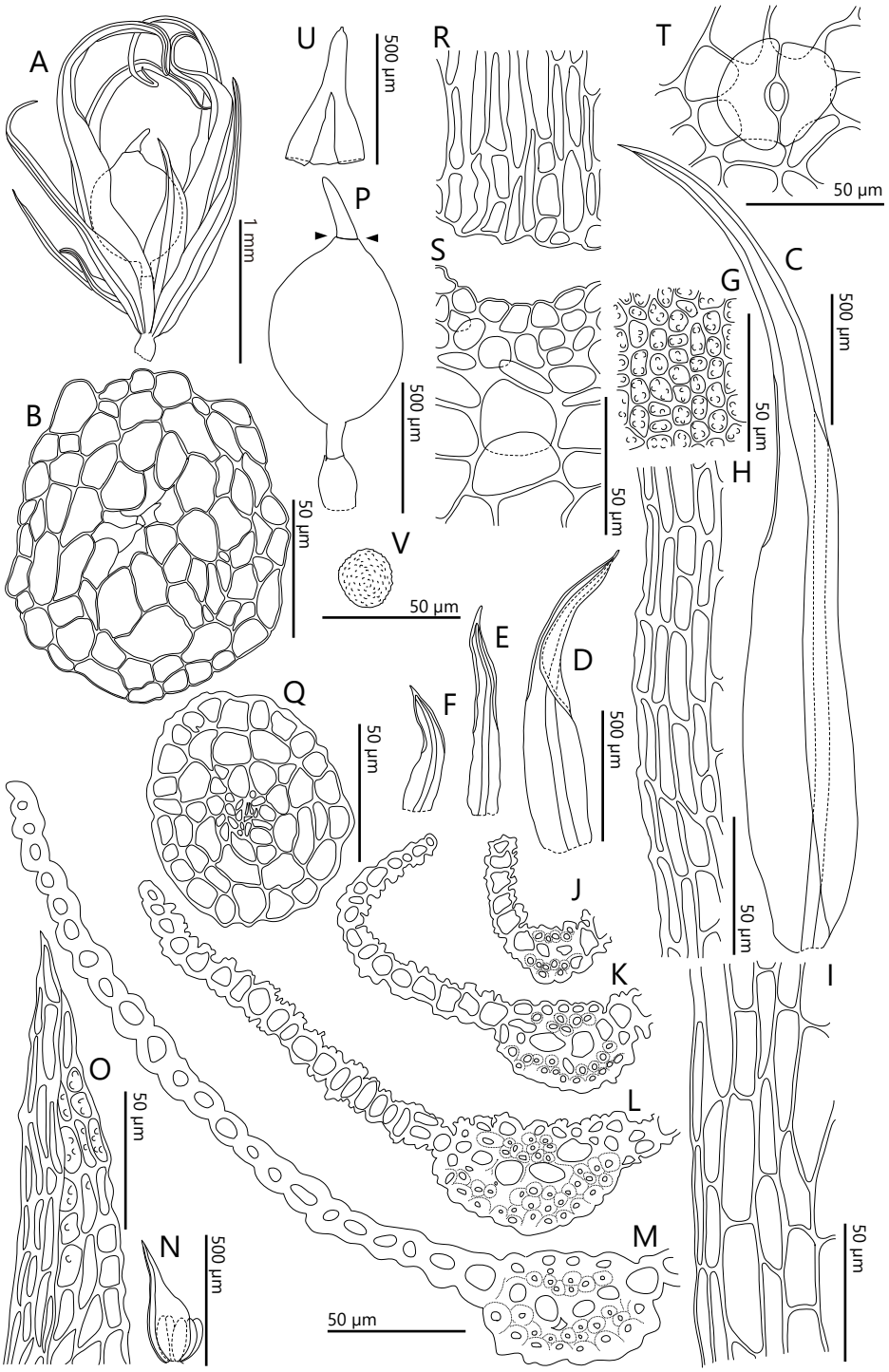

Fig. 3.5. *Weissia japonica*. A, Habit (dry); B, Cross section of stem; C, Perichaetial leaf; D–F, Vegetative leaves; G, Upper laminal cells of perichaetial leaf; H, Laminal cells at shoulder part of perichaetial leaf base; I, Basal laminal cells of perichaetial leaf; J–M, Cross sections of perichaetial leaf; N, Perigonial leaf with antheridia; O, Upper portion of perigonial leaf; P, Capsule (Arrowheads point dehiscent part); Q, Cross section of seta; R & S, Dehiscence part of capsule between the base of beak (R) and urn (S); T, Stoma; U, Calyptra; V, Spore. Scale bars: a for A; b for C–F, N, P, U; c for B, G–M, O, Q–S, V. All drawn from lectotype (PC 657676).

