

GÖTTINGER ZENTRUM
FÜR BIODIVERSITÄTSFORSCHUNG UND ÖKOLOGIE
– GÖTTINGEN CENTRE FOR BIODIVERSITY AND ECOLOGY –

**Taxonomy and Phylogeny of the Liverwort Genus *Thysananthus*
(Marchantiophyta: Lejeuneaceae)**

Dissertation zur Erlangung des Doktorgrades der
Mathematisch-Naturwissenschaftlichen Fakultäten der
Georg-August-Universität Göttingen

vorgelegt von

M.Sc. Botany

Phiangphak Sukkharak

aus

Nan, Thailand

Göttingen, June, 2011

Referentin/Referent:

Prof. Dr. S. Robbert Gradstein

Korreferentin/Korreferent:

PD Dr. Michael Stech

Tag der mündlichen Prüfung:

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ACKNOWLEDGEMENTS

I would like to thank my supervisor, Prof. Dr. S. Robbert Gradstein for giving me the opportunity to study at the department of Systematic Botany. The present study was initiated since July 2007 when I met him at the “World Conference of Bryology” in Kuala Lumpur, Malaysia and was invited to Göttingen for a PhD study under his guidance. I express my gratitude to him for his supervision, suggestions and many helpful discussions throughout the duration of my thesis. I am very grateful to PD Dr. Michael Stech as supervisor for my molecular work and being my co-referee. I would like to thank Dr. Agnieszka Ludwiczuk for being the co-author for my phytochemical paper and her hospitality upon my visit to her department. My study was supported by a Royal Thai government scholarship in cooperation with the German Academic Exchange Service (DAAD). Financial support from the Universitätsbund Göttingen for attending the conferences in Leiden, the Netherlands (2009), Singapore (2010) and Berlin, Germany (2011); the Royal Thai government scholarship for attending the conference in Melbourne, Australia (2011); the European Distributed Institute of Taxonomy (EDIT) grant for attending the Phylogenetic Systematics and Molecular Dating course in Copenhagen, Denmark (2011); and the SYNTHESYS Project for visiting Muséum National d'Histoire Naturelle in Paris, France (2011) are gratefully acknowledged. I express my gratitude to the directors and curators of the following herbaria for making the specimens available: Chulalongkorn University (BCU), National Park, Wildlife and Plant Conservation Department (BKF), The Natural History Museum (BM), National Botanic Garden of Belgium (BR), Herbarium Bogoriense (BZ), University of Copenhagen (C), Harvard University (FH), Conservatoire et Jardin botaniques de la Ville de Genève (G), Universität Göttingen (GOET), University of Helsinki (H), Hiroshima University (HIRO), Friedrich-Schiller-Universität Jena (JE), Nationaal Herbarium Nederland, Leiden University branch (L), Papua New Guinea Forest Research Institute (LAE), Hattori Botanical Laboratory (NICH), Royal Botanic Gardens (NSW), New York Botanical Garden (NY), Muséum National d'Histoire Naturelle (PC), Prince of Songkla University (PSU), Swedish Museum of Natural History (S), Singapore Botanic Gardens (SING), Institut de Botanique (STR), Nationaal Herbarium Nederland, Herbarium Utrecht (U) and Naturhistorisches Museum Wien (W). I am particularly indebted to Dr. Michel Hoff (Strasbourg, STR), Dr. Michelle J. Price (Geneva, G), Prof. Dr. Thaweesakdi Boonkerd (Bangkok, BCU), Dr. Rachun Pooma (Bangkok, BKF), Serena Lee (Singapore, SING), Dr. Herman Stieperaere (Meise, BR), Dr. Ruth Nielsen

(Copenhagen, C), Bruno Denetière (Paris, PC), and Len Ellis (London, BM) for their hospitality and generous assistance upon my visits to their institutions for the study of *Thysananthus*. Thanks are also due to M.C.M. Eurlings and the staff of DNAMarkerpoint (Leiden University) for technical assistance in molecular laboratory. I would like to thank Dr. Jochen Heinrichs, Dr. María Elena Reiner-Drehwald, Dr. Simone Klatt and all other staff at the department of Systematic Botany. Thanks also to Christine Gehrig-Downie for fresh liverwort material. I am also very grateful to Dr. Sahut Chantanaorrapint for fresh materials and field work. Special thanks go to Marc Appelhans for his helpful discussions and friendship over the years. Many thanks to Bernd Raufeisen, Dr. Boon-Chuan Ho, Ida Haerida, Jian Wang, Prof. Dr. Jan-Peter Frahm, Dr. Matt Renner, Prof. Dr. Rui-Liang Zhu, Soonthree Kornochalert and Thomas Hallingbäck. A big thank you to Thai students in Göttingen, especially Jakkrawadee Anuyotha and Sirinya Somching. My deepest thanks are to my family for their encouragement and support.

ABSTRACT

A systematic study of the liverwort genus *Thysananthus*, especially the subgenus *Thysananthus*, based on the results of morphological-anatomical, phytochemical and molecular phylogenetic analyses, leads to the recognition of 29 species in the genus: 15 species in subg. *Thysananthus* in two sections, sect. *Thysananthus* (eleven species) and sect. *Dendrolejeunea* (Spruce) Sukkharak (four species) and 14 species in subg. *Mastigolejeunea* (Spruce) Sukkharak. Based on the morphological-anatomical study two new species, *T. discretus* Sukkharak & Gradst. and *T. combinatus* Sukkharak, and one new variety are newly described and several new or little known morphological characters are recognized. The chemical heterogeneity of *T. convolutus*, which is congruent with variation in the dentation of leaves, underleaves and female bracts in this species, supports resurrection of *T. gottschei*, considered a synonym of *T. convolutus*, as a separate taxon. The results of a molecular phylogenetic analysis confirm the placement of *Mastigolejeunea pancheri* in *Thysananthus* and provide evidence for a broader circumscription of the genus *Thysananthus*, including the genera *Dendrolejeunea* and *Mastigolejeunea*. The molecular evidence also supports the status of *T. gottschei* and *M. humilis* (= *T. humilis*) as separate species and reveals the existence of a putative hybrid, the first one detected in Lejeuneaceae. A monographic treatment of subg. *Thysananthus* provides a synthesis of the morphological and chemical variation in the subgenus, and the new classification of the broadly defined genus *Thysananthus*. Some new taxa are described and numerous new combinations are proposed. An artificial key to the species of the genus *Thysananthus* is provided and each species of subg. *Thysananthus* is fully described and illustrated, with extensive synonymy and detailed data on habitat and distribution. An annotated list of the fourteen species in subg. *Mastigolejeunea* is also provided. The subg. *Thysananthus* is mainly characterized by *Lejeunea*-type vegetative branches, stem epidermal cells large as medullary cells or dorsal epidermal cells enlarged, leaves convolute when dry, leaf cells elongate and trigones cordate, adnate underleaves present, gynoeceal innovations present and with lejeuneoid leaf sequence, female involucre toothed, and perianth sharply 3-keeled and toothed. The subg. *Thysananthus* is pantropical in distribution, with four species ranging into warm temperate regions; the centre of diversity is in Southeast Asia. The species grow as epiphytes in tropical lowland and montane rain forests and cloud forests.

ZUSAMMENFASSUNG

Als Ergebnis einer systematischen Bearbeitung der Lebermoosgattung *Thysananthus*, insbesondere der Untergattung *Thysananthus*, auf der Basis morphologisch-anatomischer, phytochemischer und molekularphylogenetischer Analysen, werden 29 Arten anerkannt: 15 Arten in der Untergattung *Thysananthus* in zwei Sektionen, sect. *Thysananthus* (11 Arten) und sect. *Dendrolejeunea* (Spruce) Sukkharak (vier Arten), und 14 Arten in der Untergattung *Mastigolejeunea* (Spruce) Sukkharak. Die morphologisch-anatomischen Untersuchungen führen zur Neubeschreibung zweier Arten, *T. discretus* Sukkharak & Gradst. und *T. combinatus* Sukkharak, sowie einer neuen Varietät, und zur Beschreibung mehrerer neuer oder bislang wenig bekannter morphologischer Merkmale. Die chemische Heterogenität von *T. convolutus*, die mit Unterschieden in der Zähnung von Blättchen und Unterblättchen übereinstimmt, unterstützt die Wiederanerkennung der Art *T. gottschei*, welche bislang als synonym mit *T. convolutus* angesehen wurde. Die Ergebnisse der molekularphylogenetischen Analysen bestätigen die Stellung von *Mastigolejeunea pancheri* in *Thysananthus* und bieten Anhaltspunkte für eine breitere Umschreibung der Gattung *Thysananthus*, inklusive der Gattungen *Dendrolejeunea* und *Mastigolejeunea*. Die molekularen Daten unterstützen den Status von *T. gottschei* und *M. humilis* (= *T. humilis*) als eigene Arten und weisen auf die Existenz einer möglichen Hybride hin, der ersten die bislang in den Lejeuneaceae gefunden wurde. Die monographische Bearbeitung der Untergattung *Thysananthus* beinhaltet eine Synthese der morphologischen und chemischen Variabilität in der Untergattung, eine neue taxonomische Einteilung der weit gefassten Gattung *Thysananthus* mit einigen neuen Taxa und zahlreichen neuen Kombinationen, sowie einen Bestimmungsschlüssel der Arten der Gattung *Thysananthus*. Alle Arten der Untergattung *Thysananthus* werden ausführlich beschrieben und illustriert, mit detaillierten Angaben zu Synonymen, Habitaten und Verbreitung. Die 14 Arten der Untergattung *Mastigolejeunea* werden in einer kommentierten Auflistung behandelt. Die Untergattung *Thysananthus* kann im Wesentlichen durch die Kombination der folgenden Merkmale charakterisiert werden: Verzweigung der vegetativen Äste vom *Lejeunea*-Typ, Epidermiszellen der Stämmchen ebenso groß wie die Markzellen oder auf der Dorsalseite vergrößert, Blättchen im trockenen Zustand zusammengerollt, Blattzellen verlängert und mit herzförmigen Eckenverdickungen, verwachsene Unterblättchen vorhanden, gynöziale Erneuerungstriebe vorhanden und mit lejeuneoider Blattfolge, weibliches Involukrum gezähnt sowie Perianth mit drei scharfen Kielen und gezähnt. Die Untergattung *Thysananthus* ist pantropisch verbreitet mit Südostasien als Diversitätszentrum,

vier Arten strahlen in warm-gemäßigte Gebiete aus. Die Arten wachsen als Epiphyten in tropischen Tieflands- und Bergregenwäldern sowie Nebelwäldern.

I. SYNOPSIS

This dissertation is the systematic study of the liverwort genus *Thysananthus*, with a focus on a world-wide revision of subgenus *Thysananthus*, based on morphological-anatomical study of the types and other available herbarium materials, as well as using phytochemical and molecular evidence. Each chapter represents a published, accepted or submitted paper in an international peer-reviewed SCI journals or serial, except for Chapter I which is the introduction to Lejeuneaceae, the introduction to *Thysananthus* and the current state of knowledge of the genus. The general discussion (IB) summarizes results from the chapters II-VI and indicates necessary future work.