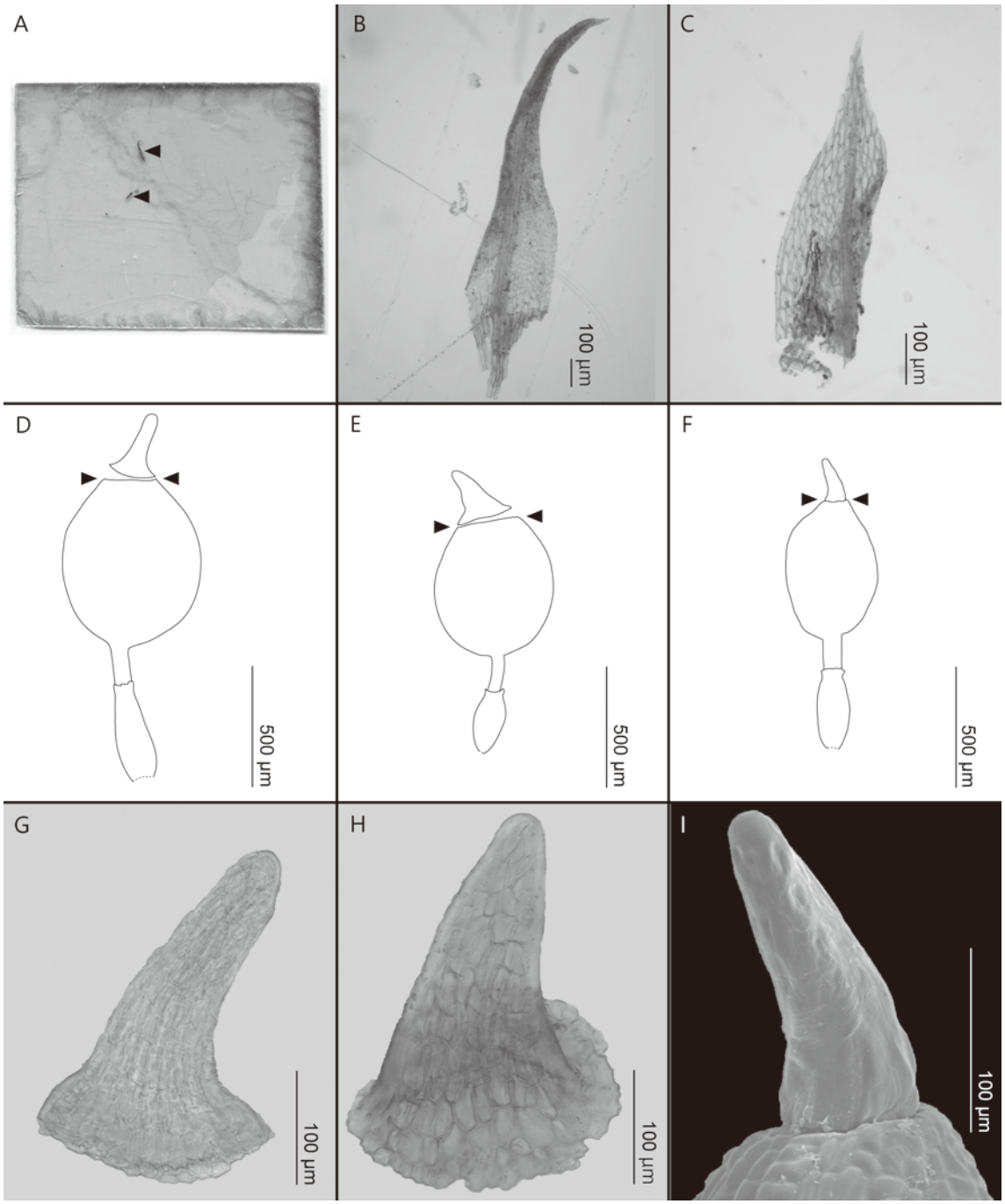

Fig. 3.6. Specimen in Roth collection (S B3524, A–C) and Dehiscence positions of *Weissia levieri* (D & G), *W. longifolia* var. *angustifolia* (E & H) and *W. japonica* (F & I). A, Overview (Arrowheads indicate leaves); B, Leaf of *Astomum japonicum* (Isolectotype of *A. japonicum*); C, Leaf of *Brachymenium* sp; D–F, Illustrations of capsule overviews (Arrowheads indicate dehiscence line); G & H, Light microscope views of opercula; I, Scanning electron microscope (SEM) view of beak attaching to urn (Preparation for SEM observation followed Inoue *et al.* 2011); D & G from *Ros & Jiménez s.n.* (MUB 10259, duplicate in HIRO); E & H from *A. Ginzberger s.n.* (holotype of *Astomum crispum* var. *angustifolium,* W-KRYPT 1964-21668); F & I from *Y. Inoue 3830* (HIRO).

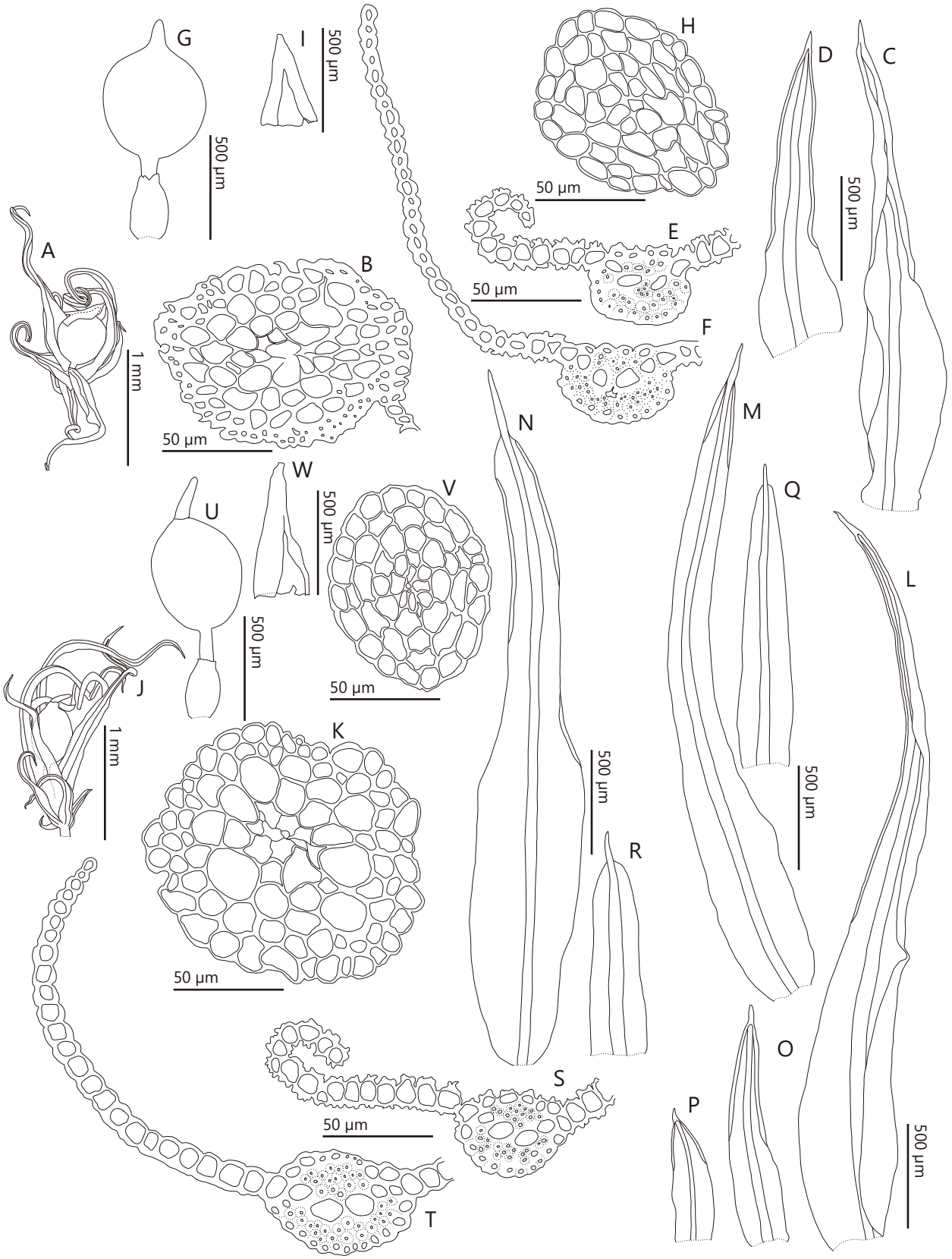

Fig. 3.7. *Weissia kiiensis* (A–I) and *W. prajaponica* (J–W). A, Habit (dry); B, Cross section of stem; C, Perichaetial leaf; D, Vegetative leaf; E & F, Cross sections of perichaetial leaf; G, Sporophyte; H, Cross section of seta; I, Calyptra; J, Habit (dry); K, Cross section of stem; L–N, Perichaetial leaves; O–R, Vegetative leaves; S & T, Cross sections of perichaetial leaf; U, Sporophyte; V, Cross section of seta; W, Calyptra. A–I drawn from *K. Minakata s.n.* (holotype of *Astomum kiiense,* NICH-M 37518); J, V from *T. Yamaguchi 36925* (paratype, HIRO); K, L, O, P, S, T, W from *Y. Inoue 3864* (holotype, HIRO); M, Q from *Y. Inoue 3925* (paratype, HIRO); N, R from *T. Yamaguchi 30497* (paratype, HIRO); U from *T. Yamaguchi 18666* (paratype, HIRO).

Appendices

Appendix A. List of words or phrases that explain abbreviations or symbols.

AU	approximately unbiased
auct. non	*auctorum non*: not of authors
BI	Bayesian inference
comb. nov.	*combinatio nova*: new combination of name and epithet
INSDC	DDBJ/EMBL/GenBank International Nucleotide Sequence Database Collaboration
ML	maximum likelihood
MP	maximum parsymony
nom. cons.	*nomen conservandum*: name conserved in International Code of Nomenclature
nom. illeg.	*nomen illegitimum*: illegitimate name
nom. inval.	*nomen invalidum*: invalid name
nom. nud.	*nomen nudum*: a designation of a new taxon published without a description or diagnosis or reference to a description or diagnosis
NP	bootstrap probability through the same theory as AU
PP	posterior probability
p.p.	*pro parte*: partly, in part
rbcL	ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit
rps4	ribosomal protein S4 subunit
s.d.	*sine die*: without a day
s.l.	*sensu lato*: in a broad sense
s.loc.	*sine loco*: without a place
s.n.	*sine numero*: without a number
sp. nov.	*species nova*: new species
s. str.	*sensu strict*: in a narrow sense
stat. nov.	*status novus*: name at new rank
syn. nov.	*synonymia novus*: new synonym
!	seen by the author
=	based on the different type, taxonomic synonym

≡ based on the same type, nomeclatural synonym

Appendix B. List of species investigated for *rbcL* and *rps4* gene sequences with the voucher information and the accession number. Bold accession numbers indicate newly obtained sequences for the chapter 1.