IA. INTRODUCTION

INTRODUCTION TO LEJEUNEACEAE

Lejeuneaceae, nested within the liverwort order Porellales, are sister to the families Jubulaceae and Frullaniaceae (Ahonen 2004, Heinrichs *et al.* 2005, He-Nygrén *et al.* 2006) and are the largest family of liverworts comprising ca. 1200 species in 78 genera (Frey & Stech 2009, with updates). They grow mostly as epiphytes in moist tropical forests. In rain forests more than three-fourths of the hepatic species are Lejeuneaceae (Gradstein 1994, 2006) and in montane forests 15-30% (Gradstein 1994). According to molecular dating (Wilson *et al.* 2007b, but see Yang & Wu 2010), diversification started in the Mid-Cretaceous and took place in the shadow of angiosperm evolution, as has also been shown for other lineages of extant cryptogamic plants such as Lycopodiaceae (Wikström *et al.* 2001) and ferns (Schneider *et al.* 2004). Morphological characteristics of Lejeuneaceae are incubous leaves with a small ventral lobule attached along a keel, the existence of underleaves and/or rhizoid tufts and the presence of one archegonium per perianth. Several conflicting classifications have been proposed for the family due to the high degree of morphological homoplasy and the lack of stable morphological diagnostic characters to delimit generic and infrageneric groups (Gradstein *et al.* 2003, Wilson *et al.* 2007a). Traditionally, on the basis of gametophyte characters, Lejeuneaceae was divided into two artificial groups: “Holostipae” and “Schizostipae”, based on underleaf morphology (undivided resp. bifid) and stem anatomy (robust and 10 or more rows of cortical cells resp. thinner and has only 7 rows of cortical cells) (Spruce 1884, Evans 1935, Schuster 1955).

Mizutani (1961) studied Japanese Lejeuneaceae and found that several sporophytic characters including the structure of the seta, the capsule-wall thickenings, and the elaters could be used to separate Holostipae and Schizostipae. He subsequently treated these two

groups as two subfamilies: Ptychanthoideae Mizut. (= Holostipae) and Lejeuneoideae Massal. (fide Gradstein 1975) (= Schizostipae). Later, several smaller subfamilies and tribes were established by Schuster (1963) and Gradstein (1975, 1994). Recent morphological and molecular phylogenetic analyses (Ahonen *et al.* 2003, Gradstein *et al.* 2003, Groth-Malonek *et al.* 2004, Wilson *et al.* 2004, 2007a, Heinrichs *et al.* 2005) supported the division of Lejeuneaceae into two broad subfamilies Ptychanthoideae and Lejeuneoideae. In addition, Wilson *et al.* (2007a) found molecular evidence for two further, smaller lineages in the family.

INTRODUCTION TO *THYSANANTHUS*

Thysananthus Lindenb. is a member of the family Lejeuneaceae subfamily Ptychanthoideae (Mizutani 1961, Gradstein 1975, 1994) and was first described by Lindenberg in 1844 for species with a 3-keeled, toothed perianth containing only one archegonium and being subtended by innovation. Spruce (1884) published the subgenus *Thysano-Lejeunea*, which was more or less equivalent to *Thysananthus*, as one of his 37 subgenera of a broadly defined genus *Lejeunea* Lib. (which was almost equivalent to the present family Lejeuneaceae). The subgenus *Thysano-Lejeunea* was classified in the “Holostipae” due to its undivided underleaves. *Thysananthus* had been restored at generic rank again by Schiffner (1893).

The genus *Thysananthus* as traditionally circumscribed contains about ten species and occurs mainly in tropical Asia (Gradstein 1994). One species, *T. spathulistipus* (Reinw. *et al.*) Lindenb., extends from tropical Asia to tropical Africa and *T. amazonicus* (Spruce) Schiffn. is the only species of the genus occurring in the New World tropics. The species grow as epiphytes in moist tropical forests, from sea level to the tree line.

Spruce and Schiffner, and all later authors, agreed that *Thysananthus* is morphologically very similar to the genus *Mastigolejeunea* (Spruce) Schiffn. (14 species) and some authors have even suggested that the two genera might be combined in one genus (Schuster 1980, Gradstein 1985). The two genera differ mainly by the entire perianth and enlarged dorsal epidermis cells. However, these differences are not sharp, as is discussed in Chapters V and VI.

Thysananthus is morphologically heterogeneous (Gradstein 1992) and the taxonomic significance of several characters considered diagnostic of the genus is unclear. As a result, different generic circumscriptions and intrageneric classifications have been evoked. For example, Verdoorn (1934) classified the Asiatic species of *Thysananthus* into three sections on the basis of leaf characters: (1) *T. sect. Spathulistipae* Verd. with six species characterized

by symmetric and rather plane leaves without vitta; (2) *T. sect. Convolutae* Verd. with two species characterized by asymmetric and deeply concave leaves without vitta; and (3) *T. sect. Vittatae* Verd. with three species characterized by symmetric, vittate leaves. Thiers and Gradstein (1989) classified the species from Australia into two subgenera: subg. *Thysananthus* and subg. *Sandeanthus* B. Thiers & Gradst., based on differences in leaf position and areolation. Gradstein (1992) placed the neotropical *T. evansii* Fulford and *T. pterobryoides* (Spruce) Schiffn. in the new genus *Fulfordianthus* Gradst., based on the dendroid habit, the isodiametric leaf cells with evenly thickened walls, lacking any trace of trigones, the lack of oil bodies, etc. Moreover, the genus *Dendrolejeunea* (Spruce) Lacout. was reinstated for the Asiatic *T. fruticosus* (Lindenb. & Gottsche) Schiffn., also based on the dendroid habit. The remaining species of *Thysananthus* were attributed to the two subgenera recognized by Thiers and Gradstein (1989).

In the papers of Chapters II-V the genus *Thysananthus* is circumscribed in the **traditional narrow sense**, maintaining *Dendrolejeunea* and *Mastigolejeunea* as separate genera. In Chapter VI, however, *Dendrolejeunea* and *Mastigolejeunea* are united with *Thysananthus* based on the results of molecular analysis. As a consequence, *Thysananthus* is treated in a **much wider sense** in the final chapter of this study.

MORPHOLOGICAL AND ANATOMICAL STUDY

Thysananthus was first described based essentially on the sharply 3-keeled, dentate-laciniate perianth (Lindenberg 1844). Further differential characters have been added by later authors, viz. toothed leaves (Spruce 1884), elongate leaf cells (Stephani 1912), possession of purely existence of *Lejeunea*-type branches, leaves convolute when dry, epidermal cells as large as medullary cells and trigones cordate, often become coalesced, (Gradstein 1975), and lejeuneoid leaf sequence of innovations (Thiers & Gradstein 1989).

Mizutani (1969, 1977), Kitagawa (1973) and Mizutani and Piippo (1986) have paid attention to the occurrence of connate leaves and underleaves in *Thysananthus*, but the taxonomic relevance of this feature has remained controversial. The study of more than 1600 herbarium materials from various museums and herbaria worldwide as well as fresh specimens of *Thysananthus* resulted in a better understanding of the morphological and anatomical characters in the genus, especially the connate leaves and underleaves and appendages on the keel of leaves, bracts and perianths. In addition, not only the appendage which is attached to the lobule bases and the stem epidermis cells on both sides of the stem was newly observed but also *T. discretus* Sukkharak & Gradst., was newly described based on

hitherto neglected morphological characters of the underleaves. *Thysananthus discretus* is described and illustrated in Chapter II and Chapter III deals with some new or little known morphological characters.

CHEMICAL STUDY

Liverworts are able to synthesize large quantities of terpenoids, especially sesquiterpenoids, diterpenoids, and lipophilic aromatic compounds, which are stored in oil bodies (e.g., Gradstein *et al.* 1985). These substances, especially terpenoids, often show strong biological activity and may play an important role in the defence of the plants against environmental hazards (Gradstein 1994) or predators (Harinantenaina *et al.* 2006). Several studies have been conducted on the terpenoids and aromatic compounds of the members of Ptychanthoideae (e.g., Asakawa 1982, 1995, 2004, Asakawa *et al.* 1980a, 1980b, Gradstein *et al.* 1981, 1985, 1988, Kruijt *et al.* 1986, Harinantenaina *et al.* 2006).

Seven species of *Thysananthus*: *T. amazonicus*, *T. appendiculatus* Steph., *T. convolutus* Lindenb., *T. discretus* (under *T. convolutus* sample nr. 49 in Gradstein *et al.* 1985), *T. mollis* Steph., *T. retusus* (Reinw. *et al.*) B. Thiers & Gradst. (under *T. fruticosus* in Gradstein *et al.* 1985) and *T. spathulistipus*, have been investigated for the occurrence of terpenoids, flavonoids, sterols, and aromatic compounds. The results showed that most species elaborate large amounts of sesquiterpenoids and unidentified diterpenoids. At least six different flavonoids are detected in *T. appendiculatus*. Stigmasterol is reported from all these species. No trace of aromatic compounds can be detected in studied species except in *T. appendiculatus* (Gradstein *et al.* 1985, Kruijt *et al.* 1986, Harinantenaina *et al.* 2006).

Fresh material of four species of *Thysananthus*: *T. comosus* Lindenb., *T. convolutus*, *T. retusus*, *T. spathulistipus*, and *Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout. from Thailand and Malaysia, enabled chemical study. Chapter IV deals with the terpenoid chemistry of these materials.

PHYLOGENETIC STUDY

Gradstein (1994), in his revision of neotropical Ptychantheae and Brachiolejeuneae, included a cladistic analysis of these two tribes of Lejeuneaceae using 26 morphological characters. Later, a comprehensive phylogenetic investigation of generic relationships within the Lejeuneaceae using 67 morphological characters and one chemical character in 69 genera was published by Weis (2001). She recognized three subfamilies: Nipponolejeuneoideae (genus *Nipponolejeunea* only; basal clade), Ptychanthoideae and Lejeuneoideae. The first

molecular phylogenetic analysis of 12 genera of Lejeuneaceae using three markers (plastid *rbcL*, *trnL-F*, nrITS2) was conducted by Ahonen *et al.* (2003). In addition, Gradstein *et al.* (2003) published a morphological phylogenetic analysis and classification of 69 genera of Lejeuneaceae. The division of Lejeuneaceae into the subfamilies Ptychanthoideae and Lejeuneoideae was supported by their analyses as well as later authors (Groth-Malonek *et al.* 2004, Wilson *et al.* 2004, 2007a, Heinrichs *et al.* 2005).

Morphological phylogenetic analysis of the Ptychanthoideae (Gradstein 1994, Gradstein *et al.* 2003) recovered *Thysananthus* as a member of the Ptychanthinae clade together with *Bryopteris* (Nees) Lindenb., *Mastigolejeunea*, *Ptychanthus* Nees and *Schiffneriolejeunea* Verd. However, *Dendrolejeunea* was not included in the analysis because sporophytes were unknown. Wilson *et al.* (2007a) in a molecular phylogenetic analysis of the family based on four markers (plastid *rbcL*, *psbA*, *trnL-F*, nrITS) recovered *Thysananthus* (4 species sampled) in a robust clade together with *Dendrolejeunea* and *Mastigolejeunea*, being sister to a clade containing *Ptychanthus* and *Spruceanthus* Verd. *Bryopteris* and *Schiffneriolejeunea* appeared to be more distantly related to *Thysananthus*. All studies revealed *Thysananthus* as monophyletic.

Phylogenetic inference of Lejeuneaceae is often hampered by meagre taxon and/or marker sampling (Wilson *et al.* 2007a). In Chapter V, however, samples of all currently recognized species of *Thysananthus*, covering almost the entire range of morphological variation within the genus, and from a representative species set of related genera, have been used to generate DNA sequence information. The molecular data from five markers (plastid *psbA-trnH*, *trnG*, *trnL-F*, *trnS-rps4*, nrITS), morphological characters of all molecularly analyzed specimens as well as phytochemical (terpenoid) data from selected *Thysananthus* species and *Dendrolejeunea fruticosa* were analyzed comparatively in a phylogenetic framework for the first time in Lejeuneaceae.