Amphidium californicum (Hampe ex Müll.Hal.) Broth., AF226812/AF226762; *Amphidium lapponicum* (Hedw.) Schimp., AF005543/AF222896; *Arctoa fulvella* (Dicks.) Bruch & Schimp., AF231293/AF231266; *Aulacopilum hodgkinsoniae* (Hampe & Müll.Hal.) Broth., AF005545/AF222897; *Barbula unguiculata* Hedw., AB670696/AF480952; *Bartramia halleriana* Hedw., AF231090/AF265358; *Blindia acuta* (Hedw.) Bruch & Schimp., AF226817/AF023781; *Brothera leana* (Sull.) Müll.Hal., AB122033/AY908129; *Bryoxiphium norvegicum* (Brid.) Mitt., AF231294/AF231267; *Buxbaumia aphylla* Hedw., AF231062/AF306959; *Calymperes afzelii* Sw., AF226788/AF226744; *Campylopus umbellatus* (Schwägr. & Gaudich. ex Arn.) Paris, AF226814/AF226764; *Catoscopium nigritum* (Hedw.) Brid., **AB914712/AB914711**, Austria, Styria, Hochschwab Mts., CBFS 15674 (duplicate in HIRO); *Ceratodon purpureus* (Hedw.) Brid., DQ463103/AY908122; *Chrysoblastella chilensis* (Mont.) Reimers, **AB914714**/**AB914713**, Australia, Tasmania, Mt. Wellington, *R. D. Seppelt 26697* (duplicate in HIRO); *Cynodontium jenneri* (Schimp.) Stirt., AF231318/AF231271; *Dicnemon semicryptum* Müll.Hal., AF478228/AF478274; *Dicranella heteromalla* (Hedw.) Schimp., AF231296/AF231272; *Dicranodontium denudatum* (Brid.) E.Britton, AF231317/AF231273; *Dicranoweisia cirrata* (Hedw.) S.O.Lindberg, AF478227/AF478279; *Dicranum scoparium* Hedw., AF231300/AF231277; *Diphyscium fulvifolium* Mitt., AF478222/AF478266; *Discelium nudum* (Dicks.) Brid., EU095320/AF223063; *Distichium capillaceum* (Hedw.) Bruch & Schimp., **AB853072**/**AB853082**, Japan, Ngano-ken, Mt. Shiomi, *Y. Inoue 1236* (HIRO); *Distichium inclinatum* (Hedw.) Bruch & Schimp., **AB914716**/**AB914715**, Czech Republic, NE Bohemia, Krkonoše Mts., CBFS 8013 (duplicate in HIRO); *Ditrichum flexicaule* (Schwägr.) Hampe, **AB914718**/**AB914717**, Austria, Styria, Totes Gebirge Mts., CBFS 12464 (duplicate in HIRO); *Ditrichum pallidum* (Hedw.) Hampe, AF231302/AF231279; *Dozya japonica* Sande Lac., AB125593/AY908262; *Drummondia obtusifolia* Müll. Hal., AF232697/AF223038; *Drummondia prorepens* (Hedw.) E.Britton, AF005542/AF306977; *Drummondia sinensis* Müll.Hal.,

AB853071/**AB853081**, Japan, Hiroshima-ken, Miyajima Isl., *H. Tsubota 7707* (HIRO); *Encalypta streptocarpa* Hedw., AF478239/AF478282; *Ephemerum spinulosum* Bruch & Schimp., AB194719/AF223055; *Eucamptodon muelleri* Hampe & Müll.Hal., AF231319/AF231280; *Eustichia longirostris* (Brid.) Brid., GQ497665/AY908091; *Fissidens dubius* P.Beauv., AF231303/AF231281; *Fissidens mooreae* H.Whittier & H.A.Mill., AF226810/AF226760; *Funaria hygrometrica* Hedw., AF005513/AJ845203; *Gigaspermum repens* (Hook.) Lindb., AF231064/JN088984; *Glyphomitrium humillimum* (Mitt.) Cardot, AB125585/EU246851; *Grimmia pulvinata* (Hedw.) Sm., AF231305/AF222900; *Hedwigia ciliata* (Hedw.) P.Beauv., AF478234/AF478289; *Holomitrium vaginatum* (Hook.) Brid., AF226811/AF226761; *Hookeria acutifolia* Hook. & Grev., AF158170/AF143071; *Hymenoloma brevipes* (Müll.Hal.) Ochyra, AB914720/AB914719, Chile, Prov. de Tierra del Fuego, J. Larrain s.n., CBFS 14901 (duplicate in HIRO); *Hyophila propagurifela* Broth., **AB853074**/**AB853084**, Japan, Hiroshima-ken, Kami-kamagari-jima Isl., *Y. Inoue 1745* (HIRO); *Hypnodendron vitiense* Mitt., AY524443/AY524471; *Hypnodontopsis apiculatus* Z.Iwats. & Nog., **AB853073**/**AB853083**, Japan, Aichi-ken, Yanai Shrine, *Y. Inoue 1815* (HIRO); *Hypodontium dregei* (Hornsch.) Müll.Hal., AF226804/AF226755; *Hypodontium pomiforme* (Hook.) Müll.Hal., AF226803/AJ554020; *Kiaeria blyttii* (Bruch & Schimp.) Broth., AF231283/AF231306; *Leucobryum sanctum* (Nees ex Schwägr.) Hampe, AF226769/AF226826; *Leucoloma serrulatum* Brid., AF231286/AF231309; *Leucophanes albescens* Müll.Hal., AF226751/AF226798; *Luisierella barbula* (Schwägr.) Steere, **AB853077**/**AB853085**, Japan, Hiroshimaken, Taishaku-kyo Gorge, *S. Ideshita 2139* (HIRO); *Luisierella barbula* (Schwägr.) Steere, **AB853076**/**AB853086**, Japan, Shizuoka-ken, Mt. Okami-yama, *Y. Inoue 1834* (HIRO); *Mitthyridium obtusifolium* (Lindb.) H.Rob., AF226777/AF226733; *Octoblepharum albidum* Hedw., AF226794/AF226747; *Oncophorus wahlenbergii* Brid., AF231310/AF231287; *Orthotrichum obtusifolium* Schrad. ex Brid., AF005537/AF306969; *Pachyneuropsis miyagii* T.Yamag., **AB853078**/**AB759969**, Japan, Okinawa-ken, Mt. Boujimui, *T. Yamaguchi 34243* (HIRO); *Paraleucobryum longifolium* (Ehrh. ex Hedw.) Loeske, AF226829/AF226772; *Parisia laevipila* (Cardot & Thér.) Tixier, HM236405/HM236404; *Physcomitrella patens* (Hedw.) Bruch & Schimp. subsp. *patens*, AP005672/AP005672; *Pleuridium acuminatum* Lindb., AF231312/AF231289;

Pseudosymblepharis schimperiana (Paris) H.A.Crum, AF226805/AF226756; *Ptychomitrium gardneri* Lesq., AF231313/AF231290; *Ptychomnion aciculare* (Brid.) Mitt., DQ196094/DQ186845; *Ptychostomum capillare* (Hedw.) Holyoak & N.Pede, AY163027/AF521682; *Rhizogonium distichum* (Sw.) Brid., AY524433/AY524461; *Schistomitrium robustum* Dozy & Molk., AF226825/AF226768; *Schistostega pennata* (Hedw.) F.Weber & D.Mohr, AY631206/AY631171; *Scopelophila cataractae* (Mitt.) Broth., **AB853075**/**AB853087**, Japan, Kochi-ken, Mt. Yokogugra-yama, *Y. Inoue 318* (HIRO); *Scouleria aquatica* Hook., AF226822/AF023780; *Stegonia latifolia* (Schwägr.) Venturi ex Broth., AF231314/AF222901; *Streptopogon calymperes* Müll.Hal., AF478231/AF478285; *Syntrichia ruralis* (Hedw.) F.Weber & D.Mohr, FJ546412/FJ546412; *Syrrhopodon fimbriatulus* Müll.Hal., AF226786/AF226742; *Timmia megapolitana* Hedw., AY312938/AY908619; *Timmiella anomala* (Bruch & Schimp.) Limpr., **AB853079**/**AB853088**, Japan, Hiroshima-ken, Miyajima Isl., *Y. Inoue 111* (HIRO); *Timmiella anomala* (Bruch & Schimp.) Limpr., **AB914722**/**AB914721**, Spain, Andalucia, Prov. de Sierra Nevada, CBFS 5479 (HIRO); *Timmiella barbuloides* (Brid.) Mönk., **AB914724**/**AB914723**, Spain, Andalucia, Prov. de Málaga, CBFS 10739 (HIRO); *Timmiella crassinervis* (Hampe) L.F.Koch, AF478236/AF478275; *Tortella tortuosa* (Hedw.) Limpr., **AB853080**/**AB853089**, Japan, Ngano-ken, Mt. Shiomi, *Y. Inoue 1297* (HIRO); *Tortula caucasica* S.O.Lindberg, AB670694/AB759970; *Venturiella sinensis* (Venturi) Müll.Hal., AB125591/AY908117.

Appendix C. List of primer sequences used for PCR amplification and DNA sequencing of the *rbcL* and *rps4* genes.

Primer name	Sequence (5'–3')	Target region	Reference	Note
Forward				
rbcL-53h	TCGAGTAGAC CTTATCCTTG C	*rbcL*	Inoue & Tsubota (2014)	PCR
HrL1	ATGTCACCAC AAACGGAGAC TAAAGCAGG	*rbcL*	Masuzaki *et al.* (2010)	PCR
rbcL7	TGGATTTAAA GCTGGTGTTA AAG	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL152	GAATCCTCCA CTGGTACATG	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL862	CAATGCATGC AGTTATTGAC	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL919G	CATGGTATGC ATTTCCGTGT A	*rbcL*	Tsubota *et al.* (2001)	Sequencing
rbcL921G	GGTATGCATT TCCGTGTATT AGC	*rbcL*	Tsubota *et al.* (2001)	Sequencing
trnT36R	GTAATGCGAT GGTCATCGGT TCGACTCCGA TA	*rps4*	Inoue *et al.* (2012)	PCR
rps5'	ATGTCCCGTT ATCGAGGACC T	*rps4*	Nadot *et al.* (1994)	Sequencing
rps4_1R	ATGTCCCGTT ATCGAGGACC TCGTGTA	*rps4*	Inoue *et al.* (2012)	Sequencing
rps4_19Fi	CCTCGTGTAA GAATAATACG TC	*rps4*	Inoue & Tsubota (2014)	Sequencing
Reverse				
trnR66R	GAAGGGATTC GAACCCTTG	*rbcL*	Tsubota *et al.* (1999)	PCR
trnR24R	CTCTAATCCA CTGAGCTACA	*rbcL*	Tsubota *et al.* (1999)	PCR
rbcL1346hR	GCAGCTAATT CAGGACTCC	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL1301RL	CTTCATTACG TGCTTGTACA CAAGCTTCTA	*rbcL*	Inoue *et al.* (2011)	PCR
rbcL1145R	TTAATGCTGG CATATGCCAA AC	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL1098R	AACACCTGGT AAAGAAACC	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL804hR	TGCAGTAAAA CCACCTG	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL650Rmas	CGATCTCTCC AACGCA	*rbcL*	Masuzaki *et al.* (2010)	Sequencing
rbcL600R	GTGAAATCAA GTCCACCACG	*rbcL*	Tsubota *et al.* (1999)	Sequencing
rbcL270R	GCAATATATT GATTTTCTTC TCCAG	*rbcL*	Tsubota *et al.* (1999)	Sequencing
psaA340F	CTTGAGCACT AGGTTTAATA TGAGTAGGAT CA	*rps4*	Inoue *et al.* (2012)	PCR
trnS	TACCGAGGGT TCGAATC	*rps4*	Souza-Chies *et al.* (1997)	PCR
rps4_609RL	TTAAGCTTGA CGAGAATAAT ATTC	*rps4*	Masuzaki *et al.* (2010)	PCR
rps4_602Fn	TGACGAGAAT AATATTCTAC AACTA	*rps4*	Inoue & Tsubota (2014)	Sequencing
rps3'	ATATTCTACA ACTAACAACT C	*rps4*	Nadot *et al.* (1994)	Sequencing
rps4_578Ri	CGAGAATAAT ATTCTACAAC TA	*rps4*	Inoue & Tsubota (2014)	Sequencing

Appendix D. Voucher specimens used for morphological observations in the chapter 1. The list includes the name of taxon, locality and specimen number.
Luisierella barbula: America, Florida, Wakulla, 27 April 1956, *R. A. Pursell 632* (HIRO). *Timmiella acaulon*: Argentina, Prov. Córdoba, Villa Allende, 1 May 1931, *C. C. Hosseus 396* (HIRO). *Timmiella anomala*: Japan, Honshu, Hiroshima-ken, Kure-shi, Kurahashi-jima Isl., 22 May 2013, *Y. Inoue 1910* (HIRO). *Timmiella barbuloides*: Greece, Peloponnese, Mistra, nr. Sparta, 15 April 1964, ex herb. *C. C. Townsend* (HIRO). *Timmiella crassinervis*: America, Georgia, Saturna Beach, Saturna Isl., *W. B. Schofield 14404* (HIRO). *Timmiella diminuta*: China, Peking, Hai-daian, Oct. 1953, C. *Y. Chang s.n.* (TNS 37219).