MONOGRAPH OF *THYSANANTHUS* SUBGENUS *THYSANANTHUS*

The taxonomic revision of Asiatic *Thysananthus* by Verdoorn (1934) marks the beginning of modern research in the genus. Several regional revisions of *Thysananthus* have been undertaken later (e.g., Fulford 1941, Vanden Berghen 1950, Thiers & Gradstein 1989, Gradstein 1992, 1994). However, Gradstein (1985) and Thiers and Gradstein (1989) noted that *Thysananthus* is in need of revision on a world-wide basis. Based on the molecular results in Chapter V, *Dendrolejeunea* is returned to *Thysananthus* in Chapter VI and *Mastigolejeunea* (fourteen spp.) is combined with *Thysananthus*, as *T.* subg. *Mastigolejeunea* (Spruce)

Sukkharak. In Chapter VI, a world-wide revision of subg. *Thysananthus* leads to the recognition of fifteen species in this subgenus, in two sections: sect. *Thysananthus* (eleven species) and sect. *Dendrolejeunea* (Spruce) Sukkharak (four species). The two sections are characterized by the absence resp. presence of a vitta in the leaves. One species, *T. combinatus* Sukkharak and one variety are newly described, and numerous new combinations are proposed. An artificial key to the species of the genus *Thysananthus* is provided and each species of subg. *Thysananthus* is fully described and illustrated, with extensive synonymy and detailed data on habitat and distribution. An annotated list of the species in subg. *Mastigolejeunea* is also provided.

IB. GENERAL DISCUSSION

A study of a large series of specimens of all species of subg. *Thysananthus* leads to the recognition of new species, *Thysananthus discretus*, in Chapter II and a better understanding of new or little known morphological characters in Chapter III. *Thysananthus discretus* is described from Western Melanesia (New Guinea, Solomon Islands). The new species stands out within *Thysananthus* on account of the leaves when moist clasping the stem, free underleaf bases with the well-developed auricles, and the strongly rigid stems with 14-18 cells wide ventral merophytes. Free underleaf bases, which are not connate with the leaves, is an unusual character in *Thysananthus* and occur otherwise in the New Guinean endemics *T. mollis* and *T. montanus* Gradst. *et al.*, and occasionally in the widespread *T. retusus*. Whereas, the presence of adnate underleaves that are connected to leaf bases appears to be a stable and taxonomically relevant feature of *T. aculeatus* Herzog, *T. amazonicus*, *T. appendiculatus*, *T. comosus*, *T. convolutus*, *T. laceratus* Steph. (= *T. convolutus* var. *laceratus* (Steph.) Sukkharak) and *T. spathulistipus*. Interestingly, the adnation of underleaves on branches occurs in a distinct left-right symmetry pattern, on right-hand branches being connected to leaves on the left side and on left-hand branches on the right-hand side. The further morphological feature, relative to leaf bases, is a small “appendage” that may be developed on leaves, female bracts and perianths. In *T. appendiculatus*, *T. discretus* and *T. laceratus* the appendages are found on the keel of leaves and inserted partially on the stems. In all *Thysananthus* species wing-like appendages may be occur on the keels of the female bracts, on one or both sides of the stem. In addition, a small appendage may be found on the mid-basal portion of the bract lobules and on the base of the keels of the perianth. Moreover, an appendage which is attached to the lobule bases and the stem epidermis cells on both sides of the stem was newly observed in *T. mollis*, *T. montanus* and *T. retusus*.

Noteworthy of the results of chemical analysis dealing with the terpenoid in Chapter IV is the chemical heterogeneity of *Thysananthus convolutus*, which is congruent with variation of the dentation of leaves, underleaves and female bracts in this species. The edentate form has been called *T. gottschei* (Jack & Steph.) Steph., which was reduced to a synonym of *T. convolutus* (Grolle & Piippo, 1984). The results in Chapter IV suggest that *T. gottschei* may have to be resurrected as a separate taxon. In addition, chemical composition of *Dendrolejeunea fruticosa* detected in this study is very different from *Thysananthus* species. In other instances, however, the chemical findings do not coincide with morphology. For instance, unidentified compound (M^+)302, 190(100), 81(95) was detected in *T. convolutus* and in one sample of *T. comosus*, and the unidentified (M^+)320, 207(100), 81(83) in *T. spathulistipus* sample 2 and Malaysian *T. convolutus* but not in other samples of these species. Furthermore, pinguisane sesquiterpenoids were only found in the morphologically very different species *T. retusus* and *T. spathulistipus*.

Phylogenetic analyses in Chapter V have provided us a better understanding into the systematic relationships and diversification pattern within *Thysananthus*. The species of *Thysananthus* are resolved into two major clades, which also include *Dendrolejeunea fruticosa* and *Mastigolejeunea pancheri* Steph. The clade of *D. fruticosa*, *T. mollis*, *T. montanus* and *T. retusus* stands out by the presence of vitta and corresponds to a section recognized in early classifications. The well-supported sister relationship between the *T. anguiformis* (Hook. f. & Taylor) Steph.-*M. pancheri* and *Thysananthus* s. str. clades is noteworthy as *M. pancheri* has long been separated from *Thysananthus* by its entire female involucre and presence of a stem hyalodermis. Within *Thysananthus* s. str., *T. comosus*, *T. convolutus* and *T. spathulistipus* were polyphyletic, but the molecular clades largely fit with formerly recognized but later synonymised species, *T. gottschei*, and in one case with a novel species that is also recognizable morphologically. Incongruence between plastid and ITS data in *M. pancheri* indicated the occurrence of a putative hybrid, the first one recorded in Lejeuneaceae and the first in liverworts inferred from phylogenetic data. Interestingly, the molecular evidence of Wilson *et al.* (2007a) and the present study suggests that the Asiatic and neotropical populations of *M. auriculata* (Wils.) Schiffn. represent different taxa. The plants from Asia and Neotropics are also morphologically different. The Asian populations of *M. auriculata* were originally described as *M. humilis* (Gottsche) Schiffn.; later taxonomic work (e.g., Gradstein & Inoue 1980, Gradstein 1994) suggested that *M. humilis* cannot be sharply separated morphologically from *M. auriculata*, described from the Neotropics. The

molecular results in Chapter V, however, clearly support the recognition of the Asiatic *M. humilis* as a separate species.

Based on the results of morphological-anatomical, phytochemical and molecular phylogenetic analyses, the genus *Thysananthus* is divided in Chapter VI into 2 subgenera: subg. *Thysananthus* (15 spp., 4 varieties, 2 subspecies) and subg. *Mastigolejeunea* (14 spp.). The classification of *Thysananthus* in Chapter VI is as follows:

Thysananthus subg. *Thysananthus*

sect. *Thysananthus*

ser. *Thysananthus*

1. *T. aculeatus* Herzog
2. *T. amazonicus* (Spruce) Schiffn.
3. *T. appendiculatus* Steph.
4. *T. combinatus* Sukkharak
5. *T. comosus* Lindenb.
6. *T. convolutus* Lindenb.
 var. *convolutus*
 var. *laceratus* (Steph.) Sukkharak
7. *T. discretus* Sukkharak & Gradst.
8. *T. gottschei* (Jack & Steph.) Steph.
 var. *gottschei*
 var. *continuus* Sukkharak
9. *T. spathulistipus* (Reinw. *et al.*) Lindenb.

ser. *Anguiformes* Sukkharak

10. *T. anguiformis* (Hook. f. & Taylor) Steph.
11. *T. pancheri* (Steph.) Hürl.

sect. *Dendrolejeunea* (Spruce) Sukkharak

ser. *Dendrolejeunea*

12. *T. fruticosus* (Lindenb. & Gottsche) Schiffn.

ser. *Sandeanthus* (B. Thiers & Gradst.) Sukkharak

13. *T. mollis* Steph.
14. *T. montanus* Gradst. *et al.*
15. *T. retusus* (Reinw. *et al.*) B. Thiers & Gradst.
 subsp. *retusus*

subsp. *sellingii* (Hürl.) Sukkharak

Thysananthus subg. *Mastigolejeunea* (Spruce) Sukkharak

16. *T. auriculatus* (Wils.) Sukkharak
17. *T. calcaratus* (Steph.) Sukkharak
18. *T. floreus* (Mitt.) Sukkharak
19. *T. humilis* (Gottsche) Sukkharak
20. *T. integrifolius* Steph.
21. *T. innovans* (Spruce) Sukkharak
22. *T. ligulatus* (Lehm. & Lindenb.) Sukkharak
23. *T. plicatiflorus* (Spruce) Sukkharak
24. *T. reconditus* (Steph.) Sukkharak
25. *T. recurvifolius* (Mizut.) Sukkharak
26. *T. repletus* (Taylor) Sukkharak
27. *T. truncatus* (Mizut.) Sukkharak
28. *T. undulatus* (Gradst. & Grolle) Sukkharak
29. *T. virens* Ångstr.

In its current circumscription, subg. *Thysananthus* is mainly characterized by (1) *Lejeunea*-type vegetative branches, (2) stem epidermal cells large as medullary cells (dorsal epidermal cells enlarged in *T. combinatus*, *T. anguiformis*, *T. pancheri*), (3) leaves convolute when dry (spread out widely in *T. retusus*), (4) Leaf cells elongate and trigones cordate (isodiametric and trigones faint in *T. retusus*), (5) adnate underleaves present (absent in *T. discretus*, *T. fruticosus*, *T. mollis*, *T. montanus*), (6) gynoecial innovations present and with lejeuneoid leaf sequence, (7) female involucre toothed (entire in *T. anguiformis*, *T. pancheri*), and (8) perianth sharply 3-keeled and toothed (entire in *T. montanus*).

FUTURE PROSPECTS

The chemotaxonomic conclusions presented in Chapter IV are still preliminary. The results obtained in the study will be substantiated by isolation and identification of the detected unidentified compounds, which is in progress (Ludwiczuk, in prep.).

Molecular phylogenetic results presented in Chapter V revealed that *Thysananthus comosus*, *T. convolutus* (as traditionally circumscribed) and *T. spathulistipus* are polyphyletic. Increased taxon sampling is needed to clarify the relationships of these taxa. Incongruence between plastid and ITS data in one sample of *M. pancheri* led to the first report of a putative

hybrid in Lejeuneaceae, and the first one in liverworts inferred from phylogenetic data. However, inference from a more detailed dated phylogeny of Ptychanthoideae may confirm the putative young age of the hybridization event. Further analyses including chromosome counts may determine a possible polyploidy of the hybrid.

Finally, the fourteen species currently accepted in *Mastigolejeunea* are transferred to *Thysananthus* in Chapter VI but are only briefly listed in the recent monograph. A full treatment of the subg. *Mastigolejeunea* should be the subject of future work.

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Cryptogamie, Bryologie, 2010, 31 (2): 113-119
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Studies on the genus *Thysananthus* (Marchantiophyta: Lejeuneaceae)

1. *Thysananthus discretus* Sukkharak *et* Gradst. sp. nov.

Phiangphak SUKKHARAK* & Robbert GRADSTEIN

Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences,
 University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

(Received 10 November 2009, accepted 5 January 2010)

Abstract – The liverwort, *Thysananthus discretus* Sukkharak *et* Gradst. sp. nov. (Lejeuneaceae) is described from Western Melanesia (New Guinea, Solomon Islands). The new species stands out within *Thysananthus* on account of the leaves when moist clasping the stem, free underleaf bases with the well-developed auricles, and the strongly rigid stems with 14-18 cells wide ventral merophytes.

Lejeuneaceae / liverworts / morphology / taxonomy / *Thysananthus discretus* / Western Melanesia

INTRODUCTION

Thysananthus Lindenb. is a member of Lejeuneaceae subfamily Ptychanthoideae Mizut. (Mizutani, 1961; Gradstein, 1975) and probably contains about ten species, growing as epiphytes in rain forests and montane cloud forests throughout the tropics. The centre of diversity of the genus is in Southeast Asia with eight species occurring in the area (*T. aculeatus* Herzog, *T. appendiculatus* Steph., *T. comosus* Lindenb., *T. convolutus* Lindenb., *T. mollis* Steph., *T. montanus* Gradst. *et al.*, *T. retusus* (Reinw. *et al.*) B. Thiers *et* Gradst. and *T. spathulistipus* (Reinw. *et al.*) Lindenb.). One species is known from the New World tropics (*T. amazonicus* (Spruce) Schiffn.).

In the course of a world-wide revision of *Thysananthus* we found that some collections from New Guinea and Solomon Islands represent a hitherto undescribed taxon. The new species, *Thysananthus discretus* Sukkharak *et* Gradst., is described and illustrated in this paper. In addition a key to the species is provided.

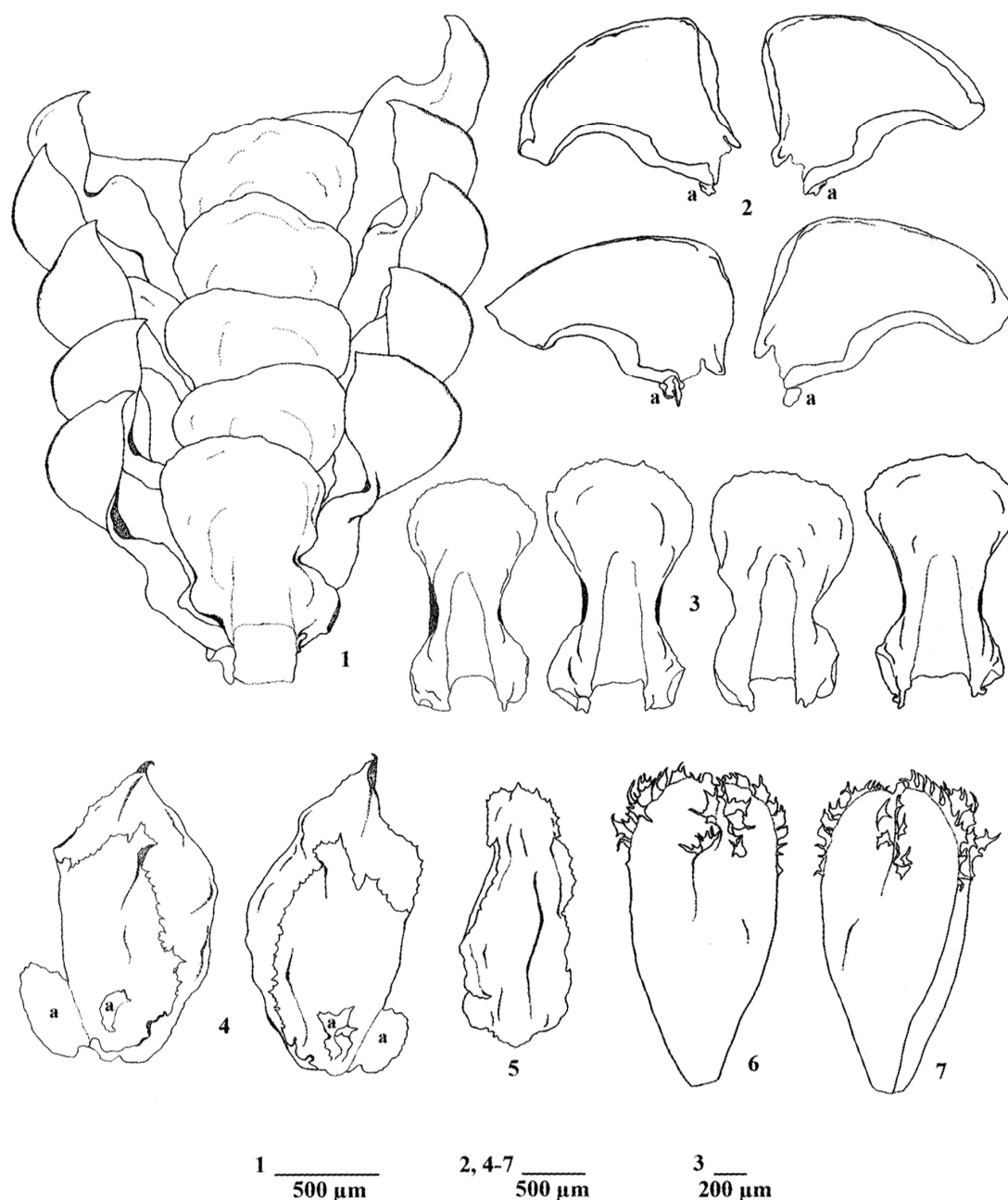
SYSTEMATIC TREATMENT

Thysananthus discretus Sukkharak *et* Gradst., sp. nov.

Figs 1-21

Type. Indonesia, Papua [“Netherlands New Guinea, distr. Hollandia”], Cycloop Mountains, path Ifar-Ormoe, alt. 1220 m, 21 Aug 1961, Royen & Sleumer 5896 (**holotype**, L; **isotypes**, JE, S). The epithet *discretus* refers to the free underleaf bases, which are not connate with the leaves.

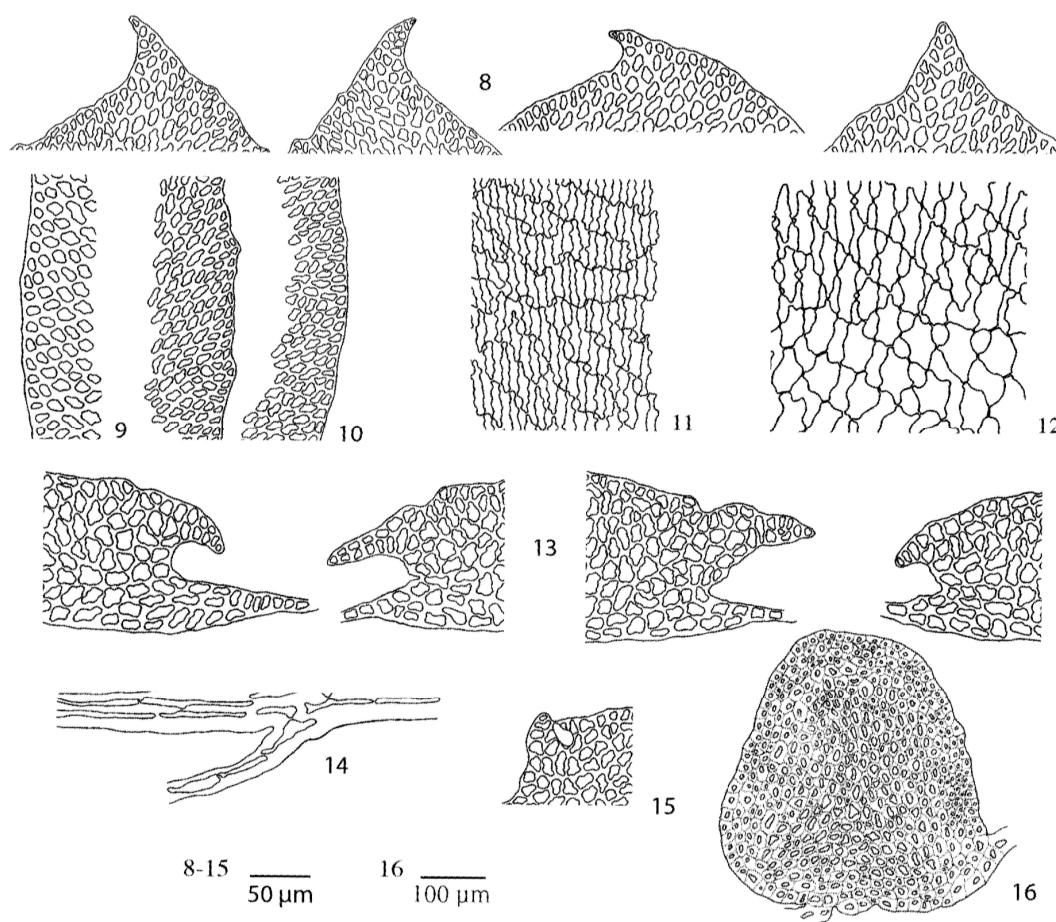
* Correspondence and reprints: ppsukk@gmail.com



Figs 1-7. *Thysananthus discretus* Sukkharak et Gradst. **1.** Portion of shoot, ventral view. **2.** Leaves, ventral view. **3.** Underleaves. **4.** Female bracts. **5.** Female bracteole. **6.** Perianth, dorsal view. **7.** Perianth, ventral view. (1-3 from the holotype; 4-7 from Royen & Sleumer 5907 [L]). a = appendage.

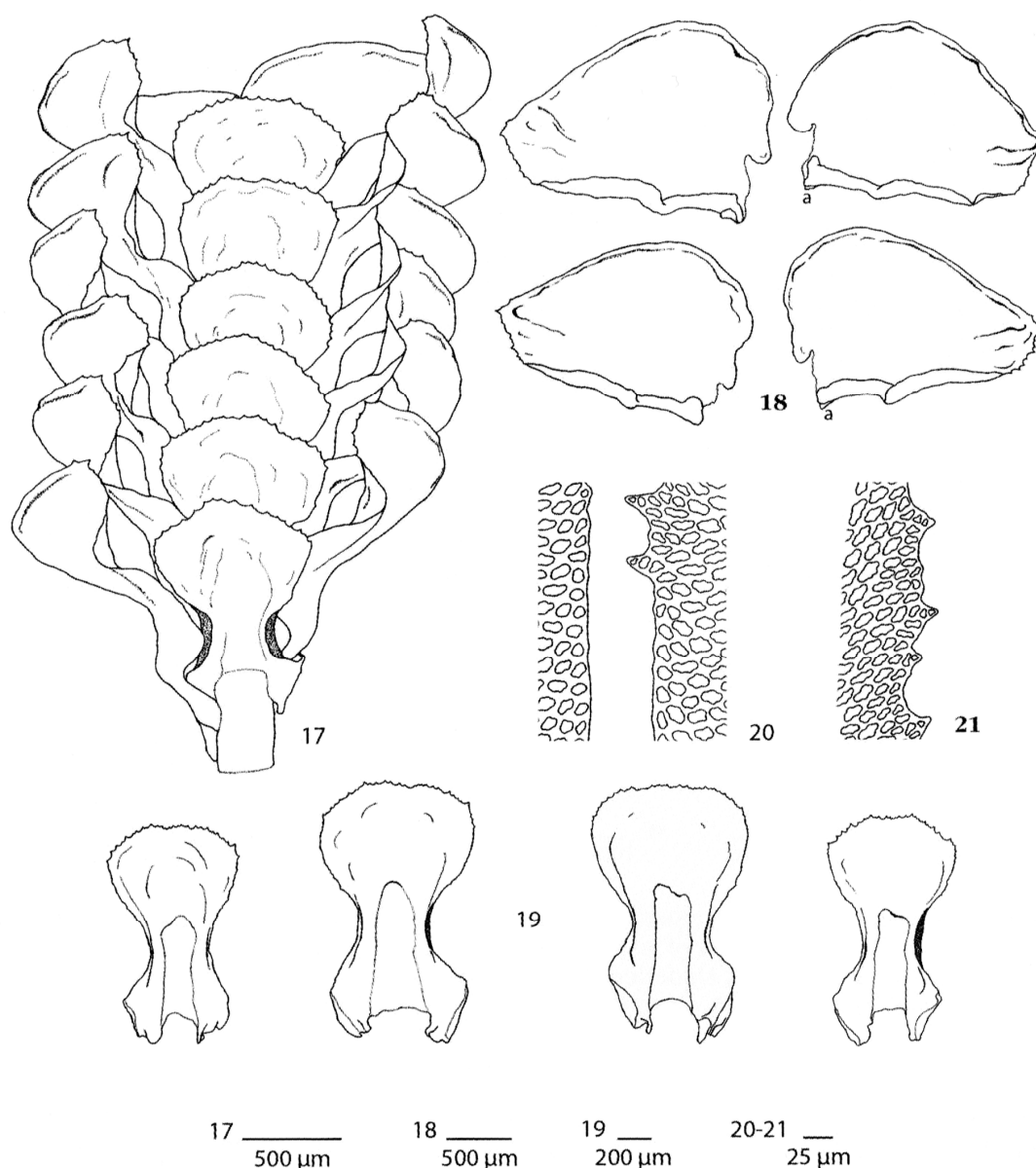
Caulis rigida, 14-18 cellulis lata ventralibus. Folia asymmetrica rotundata. Amphigastria libera, ad basim auriculata.