Appendix E. List of species investigated for *rbcL* and *rps4* gene sequences with the voucher information and the accession number. Bold accession numbers indicate newly obtained sequences for the chapter 2.

Ardeuma aurantiacum (Mitt.) R.H.Zander & Hedd., **LC176249**/**LC176270**, Japan, Yamaguchi Pref., *Y. Inoue 4007* (HIRO); *Ardeuma recurvirostrum* (Hedw.) R .H.Zander & H edd., **LC176251**/**LC176272**, Japan, Nagano Pref., *Y. Inoue 1323* (HIRO); *Barbula unguiculata* Hedw., AB670696/**LC176265**, Japan, Hiroshima Pref., *Y. Inoue 113* (HIRO); *Chionoloma angustata* (Mitt.) M.Menzel, LC176254/LC176276, Japan, Miyazaki Pref., *Y. Inoue 3238* (HIRO); *Chionoloma tenuirostre* (Hook. & Taylor) M.Alonso, M.J.Cano & J.A.Jiménez, **LC176252**/**LC176274**, Japan, Hiroshima Pref., *Y. Inoue 3218* (HIRO); *Didymodon constrictus* (Mitt.) K .Saito var. *flexicuspis* (P.C.Chen) K.Saito, **LC176245**/**LC176266**, Japan, Nagano Pref., *Y. Inoue 4040* (HIRO); *Ditrichum heteromallum* (Hedw.) E.Britton, **LC176243**/**LC176263**, Japan, Niigata Pref., *H. Sato 284* (HIRO); *Ephemerum crassinervium* (Schwägr.) Hampe, **LC176246**/**LC176267**, Japan, Tochigi Pref., *T. Kamiyama 8980* (HIRO); *Eucladium verticillatum* (With.) Bruch & Schimp., **LC176247**/**LC176268**, Japan, Kanagawa Pref., Y. Inoue 1803 (HIRO); *Gymnostomiella longinervis* Broth., **LC176248**/**LC176269**, Japan, Okinawa Pref., *Y. Inoue 3902* (HIRO); *Hydrogonium hiroshii* (K.Saito) Jan Kučera, **LC176250**/**LC176271**, Japan, Shizuoka Pref., *T. Suzuki 61397* (HIRO); *Hyophila propagulifera* Broth., AB853074/AB853084, Japan, Hiroshima Pref., *Y. Inoue 1745* (HIRO); *Leptophascum leptophyllum* (Müll.Hal.) J.Guerra & M .J.Cano, AB670695/**LC176273**, Japan, Ehime Pref., *Y. Inoue 57* (HIRO); *Pachyneuropsis miyagii* T.Yamag., AB853078/AB759969, Japan, Okinawa Pref., *T. Yamaguchi 34243* (HIRO); *Pottiopsis caespitosa* (Bruch ex Brid.) Blockeel & A.J.E.Sm., **LC176253**/**LC176275**, Czech Republic, S. Moravia, CBFS 14602 (duplicate in HIRO); *Scopelophila cataractae* (Mitt.) Broth., AB853075/AB853087, Japan, Kochi Pref., *Y. Inoue 318* (HIRO); *Pseudephemerum nitidum* (Hedw.) Loeske, **LC176244**/**LC176264**, Japan, Hiroshima Pref., *H. Sato 820* (HIRO); *Stegonia latifolia* (Schwägr.) Venturi ex Broth., AF231314/AF222901, Canada, Alberta, *La Farge s.n.* (ALTA); *Streblotrichum convolutum* (Hedw.) P.Beauv., **LC176255**/**LC176277**, Japan, Hiroshima Pref., *H. Tsubota 7997* (HIRO); *Streptopogon calymperes* Müll.Hal., AF478231/AF478285, Bolivia, La Paz, *Z. L. K. Magombo 5695* (MO); *Syntrichia ruralis* (Hedw.) F.Weber & D.Mohr, FJ546412/FJ546412, Canada,

Alberta (CAVA); *Tortella tortuosa* (Schrad. ex Hedw.) Limpr., AB853080/AB853089, Japan, Nagano Pref., *Y. Inoue 1297* (HIRO); *Tortula caucasica* Lindb., AB670694/AB759970, Japan, Ehime Pref., *Y. Inoue 56* (HIRO); *Trichostomum brachydontium* Bruch, **LC176256**/**LC176278**, Spain, Murcia, CBFS13652 (duplicate in HIRO); *Trichostomum crispulum* Bruch, **LC176257**/**LC176279**, Spain, Asturias, MUB 45068 (duplicate in HIRO); *Trichostomum platyphyllum* (Broth. ex Iisiba) P.C.Chen, **LC176258**/**LC176280**, Japan, Okinawa Pref., *Y. Inoue 3869* (HIRO); *Tuerckheimia svihlae* (E.B.Bartram) R.H.Zander, **LC176259**/**LC176281**, Japan, Fukuoka Pref., *T. Suzuki 61444* (HIRO); *Uleobryum naganoi* Kiguchi, I.G.Stone & Z.Iwats., AB194717/LC176282, Japan, Kagawa Pref., *H. Sato 377* (HIRO); *Weisiopsis anomala* (Broth. & Paris) Broth. & Paris, **LC176260**/**LC176283**, Japan, Tokyo Pref., *Y. Inoue 2812* (HIRO); *Weissia controversa* Hedw., **LC176261**/**LC176284**, Japan, Hiroshima Pref., *Y. Inoue 2568* (HIRO); *Weissia exserta* (Broth.) P.C.Chen, **LC176262**/**LC176285**, Japan, Hiroshima Pref., *Y. Inoue 794* (HIRO).