Plants with vigorous shoots, yellowish brown in herbarium specimens, up to 6.5 cm long \times 2-3 mm wide, habit deliquescent with projecting growth, turning upwards and becoming ascending to erect, irregularly (1)-pinnate, branches *Lejeunea*-type. **Stems** strongly rigid; ventral merophyte 14-18 cells wide; in cross



Figs 8-16. *Thysananthus discretus* Sukkharak et Gradst. **8.** Leaf apices. **9.** Dorsal margin cells of leaf lobe. **10.** Ventral margin cells of leaf lobe. **11.** Median cells of leaf lobe. **12.** Basal cells of leaf lobe. **13.** Leaf lobule apices. **14.** Underleaf base in longitudinal section. **15.** Inner surface of lobule apex showing hyaline papilla. **16.** Cross section of stem. (All from the holotype).

section orbicular-subelliptic in shape, 360-500 µm high × 260-445 µm wide, composed of 76-80 epidermal cells surrounding 365-381 medullary cells in 16-22 layers, epidermal cells not larger than medullary cells, all cells with thickened walls, walls of epidermal cells brownish, those of medullary cells hyaline. **Leaves** imbricate, when dry suberect and strongly convolute, when moist clasping the stem (not spreading outwards), attached to the axis along a J-shaped line of insertion and covering the whole length of the straight lateral merophytes; dorsal lobes asymmetrically ovate, 1.4-2.3 × 1-1.8 mm, strongly concave in ventral view, apex apiculate, dorsal base auriculate, auricle 100-150 × 125-160 µm, dorsal margin entire or with 1-4 triangular teeth, the teeth consisting of up to 4 cells, being 2-3 cells wide at base and ending in a row of 1-2 cells, ventral margin upcurved over most of its length, becoming flat near the apex, entire or with 3-8 triangular teeth, the teeth consisting of up to 5 cells, 2-3 cells wide at base and ending in a row of 1-2 cells; leaf cells elongate-hexagonal with acute ends, marginal lobe cells 10-12 × 10-12 µm, median cells 32-45 × 5-7 µm, basal cells 37-62 × 17-25 µm, vitta cells absent, cells wall thick, trigones large, cordate to bulging and irregularly rounded, often becoming coalesced, intermediate thickenings 0-1 per cell wall, the cell lumen appearing vermicular; oil bodies *Calypogeia*-type, 4-5 per cell, toward leaf base more numerous, up to 8 per cell (Gradstein 3894). **Lobules** rectangular,



Figs 17-21. *Thysananthus discretus* Sukkharak et Gradst. **17.** Portion of shoot, ventral view. **18.** Leaves, ventral view. **19.** Underleaves. **20.** Dorsal margin cells of leaf lobe. **21.** Ventral margin cells of leaf lobe. (All from Streimann 13622 [JE]). a = appendage.

0.6-0.7 × 0.1-0.2 mm, ± 1/4 × lobe length, inflated, keel curved, the surface smooth; foliar appendages under keel on one or both sides or not developed, orbicular-oblong, 215-375 × 85-150 µm; the free margin and keel meeting each other at an oblique angle of ca. 45°, free margin slightly upcurved, apex with one triangular tooth, the tooth consisting of 5-12 cells, 2-4 cells wide at base and ending in a row of 1-2 cells; hyaline papilla pyriform, 25-27 × 12-15 µm, at or near the proximal base of the tooth on the inner surface of the lobule. **Underleaves** imbricate, broadly oblong to rectangular, 1.2-1.9 × 0.8-1.4 mm, 2-2.5 × stem width, apex broadly rounded to truncate, toothed, the teeth consisting of 1-6 cells, 2-3 cells wide at base and ending in a row of 1-2 cells, margins entire, recurved, central region gibbous, underleaf bases auriculate, the auricles 100-275 × 200-400 µm,

underleaf bases not connected with leaves, insertion line slightly arched; cells $20\text{--}25 \times 5\text{--}7 \mu\text{m}$, becoming longer towards the base of the underleaf; underleaf attachment bistratose. **Dioicous.** **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 6-10 pairs, bracts hypostatic, ovate, $0.7\text{--}0.8 \times 0.5\text{--}0.6 \text{ mm}$, apex acute, margins entire, lobules strongly inflated; bracteoles similar to underleaves; antheridia 2 per bract. **Gynoecia** terminal on elongated branches, with 2 lejeuneoid innovations, innovations repeatedly fertile, forming a dichasial pattern; bracts in one pair, obliquely spreading to subsquarrose, lobe ovate, $2.4\text{--}2.7 \times 1.2\text{--}1.5 \text{ mm}$, apex apiculate, with 8-9 triangular teeth, the teeth consisting of 3-5 cells, 2-3 cells wide at base and ending in a row of 1-2 cells, appendages under keel on one or both sides or not developed, orbicular-oblong $48\text{--}95 \times 25\text{--}55 \mu\text{m}$; lobules broadly ovate, $2/3 \times$ lobe length, apex apiculate, appendages on middle of basal part or not developed, orbicular-oblong $30\text{--}42 \times 13\text{--}25 \mu\text{m}$; bracteoles spatulate, $2.3\text{--}2.4 \times 1.1\text{--}1.3 \text{ mm}$, apex emarginate, $1/2 \times$ bracteole length with triangular teeth, the teeth consisting of 3-7 cells, 2-3 cells wide at base and ending in a row of 1-2 cells, margins entire, slightly recurved, central region gibbous. **Perianths** exerted to $1/2$, oblong, $2.5\text{--}2.6 \times 1.1\text{--}1.3 \text{ mm}$, apex truncate, surface sharply 3-keeled, keels in upper $1/3$ with numerous lacinate teeth, the teeth 3-9 cells long; beak $97\text{--}125 \mu\text{m}$, 4-7 cells long; appendages on basal part of keel or not developed. **Sporophyte** not seen. **Chemistry:** sesquiterpenes, diterpenes and sterols (Gradstein *et al.*, 1985, under *T. convolutus* sample nr. 49).

Distribution and ecology: *Thysananthus discretus* is thus far known only from Western Melanesia: Papua (Indonesia), Papua New Guinea and the Solomon Islands. It occurs in rain forests and montane cloud forests and was collected at 760-2700 m. The new species grows as an epiphyte on tree trunks, branches and stems of treelets. In the view of its local abundance, it indicates that the flora of Western Melanesia still remains poorly known and that exciting discoveries may still be made in this floristically unusually rich part of the world.

Additional illustration: Gradstein *et al.* (2002, p. 73, Fig. 45, as *T. convolutus*).

Specimens examined:

INDONESIA. PAPUA: the type specimens; Cycloop Mts., Royen & Sleumer 5907 (JE, L). — **WEST PAPUA:** Eipomek-Tal, $4^{\circ} 25' \text{ S } 140^{\circ} 01' \text{ E}$, Hiepko & Schultze-Motel 2218, 2403 (JE).

PAPUA NEW GUINEA. CENTRAL: Boridi, Carr 13531 (JE). — **EASTERN HIGHLANDS:** Daulo Pass, $6^{\circ} 03' \text{ S } 145^{\circ} 14' \text{ E}$, Streimann 17990 (JE); Gahavisuka Provincial Park, $6^{\circ} 01' \text{ S } 145^{\circ} 25' \text{ E}$, Streimann 18201 (JE). — **MOROBE:** Wau, Mt. Kaindi, Gradstein 3778, 3856, 3894, 3910 (GOET), Schuster 67-5786, 67-5787, 67-5792, 67-5791/c, 67-6282 (JE), Streimann 22497 (JE, LAE), Streimann & Bellamy 17690 (JE, S, W); Araulu logging area, $7^{\circ} 28' \text{ S } 146^{\circ} 48' \text{ E}$, Streimann 13622 (JE, LAE); Slate Creek & Gumi Creek Divide, $7^{\circ} 10' \text{ S } 146^{\circ} 28' \text{ E}$, Streimann 13861 (JE); Spreader Divide, $7^{\circ} 16' \text{ S } 146^{\circ} 06' \text{ E}$, Streimann & Tamba 11878 (JE, LAE), Streimann 11846 (LAE), Streimann 26036 (JE); Aseki-Bulolo Road, Streimann 20051, 20103, 26135 (JE). — **WESTERN HIGHLANDS:** Jimi-Waghi Divide, $5^{\circ} 43' \text{ S } 144^{\circ} 38' \text{ E}$, Streimann 20916 (JE, LAE), 20911 (LAE).

SOLOMON ISLANDS. GUADALCANAL: Mt. Papomanatsen, Braithwaite 4773 (JE).

DISCUSSION

Thysananthus is subdivided into two subgenera, subgen. *Thysananthus* and subgen. *Sandeanthus* B. Thiers et Gradst., based on differences in leaf position and areolation (Thiers & Gradstein, 1989). The new species *T. discretus* is a member of

subgenus *Thysananthus* and is recognized the underleaf bases, which are not connate with the leaves, the presence of well-developed auricles at underleaf bases, the strongly rigid stems with 14-18 cells wide ventral merophytes, and the leaves which, when moist, are clasping the stem. Free underleaf bases, which are not connate with the leaves, is an unusual character in *Thysananthus* and occur otherwise in the New Guinean endemics *T. mollis* and *T. montanus*, and (occasionally) in the widespread *T. retusus*. These three species are readily distinguished from *T. discretus* by the vittate leaves. All other species of *Thysananthus* have leaves that are connate with the underleaf bases on one side (Sukkharak & Gradstein, submitted). The differences between *T. discretus* and other members of the genus are shown in the key to species of *Thysananthus* given below.

Collections of *Thysananthus discretus* were previously identified as "*T. appendiculatus*", "*T. convolutus*", or "*T. sp.*". The new species is most closely related to widespread Malesian *T. convolutus* and was illustrated as *T. convolutus* by Gradstein *et al.* (2002: Fig. 45). The illustration clearly shows the free underleaves characteristic of the new species, which are not connected with the leaves, and the presence of well-developed auricles at the underleaf bases. *T. discretus* shares with *T. convolutus* the asymmetric leaves but differs from the latter by (1) leaves when moist clasping the stem (squarrose in *T. convolutus*), (2) free underleaf bases, with well-developed auricles (underleaf bases connate with leaves on one side and without auricles in *T. convolutus*), and (3) strongly rigid stems, with 14-18 cells wide ventral merophytes and medulla 16-22 cell layers high (less rigid stems, with 8-10 cells wide ventral merophytes and 14-17 layers high medulla in *T. convolutus*). The new species may also be confused with *T. appendiculatus*, a species endemic to New Guinea which may possess auricled underleaf bases like *T. discretus*. However, the leaf lobes in *T. appendiculatus* are symmetric and widely spreading when moist, while in *T. discretus* they are asymmetric and clasping the stem when moist. In addition, leaf and underleaf bases are connected in *T. appendiculatus* while in *T. discretus* they are never connected.

A foliar appendage is developed at the base of the keel in leaves (Figs 2, 18) and bracts, the mid-basal portion of bract lobules (Fig. 4), and perianths of *Thysananthus discretus*. Foliar appendages may occur on bracts and perianths in all species of *Thysananthus* but are rare on vegetative leaves (only in *T. discretus*, *T. appendiculatus* and *T. convolutus*; Sukkharak & Gradstein, submitted). In *T. discretus* the appendages are present on one or both sides of the stem and are sometimes lacking, while in *T. appendiculatus* and *T. convolutus* they are always found on one side of the stem only, on leaves that are free from underleaf bases and opposite to leaves that are connected with underleaf bases. Moreover, the foliar appendages of *T. convolutus* are always curved towards the stem while in *T. discretus* and *T. appendiculatus* they are straight or curved.

Thysananthus discretus is a rather polymorphic species with respect to the dentation of leaves, which varies from edentate (Figs 1, 2) to \pm strongly dentate (Figs 17, 18). The variation in leaf dentation observed in *T. discretus* is not uncommon in Lejeuneaceae, however, and also occurs in, e.g., *T. convolutus*, *Bryopteris filicina* (Swartz) Nees (Gradstein, 1994), *Archilejeunea planiuscula* (Mitt.) Steph. (Thiers & Gradstein, 1989; Gradstein *et al.*, 2002), and in the genus *Lejeunea* (Reiner-Drehwald & Goda, 2000).

Key to the species of *Thysananthus*

1. Leaves when dry convolute. Leaf cells elongate (*Thysananthus* subgen. *Thysananthus*)..... 2

1. Leaves when dry widely spreading, loosely reflexed or plane. Leaf cells (except for vitta) subisodiametric (*Thysananthus* subgen. *Sandeanthus*) *T. retusus*
2. Leaf lobes without vitta. Underleaf bases free or connected with leaves on one side 3
2. Leaf lobes with vitta. Underleaf bases free. 9
3. Leaf lobes asymmetrical with the apex positioned towards the ventral side of the leaves 4
3. Leaf lobes symmetrical, apex not positioned towards the ventral side of the leaves 8
4. Leaves when moist squarrose or clasping the stem. Underleaf bases free or connected with leaves on one side 5
4. Leaves when moist spreading out widely. Underleaf bases connected with leaves on one side 6
5. Ventral merophyte 14-18 cells wide. Leaves when moist clasping the stem. Underleaf bases free, with well-developed auricles *T. discretus*
5. Ventral merophyte 8-10 cells wide. Leaves when moist squarrose. Underleaf bases connected with leaves on one side, without auricles *T. convolutus*
6. Underleaves spatulate, recurved. Male bract lobules epistatic or hypostatic. Neotropical *T. amazonicus*
6. Underleaves obovate, flat or channeled/hollow. Male bract lobules hypostatic. Paleotropical 7
7. Dorsal base of leaves auriculate. Underleaves flat. Perianth laciniate, teeth 3-5 cells long *T. comosus*
7. Dorsal base of leaves without auriculate. Underleaves channeled/hollow. Perianth dentate, teeth 1-2 cells long. *T. aculeatus*
8. Keel of leaves on one side of the stems with a foliar appendages (on the side where leaves and underleaves are free) *T. appendiculatus*
8. Keel of leaves without foliar appendage. *T. spathulistipus*
9. Leaves when dry convolute or laterally appressed to the stem. Leaves lanceolate, toothed *T. mollis*
9. Leaves when dry convolute. Leaves oblong, entire. *T. montanus*

Acknowledgments. The research of the first author was supported by a Royal Thai government scholarship in cooperation with the German Academic Exchange Service (DAAD).

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On the occurrence of adnate underleaves and appendages in *Thysananthus* (Lejeuneaceae). Studies on the genus *Thysananthus*, 2.

Fusion of underleaf bases with the bases of adjacent leaves is a rather common phenomenon in the order Jungermanniales (Heinrichs *et al.* 2005; He-Nygrén *et al.*, 2006), especially in species of *Bazzania* and Lophocoleaceae (*Chiloscyphus*, *Clasmatocolea*, *Heteroscyphus*, *Leptoscyphus*, etc.) (e.g. Fulford, 1963, 1976; Engel, 1980; Piippo, 1985; Srivastava & Srivastava, 2002). Underleaves in these groups may be adnate with leaves on one or both sides, or free, and this character may sometimes be useful to separate closely related species. In contrast, adnate underleaves are very rare in the order Porellales (Frullaniaceae, Lejeuneaceae, Porellaceae, etc.) where they occur commonly only in the genus *Thysananthus* (but adnate female bracteoles occur in *Ceratolejeunea*, *Drepanolejeunea*, *Lejeunea* and *Leptolejeunea*; Zhu & So, 2001; Dauphin, 2003; Zhu & Grolle, 2003). Several authors have paid attention to the occurrence of adnate underleaves in *Thysananthus* but the descriptions and taxonomic interpretations were sometimes contradictory. In this paper, we briefly examine the occurrence of adnate underleaves, and some further little-known leaf-base features, in the genus *Thysananthus*.

Thysananthus (Lejeuneaceae subfamily Ptychanthoideae) is a genus of about 11 species occurring mostly in Southeast Asia and is a characteristic element of tropical lowland and montane rainforests (Sukharak, in prep.). Mizutani (1969) first

observed that underleaves of *T. spathulistipus* were connected with the basal part of keels of the leaves. He showed that when an underleaf is removed from the stem, the basal portion of the underleaf remains attached to the base of the keel of the lateral leaves, as an appendage. Later, Mizutani (1977) reported adnate underleaves in *T. aculeatus* Herzog and *T. convolutus* Lindenb. (and its synonym *T. gottschei* (Jack & Steph.) Steph.), and concluded that these species were therefore closely related. Kitagawa (1973) observed adnate underleaves in *T. appendiculatus* Steph., a species having large appendages where underleaves are detached (hence the name *appendiculatus*), and concluded that separation of this species from *T. spathulistipus* was not warranted. Mizutani & Piippo (1986), however, noted that appendages in *T. appendiculatus* occur on both sides of the stem while being absent or on one side of stem only in *T. spathulistipus*, and maintained the two as separate species.

Our study of a large series of specimens of all species of *Thysananthus* shows that underleaves in *Thysananthus* may be free or adnate to the keel of the leaves on one side of the stem, never on both sides (Fig. 1A, B and D; adnate portion running from the base of the underleaf to 'e'). We are unable to confirm the observation of Mizutani & Piippo (1986) that underleaves in *T. appendiculatus* are adnate on both sides. The presence of adnate underleaves appears to be a stable and taxonomically relevant feature of *T. aculeatus*, *T.*

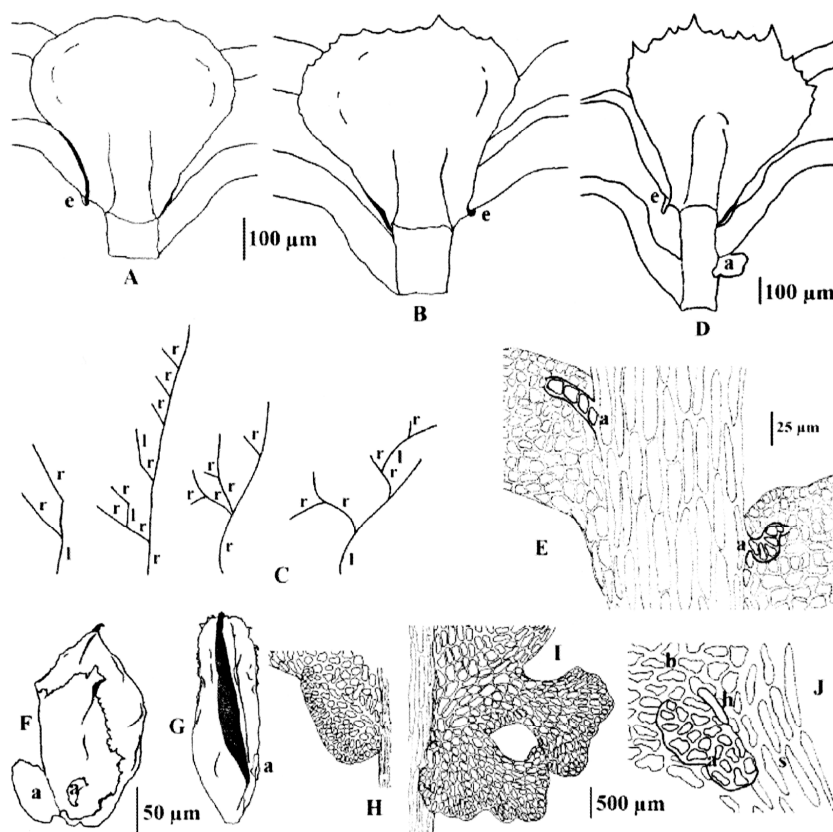


Figure 1. Adnate underleaves and appendages in *Thysananthus*. (A and B) Stem in ventral view showing adnate underleaf; e=distal end of the connection between leaf and underleaf. (C) Diagrams of branch systems; l=underleaves adnate on left-hand side, r=underleaves adnate on right-hand side. (D) Appendage (a) at keel of leaf. (E) Appendage (a) at lobule base. (F) Appendages (a) at keel and lobule base of female bract. (G) Appendages (a) at perianth base. (H–I) Appendages of leaf keels. (J) Appendage of lobule base; a=appendage, b=lobule, h=hyaline papilla, s=stem (A–C drawn from *T. comosus*, Wallich s.n. (BM); D drawn from *T. appendiculatus*, Clemens 5414 (W); E drawn from *T. retusus*, Sukkharak 733 (GOET); F and H drawn from *T. discretus*, van Royen & Sleumer 5896 (L); G drawn from *T. mollis*, Gradstein 3795 (GOET); I drawn from *T. appendiculatus*, Gradstein 3875 (GOET); J drawn from *T. montanus*, Streimann 13639 (LAE)).

amazonicus (Spruce) Schiffn., *T. appendiculatus*, *T. comosus* Lindenb., *T. convolutus*, *T. laceratus* Steph. and *T. spathulistipus* (Reinw. et al.) Lindenb.; in the other species of the genus (*T. discretus* Sukkharak & Gradst. (Sukkharak & Gradstein, 2010), *T. mollis* Steph., *T. montanus* Gradst., X.-L. He & Piippo and *T. retusus* (Reinw. et al.) B. Thiers & Gradst.) underleaf bases are usually free.