Appendix F. List of species investigated for *rbcL* and *rps4* gene sequences with the voucher information and the accession number. Bold accession numbers indicate newly obtained sequences for the chapter 3.

Ingroup species: *Ardeuma aurantiacum* (Mitt.) R.H.Zander & Hedd., LC176249/LC176270, Japan, Yamaguchi Pref., *Y. Inoue 4007* (HIRO); *Ardeuma recurvirostrum* (Hedw.) R.H.Zander & Hedd., LC176251/LC176272, Japan, Nagano Pref., *Y. Inoue 1323* (HIRO); *Chionoloma angustata* (Mitt.) M.Menzel, LC176254/LC176276, Japan, Miyazaki Pref., *Y. Inoue 3238* (HIRO); *Chionoloma tenuirostre* (Hook. & Taylor) M.Alonso, M.J.Cano & J.A.Jiménez, LC176252/LC176274, Japan, Hiroshima Pref., *Y. Inoue 3218* (HIRO); *Ephemerum crassinervium* (Schwägr.) Hampe, LC176246/LC176267, Japan, Tochigi Pref., *T. Kamiyama 8980* (HIRO); *Eucladium verticillatum* (With.) Bruch & Schimp., LC176247/LC176268, Japan, Kanagawa Pref., *Y. Inoue 1803* (HIRO); *Gymnostomiella longinervis* Broth., LC176248/LC176269, Japan, Okinawa Pref., *Y. Inoue 3902* (HIRO); *Hydrogonium hiroshii* (K.Saito) Jan Kučera, LC176250/LC176271, Japan, Shizuoka Pref., *T. Suzuki 61397* (HIRO); *Hyophila propagulifera* Broth., AB853074/AB853084, Japan, Hiroshima Pref., *Y. Inoue 1745* (HIRO); *Pachyneuropsis miyagii* T.Yamag., AB853078/AB759969, Japan, Okinawa Pref., *T. Yamaguchi 34243* (HIRO); *Pottiopsis caespitosa* (Bruch ex Brid.) Blockeel & A.J.E.Sm., LC176253/LC176275, Czech Republic, S Moravia, CBFS 14602 (duplicate in HIRO); *Tortella tortuosa* (Schrad. ex Hedw.) Limpr., AB853080/AB853089, Japan, Nagano Pref., *Y. Inoue 1297* (HIRO); *Trichostomum brachydontium* Bruch, LC176256/LC176278, Spain, Murcia, CBFS 13652 (duplicate in HIRO); *Trichostomum crispulum* Bruch, LC176257/LC176279, Spain, Asturias, MUB 45068 (duplicate in HIRO); *Trichostomum platyphyllum* (Broth. ex Iisiba) P.C.Chen, LC176258/LC176280, Japan, Okinawa Pref., *Y. Inoue 3869* (HIRO); *Tuerckheimia svihlae* (E.B.Bartram) R.H.Zander, LC176259/LC176281, Japan, Fukuoka Pref., *T. Suzuki 61444* (HIRO); *Uleobryum naganoi* Kiguchi, I.G.Stone & Z.Iwats., AB194717/LC176282, Japan, Kagawa Pref., *H. Sato 377* (HIRO); *Weissia condensa* (Voit) Lindb., **LC183764**/**LC183797**, Spain, Málaga, MUB 41163 (duplicate in HIRO); *Weissia controversa* Hedw. 1, **LC183769**/**LC183802**, Japan, Ehime Pref., *Y. Inoue 2580* (HIRO); **LC183766**/**LC183799**, Japan, Oita Pref., *Y. Inoue 1783* (HIRO); *Weissia controversa* Hedw. 2, **LC183767**/**LC183800**, Japan, Fukushima Pref., *Y. Inoue*