Interestingly, it appeared that the adnation of underleaves on branches occurs in a distinct left–right symmetry pattern, on right-hand branches being connected to leaves on the left side and on left-hand branches on the right-hand side (Fig. 1C). The left–right correlation between branches and underleaf adnation observed in *Thysananthus* has, to our knowledge, not yet been reported from liverworts and deserves further study in other genera with adnate underleaves. A more detailed analysis might be rewarding and could shed more light on the evolutionary and systematic implications of this phenomenon.

Associated with leaf bases, we have observed an additional morphological feature in *Thysananthus*. In all species of *Thysananthus*, a small foliar ‘appendage’ may be developed on leaves, female bracts and perianths (Fig. 1D–G). These appendages, which are not to be confused with the ones

discussed above, are irregular in shape (Fig. 1H–J) and vary somewhat in size and position. In *T. appendiculatus*, *T. laceratus* and *T. discretus*, the appendages are found on the keel of leaves and inserted partially on the stems. In *T. appendiculatus* and *T. laceratus*, they are always found on one side of the stem only, on the side where underleaves are free and being opposite to the adnate ones (Fig. 1D). In species with free underleaves such as *T. discretus*, however, the position of the appendages is variable and may be on one or both sides of the stems (or lacking). These observations are further evidence for the left–right symmetry on branches in *Thysananthus*. In *T. mollis*, *T. montanus* and *T. retusus*, moreover, we observed an appendage which is attached to the lobule bases and the stem epidermis cells (Fig. 1E). The appendage is oblong in shape, 45–85 × 22–45 µm in size (Fig. 1J) and developed on both sides of the stem. This structure should not be confused with the stylus, which is the characteristic of Frullaniaceae, Jubulaceae and Lejeuneaceae (*Cololejeunea* and *Lejeunea*) (e.g. Leitgeb, 1880, p. 12; Benedix, 1953; Grolle, 1975; Reiner-Drehwald, 2000; Wigginton, 2006). By its position, these structures are different. The appendage runs below the margin base of

lobule and is also inserted on the stem, whereas the stylus is always inserted on the margin base of a lobule.

In all *Thysananthus* species, wing-like appendages occur on the keels of the female bracts, on one or both sides of the stem (or lacking) and partially inserted on the associated innovation. In addition, a small appendage may be found on the mid-basal portion of the bract lobules and on the base of the keels of the perianth (Fig. 1F–G). The appendages on the female bracts are not associated with left–right symmetry and their presence is a generic feature of *Thysananthus*, without relevance for species recognition. The presence of an appendage along the keel of the female bracts is also characteristic of *Brachiolejeunea*, *Frullanoides* and *Harpalejeunea*, and occurs furthermore also in *Blepharolejeunea*, *Lindigianthus*, *Neurolejeunea*, *Mastigolejeunea* and *Spruceanthus* where it is small and sometimes lacking (van Slageren, 1985; Gradstein, 1994; Daniels, Kariyappaa & Daniel, 2010). The available evidence indicates that appendages on female bracts occur widely in family Lejeuneaceae.

The taxonomic value of the adnate underleaves and appendages in *Thysananthus* is shown in the following key to the species of the genus:

1. Underleaf bases connected with leaves on one side 2
 1. Underleaf bases usually free 3
 2. Keel of leaves on one side of the stems with a small foliar appendage (on the side where leaves and underleaves are free). *T. appendiculatus* and *T. laceratus*
 2. Keel of leaves without foliar appendage ... *T. aculeatus*, *T. amazonicus*, *T. comosus*, *T. convolutus* and *T. spathulistipus*
 3. Lobule bases with small appendages (attached to stem epidermis cells); keel of leaves without foliar appendage *T. mollis*, *T. montanus* and *T. retusus*
 3. Lobule bases without appendage; keel of leaves on one or both sides of the stem with small foliar appendage, or appendage lacking *T. discretus*

We are grateful to the curators of the herbaria BM, L, LAE and W for the loan of specimen and to Dr M. Elena Reiner-Drehwald and an anonymous reviewer for advice. Work by the first author was supported by a Royal Thai government scholarship in cooperation with the German Academic Exchange Service (DAAD).

TAXONOMIC ADDITIONS AND CHANGES: Nil.

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Studies on the genus *Thysananthus* (Marchantiophyta, Lejeuneaceae) 3.
Terpenoid chemistry and chemotaxonomy of selected species of
Thysananthus* and *Dendrolejeunea fruticosa

Phiangphak SUKKHARAK^{a*}, Agnieszka LUDWICZUK^b, Yoshinori ASAKAWA^c & Robbert GRADSTEIN^d

^aDepartment of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

^bDepartment of Pharmacognosy with Medicinal Plant Unit, Medical University of Lublin, 1 Chodzki Street, 20-093 Lublin, Poland

^cFaculty of Pharmaceutical Sciences, Tokushima Bunri University, Yamashiro-cho, Tokushima, 770-8514, Japan

^dMuséum National d'Histoire Naturelle, Dept. Systématique et Evolution, UMS 7205, Case Postale 39, 57 rue Cuvier, 75231 Paris cedex 05, France

(Received 20 October 2010, accepted 26 March 2011)

Abstract – Gas chromatography and mass spectrometry of 20 samples of *Thysananthus* (*T. comosus*, *T. convolutus*, *T. retusus*, *T. spathulistipus*) and one of *Dendrolejeunea* (*D. fruticosa*) from Malaysia and Thailand revealed the presence in most taxa of large quantities of sesquiterpenoids and unidentified diterpenoids. Isolepidozene was detected as a major component in *T. comosus*, *T. convolutus* and *T. spathulistipus*, pinguisane sesquiterpenoids as major components in *T. retusus*, and the unidentified (M⁺)304, 271(100), 105(90) as the most abundant component of *D. fruticosa*. The large chemical heterogeneity detected in *T. convolutus* correlates with the variation in leaf dentation observed in the species and supports the resurrection of *T. gottschei*, previously considered a synonym of *T. convolutus*. The subdivision of *Thysananthus* into two subgenera, subg. *Thysananthus* and subg. *Sandeanthus*, and the treatment of *Dendrolejeunea* as a separate genus, are chemically supported.

Dendrolejeunea fruticosa/ diterpenoids/ GC-MS/ liverwort/ sesquiterpenoids/
Thysananthus comosus/ *Thysananthus convolutus*/ *Thysananthus retusus*/ *Thysananthus spathulistipus*/ volatiles

INTRODUCTION

* Correspondence and reprints: ppsukk@gmail.com

Liverworts are able to synthesize large quantities of terpenoids, especially sesquiterpenoids, diterpenoids and lipophilic aromatic compounds, which are stored in oil bodies (e.g., Gradstein *et al.*, 1985). The Lejeuneaceae are the largest family of liverworts with about 1200 species in 78 genera (Frey & Stech, 2009, with updates). Several studies have been conducted on the terpenoids and aromatic compounds of Lejeuneaceae (e.g., Asakawa, 1982, 1995, 2004; Asakawa *et al.*, 1980a, 1980b; Gradstein *et al.*, 1981, 1985, 1988; Kruijt *et al.*, 1986). These substances, especially terpenoids, often show strong biological activity and may play an important role in the defence of the plants against environmental hazards (Gradstein, 1994) or predators (Harinantenaina *et al.*, 2006). The above-mentioned studies also identified some substances as taxonomic markers for members of the family.

Thysananthus Lindenb. is a member of Lejeuneaceae subfamily Ptychanthoideae Mizut. (Mizutani, 1961; Gradstein, 1975, 1994). The genus is characterized by (1) purely *Lejeunea*-type vegetative branches, (2) ventral merophyte 4-12 cells wide, (3) stem epidermis cells not larger than medullary cells, with thick, brownish walls, (4) leaves convolute when dry, usually toothed, (5) leaf cells elongate, (6) gynoeical innovations with lejeuneoid leaf sequence, and (7) perianth with 3(-10) keels (Thiers & Gradstein, 1989; Gradstein, 1992; Gradstein *et al.*, 2002; Sukkharak & Gradstein, 2010a). Thus defined, the genus contains ten species rowing as epiphytes in moist lowland forests and montane cloud forests throughout the tropics (Sukkharak & Gradstein, 2010a). The centre of diversity is in Southeast Asia with five species (*T. aculeatus* Herzog, *T. comosus* Lindenb., *T. convolutus* Lindenb., *T. retusus* (Reinw. *et al.*) B. Thiers & Gradst., *T. spathulistipus* (Reinw. *et al.*) Lindenb.). *Thysananthus spathulistipus* also reaches to tropical Africa. Three species are found in New Guinea and the Solomon Islands (*T. discretus* Sukkharak & Gradst., *T. mollis* Steph., *T. appendiculatus* Steph.) and one is only known from Papua New Guinea (*T. montanus* Gradst. *et al.*). Finally, one species, *T. amazonicus* (Spruce) Schiffn., is known from the New World tropics. The species of *Thysananthus* are attributed to the two subgenera: subg. *Thysananthus* (*T. aculeatus*, *T. amazonicus*, *T. appendiculatus*, *T. comosus*, *T. convolutus*, *T. discretus*, *T. mollis*, *T. montanus*, *T. spathulistipus*) and subg. *Sandeanthus* B. Thiers & Gradst. (*T. retusus*) (Thiers & Gradstein, 1989; Gradstein, 1992, with updates).

Dendrolejeunea is a monotypic genus, containing only *D. fruticosa* (Lindenb. & Gottsche) Lacout. from tropical Asia, northern Australia and the Pacific region. First described by Spruce (1884) as a subgenus of *Lejeunea*, *Dendrolejeunea* was long included in *Thysananthus* but was resurrected as a separate genus by Gradstein (1992). Morphologically, *Dendrolejeunea* stands out by its dendroid habit, having creeping stoloniform stems and

upright, regularly pinnate branches. In contrast, members of *Thysananthus* are never dendroid and share projecting growth and irregularly pinnate branching. Molecular data have revealed that *Dendrolejeunea* is the sister group of *Thysananthus* (Wilson *et al.*, 2007).

Seven species of *Thysananthus*: *T. amazonicus*, *T. appendiculatus*, *T. convolutus*, *T. discretus* (under *T. convolutus* sample nr. 49 in Gradstein *et al.*, 1985), *T. mollis*, *T. retusus* (under *T. fruticosus* in Gradstein *et al.*, 1985) and *T. spathulistipus*, have been screened for the occurrence of terpenoids, flavonoids, sterols, and aromatic compounds (Gradstein *et al.*, 1985; Kruijt *et al.*, 1986; Harinantenaina *et al.*, 2006). The results showed the presence of pinguisane sesquiterpenoids, clerodane diterpenoids and unidentified diterpenoids.

As part of a world-wide revision of *Thysananthus* by the first author, we hereby report the results of chemical analysis of four species of *Thysananthus* (*T. comosus*, *T. convolutus*, *T. retusus*, *T. spathulistipus*) and of the closely related *Dendrolejeunea fruticosa*.

MATERIAL AND METHODS

Plant material. Twenty samples of *Thysananthus* and one sample of *Dendrolejeunea* were collected mainly by the first author and her associates in Malaysia and Thailand in 2009 (Table 1). Dried voucher specimens were deposited in BKF and GOET.