2524 (HIRO); **LC176261**/**LC176284**, Japan, Hiroshima Pref., *Y. Inoue 2568* (HIRO); LC183765/LC183798, Japan, Kagawa Pref., *H. Tsubota 7704* (HIRO); *Weissia controversa* Hedw. 3, **LC183768**/**LC183801**, Japan, Hiroshima Pref., *Y. Inoue 2564* (HIRO); *Weissia controversa* Hedw. 4, **LC183770**/**LC183803**, Spain, Burgos, MUB 34121 (duplicate in HIRO); *Weissia exserta* (Broth.) P.C.Chen, **LC183792**/**LC183825**, Japan, Hiroshima Pref., *Y. Inoue 912* (HIRO); **LC183793**/**LC183826**, Japan, Oita Pref., *Y. Inoue 1788a* (HIRO); *Weissia japonica* (G.Roth) Y.Inoue & H.Tsubota, **LC183782**/**LC183815**, Japan, Hiroshima Pref., *Y. Inoue 3830* (HIRO); **LC183785**/**LC183818**, Japan: Fukuoka Pref., *Y. Inoue 3947* (HIRO); *Weissia kiiensis* (S.Okamura) Y.Inoue & H.Tsubota 1, **LC183772**/**LC183805**, Japan, Hokkaido Pref., *Y. Inoue 1493* (HIRO), **LC183790**/**LC183823**, Japan, Niigata Pref., *T. Sato 1430* (HIRO); **LC183788**/**LC183821**, Japan, Shizuoka Pref., *Y. Inoue 3816* (HIRO); **LC183774**/**LC183807**, Japan, Aichi Pref., *Y. Inoue 1816* (HIRO); **LC183789**/**LC183822**, Japan, Hiroshima Pref., *Y. Inoue 3826* (HIRO); **LC183787**/**LC183820**, Japan, Miyazaki Pref., *Y. Inoue 3813* (HIRO); **LC183773**/**LC183806**, Japan, Otia Pref., *Y. Inoue 1788b* (HIRO); *Weissia kiiensis* (S.Okamura) Y.Inoue & H.Tsubota 2, **LC183775**/**LC183808**, Japan, Kochi Pref., *Y. Inoue 2606* (HIRO); *Weissia kiiensis* (S.Okamura) Y.Inoue & H.Tsubota 3, **LC183777**/**LC183810**, Japan, Fukushima Pref., *Y. Inoue 3169* (HIRO); *Weissia kiiensis* (S.Okamura) Y.Inoue & H.Tsubota 4, **LC183778**/**LC183811**, Japan, Tokyo Pref., *Y. Inoue 3183* (HIRO); *Weissia lonchophylla* (G.Roth) Y.Inoue & H. Tsubota, **LC183763**/**LC183796**, Brazil, São Paulo, *O. Yano & B.L. Morretes 28820* (SP 382923); *Weissia longidens* Cardot, **LC183794**/**LC183827**, Japan, Hiroshima Pref., *Y. Inoue 918* (HIRO); *Weissia newcomeri* (E.B.Bartram) K.Saito, **LC183795**/**LC183828**, Japan, Hiroshima Pref., *Y. Inoue 2781* (HIRO); *Weissia parajaponica* Y.Inoue & H.Tsubota 1, **LC183781**/**LC183814**, Japan, Ryukyu, Miyakojima Isl., *Y. Inoue 3910* (HIRO); **LC183780**/**LC183813**, Japan, Ryukyu, Ishigakijima Isl., *Y. Inoue 3864* (HIRO); *Weissia parajaponica* Y.Inoue & H.Tsubota 2, **LC183776**/**LC183809**, Japan, Kagoshima Pref., Yakushima Isl., *Y. Inoue 3143* (HIRO); **LC183779**/**LC183812**, Japan, Ryukyu, Iriomotejima Isl., *Y. Inoue 3849* (HIRO); *Weissia parajaponica* Y.Inoue & H.Tsubota 3, **LC183791**/**LC183824**, Japan, Ryukyu, Amamioshima Isl., *Y. Inoue 3951* (HIRO); **LC183783**/**LC183816**, Japan: Ryukyu, Okinawa Isl., *Y. Inoue 3912* (HIRO); **LC183784**/**LC183817**, Japan, Ryukyu, Minamidaitojima Isl., *Y. Inoue 3925* (HIRO);

Weissia parajaponica Y.Inoue & H.Tsubota 4, **LC183771**/**LC183804**, Japan, Ogasawara, Mukojima Isl., *S. Uchida 10069* (HIRO); *Weissia parajaponica* Y.Inoue & H.Tsubota 5, **LC183786**/**LC183819**, Japan, Ogasawara, Hahajima Isl., *S. Uchida 10685* (HIRO).
Outgroup species: *Barbula unguiculata* Hedw., AB670696/LC176265, Japan, Hiroshima Pref., *Y. Inoue 113* (HIRO); *Didymodon constrictus* (Mitt.) K.Saito var. *flexicuspis* (P.C.Chen) K.Saito, LC176245/LC176266, Japan, Nagano Pref., *Y. Inoue 4040* (HIRO).

Appendix G. Exotic specimens examined for comparison in the chapter 3.

Weissia longifolia* Mitt. var. *longifolia

ENGLAND. Goldstone Barn, near Brighton, 1836, *Borrer s.n.* (holotype, NY 1408141)

***Weissia longifolia* Mitt. var. *angustifolia* (Baumgartner) Crundw. & Nyholm**

YUGOSLAVIA. Insel San Andrea wesil. von Lissa, 6–9 June 1911, *A. Ginzberger s.n.* (holotype of *Astomum crispum* (Hedw.) Hampe var. *angustifolium* Baumgartner, W-KRYPT 1964-21668)

***Weissia levieri* (Limpr.) Kindb.**

SPAIN. Albacete: Sierra del Relumbrar, 23 March 2000, *Ros & Jiménez s.n.* (MUB 10259, duplicate in HIRO)

***Weissia muhlenbergiana* (Sw.) W.D.Reese & B.A.E.Lemmon**

Morphological group 1 (Capsules without annulus):—USA. Indiana: Dearbon, Tanner's Creek near outlet with Ohio River just below Lawrenceburg, 21 April 1984, *B.H. Allen 3924* (HIRO); Dearborn, 19 March 1983, *B.H. Allen 3038* (HIRO); Texas: North side of Ft. Worth–Oakhurst Div., 18 December 1967, *D. Griffin, III s.n.* (NICH 299840); Maryland: Prince Georges Country, Hillenest Heights, Marlbororgh House, 31 January 1968, *F.S. Hermann 22294* (HIRO); Beltsville, USDA Plant Industry Station, 1 mile S., 13 April 1958, *F.J. Hermann 14210* (NICH 202584); Tennessee: Nashville, 3 May 1958, *R.F. Cain s.n.* (NICH 202585); Garden, near Lake City, ca. 335 m elev., 13 January 1957, *Z. Iwatsuki s.n.* (NICH 202588); Texas: Pasture and alluvial soil in vicinity of junction Piney River & US 63 ca. 1 mile north of Cabool, 16 April 1960. *P.L. Redfearn, Jr. 5478* (HIRO).

Morphological group 2 (Capsules with annulus):—USA. Kansas: 12.8 km E of Wilmore, 1 June 1978, *S.P. Churchill 9980* (HIRO); Louisiana: bluffs along the Ouachita River, 4 3/4 mi. se of Columbia, 13 May 1966, *W.D. Reese 9229* (NICH 290052); vic. of Pont Brule, 4 mi. due sw of Arnaudville, 18 March 1965, *W.D. Reese 1919* (NICH 242842).

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