Extraction and analysis. Plant material (0.25 g of each species) was purified, air-dried and crushed in mortar to receive fine powder. The powdered material was extracted three times with diethyl ether (3 x 3 ml) at room temperature, and the crude extract was filtered through a Pasteur pipette packed with Celite. The filtered extract was dried using anhydrous sodium sulfate as a drying agent, then evaporated to receive 100 µl of extract. One µl of the crude extract was analyzed by GC-MS using an Agilent Technologies 6890N gas chromatograph coupled with a mass selective detector (Agilent Technologies 5973), on an HP-5MS capillary column (30 m x 0.25 mm, 0.25 µm film thickness). Oven temperature was 50°C with 3 minutes initial hold, and then to 250°C temperature programmed at 5°C/min, and 15 minutes at 250°C. Injection temperature was 280°C and helium (1ml/min) was used as a carrier gas. The detector was operated in electron impact mode (70eV with 3 scans/s and mass range m/z 40-500) at 230°C. Each extract was analyzed three times. The retention indices were calculated relative to C9-C30 *n*-alkanes. Compounds were identified using a computer-supported spectral library (Hochmuth, 2008), mass spectra of reference compounds, as well as MS data from the literature (Joulain & König, 1998; Linstrom & Mallard, 2001) and the library database of the Faculty of Pharmaceutical Sciences, Tokushima Bunri University. Compound identities were confirmed by comparison of retention indices with reference

compounds and published data (Linstrom & Mallard, 2001). Quantification was done based on peak area.

RESULTS AND DISCUSSION

In total, 66 different sesquiterpenoids and diterpenoids were detected in the five investigated species (21 samples). Of these, about two-thirds (42) are unidentified compounds. The taxonomic distribution and abundance of the identified and unidentified compounds are shown in Table 2, chemical structures of identified components are depicted in Figure 1. Numbers in bold face in the text refer to the compound figure numbers. The chemotaxonomic relevance of the detected compounds is discussed below.

Thysananthus comosus Lindenb.

Three compounds were detected in all four samples of *Thysananthus comosus*: *cis*- β -elemene (**3**), isolepidozene (**13**) and the unidentified (M^+)220, 107(100), 43(80). The Malaysian specimen of this species (sample 1) produces large amounts of (M^+)302, 190(100), 81(95) which was also detected as a major component in *T. convolutus* from Malaysia. Samples 2-4 from Thailand produce three unidentified compounds (M^+)318, 207(100), 189(60), (M^+)318, 151(100), 303(32) and (M^+)318, 119(100), 134(60), which have not been detected in any other analyzed *Thysananthus* species. In ecological respect, the samples of *T. comosus* are quite distinct. Sample 1 is from rock in coastal forest at the sea shore, whereas the other samples are from inland forests. We suggest that the deviating chemical composition of sample 1 might be due to stress, induced by the salt-spray environment. The same phenomenon is observed in the widespread holarctic *Conocephalum conicum* (L.) Dumort. which is made up of different geographical and chemical races. *Conocephalum conicum* type I is widely distributed while type II occurs in coastal locations (Wood *et al.*, 1996). GC-mass-spectrometric analysis of 280 samples of *C. conicum* revealed that type I elaborates (-)-sabinene as a major compound whereas type II produces large amounts of (+)-bornyl acetate (Toyota *et al.*, 1997). Kim *et al.* (2001) studied the phylogenetic relationships among the two chemotypes of *C. conicum* using *psbA* sequences. Their results showed that the *psbA* sequences of *C. conicum* type I and II are identical, suggesting that they are conspecific. These finding indicate that the detected chemical differences within *C. conicum* are environmentally controlled, as has been suggested by Asakawa (1995) and Harinantenaina & Asakawa (2004). In *T. comosus*, however, study of a larger number of samples is needed to corroborate the observed correlation between chemical constitution and habitat.

***Thysananthus convolutus* Lindenb.**

In all samples of *T. convolutus* relatively large amounts of isolepidozene (**3**) were detected. However, the samples from Malaysia (1-3) and Thailand (4, 5) are chemically different. Large amounts of the unidentified diterpenoid (M^+)302, 190(100), 81(95) were detected in the Malaysian samples whereas those from Thailand produce large amounts of (M^+)302, 81(100), 185(60), which was absent in the samples from Malaysia. The chemical dissimilarity of the samples of *T. convolutus* is reflected in the morphology, as the samples from Malaysia have entire leaves, whereas Thai samples have toothed leaves. *Thysananthus convolutus* is a polymorphic species with respect to the dentation of leaves, underleaves and female bracts, which varies from strongly dentate to edentate. The edentate form has been called *T. gottschei* (Jack & Steph.) Steph., which was reduced to a synonym of *T. convolutus* (Grolle & Piippo, 1984). Our data suggest that *T. gottschei* may have to be resurrected as a separate taxon. This taxonomic issue will be addressed in a more broadly-based, monographic study (Sukkharak, submitted).

***Thysananthus retusus* (Reinw. et al.) B. Thiers & Gradst.**

Pinguisane sesquiterpenoids are detected as major compounds in all 4 samples of *T. retusus*. The presence of α -pinguisene (**10**) and deoxopinguisone (**19**), reported earlier from *T. retusus* (under *T. fruticosus*) by Gradstein *et al.* (1985), is confirmed. Another abundant compound occurring only in this species is an unidentified diterpenoid (M^+)318, 81(100), 206(98). The chemical constitution of the samples of *T. retusus* is rather different from that of the other analyzed *Thysananthus* species. The chemical data are supportive of the classification of *Thysananthus* into 2 subgenera, subg. *Thysananthus* and subg. *Sandeanthus*, based on morphology (Thiers & Gradstein, 1989; Gradstein, 1992). *Thysananthus mollis* and *T. planus* Sande Lac. (= *T. retusus*) were earlier placed in section *Vittatae* by Verdoorn (1934), together with *Dendrolejeunea fruticosa* (= *T. fruticosus*), but this section was broken up by Thiers & Gradstein (1989). Morphologically, *Thysananthus mollis* and *T. retusus* share the presence of a vitta in the leaves and appendages on the leaf lobules (Sukkharak & Gradstein, 2010b). Chemically, however, the two species seem to be quite different, *T. mollis* being poor in sesquiterpenoids (Gradstein *et al.*, 1985).

***Thysananthus spathulistipus* (Reinw. et al.) Lindenb.**

In all analyzed samples of *Thysananthus spathulistipus* quite large amounts of isolepidozene (**13**) were found. Five from the seven samples produce pinguisane sesquiterpenoids. Samples 3 and 5, and also sample 1 (small amount), biosynthesize the

unidentified diterpenoid (M^+)318, 125(100), 81(38). Compounds (M^+)360, 81(100), 43(80), (M^+)360, 81(100), 43(90) and (M^+)374, 43(100), 81(58) are abundantly present in samples 4, 6 and 7. Sample 2 differs from the others by the presence of large amounts of compounds (M^+)302, 95(100), 81(82) and (M^+)320, 207(100), 81(83). The latter compound is also abundantly present in the Malaysian samples of *T. convolutus*. Morphologically, however, sample 2 fits *T. spathulistipus* as currently conceived. The data suggest that *T. spathulistipus* is chemically a rather variable species.

***Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout.**

The investigated sample of *Dendrolejeunea fruticosa* differs chemically from the analyzed *Thysananthus* species by the presence of the sesquiterpenoid alcohol guaia-6,9-dien-4 β -ol (**20**) and an unidentified diterpenoid (M^+)304, 271(100), 105(90) as the two most abundant components. Interestingly, fusicocca-2,5-diene (**37**) detected in all samples of *T. retusus* was also found in the sample of *D. fruticosa*.

CONCLUSIONS

The chemotaxonomic conclusions presented here are still preliminary. Noteworthy is the chemical heterogeneity of *Thysananthus convolutus*, which is congruent with the morphological variation in this species, viz. the dentation of leaves, underleaves and female bracts. In other instances, however, the chemical findings do not coincide with morphology. For instance, unidentified compound (M^+)302, 190(100), 81(95) was detected in *T. convolutus* and in *T. comosus* sample 1, and the unidentified (M^+)320, 207(100), 81(83) in *T. spathulistipus* sample 2 and Malaysian *T. convolutus* but not in other samples of these species. Furthermore, pinguisane sesquiterpenoids were only found in the morphologically very different species *T. retusus* and *T. spathulistipus*. The separation of *Dendrolejeunea* from *Thysananthus* was confirmed by the very different chemical composition of *Dendrolejeunea fruticosa* detected in this study. The results obtained in this study will be substantiated by isolation and identification of the detected unidentified compounds, which is in progress (Ludwiczuk, in prep.), and by molecular phylogenetic analysis of DNA markers and further morphological study (Sukkharak *et al.*, submitted).

ACKNOWLEDGEMENTS. The research of the first author was supported by a Royal Thai government scholarship in cooperation with the German Academic Exchange Service (DAAD). Thanks are due to S. Chantanaorrapint for additional fresh material and field observations.

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Table 1. Voucher information and sample number.

Taxon	Sample number	Geographical origin	Collection date	Voucher number and herbarium
<i>Thysananthus comosus</i> Lindenb.	1	Pangkor Island, Malaysia	4 Mar 2009	<i>Sukkharak 730</i> (BKF, GOET)
	2	Khao Luang National Park, Thailand	24 Feb 2009	<i>Chantanaorrapint s.n.</i> (PSU)
	3	Sri Pang Nga National Park, Thailand	12 Jul 2008	<i>Chantanaorrapint 2121</i> (PSU)
	4	Ton Nga Chang waterfall, Songkhla Province, Thailand	17 Aug 2009	<i>Inuthai s.n.</i> (PSU)
<i>Thysananthus convolutus</i> Lindenb.	1	Genting Highland, Malaysia	3 Mar 2009	<i>Sukkharak 717</i> (BKF, GOET)
	2	Genting Highland, Malaysia	3 Mar 2009	<i>Sukkharak 718</i> (BKF, GOET)
	3	Genting Highland, Malaysia	3 Mar 2009	<i>Sukkharak 720</i> (BKF, GOET)
	4	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 769</i> (BKF, GOET)
	5	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 803</i> (BKF, GOET)

<i>Thysananthus retusus</i> (Reinw. <i>et al.</i>) B. Thiers & Gradst.	1	San Yen, Khao Nan National Park, Thailand	19 Feb 2009	<i>Chantanaorrapint s.n.</i> (PSU)
	2	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 733</i> (BKF, GOET)
	3	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 741</i> (BKF, GOET)
	4	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 743</i> (BKF, GOET)
<i>Thysananthus spathulistipus</i> (Reinw. <i>et al.</i>) Lindenb.	1	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 739</i> (BKF, GOET)
	2	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 751</i> (BKF, GOET)
	3	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 752</i> (BKF, GOET)
	4	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 762</i> (BKF, GOET)
	5	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak 768</i> (BKF, GOET)

Chapter IV					
<i>Dendrolejeunea fruticosa</i> (Lindenb. & Gottsche) Lacout.	6	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak</i> 788 (BKF, GOET)	
	7	San Yen, Khao Nan National Park, Thailand	10 Mar 2009	<i>Sukkharak</i> 793 (BKF, GOET)	
	1	Sri Pang Nga National Park, Thailand	12 Jul 2008	<i>Chantanaorrapint</i> 2112 (PSU)	

Table 2. The distribution of the sesqui- and diterpenoids detected in the analyzed samples of *Thysananthus* species and *Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout. RRI - relative retention indices calculated against *n*-alkanes on HP-5MS column; tr – traces (<0.2%).

No	compounds	RRI	T. comosus				T. convolutus				T. retusus				T. spathulistipus							D. fruticosa																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																	
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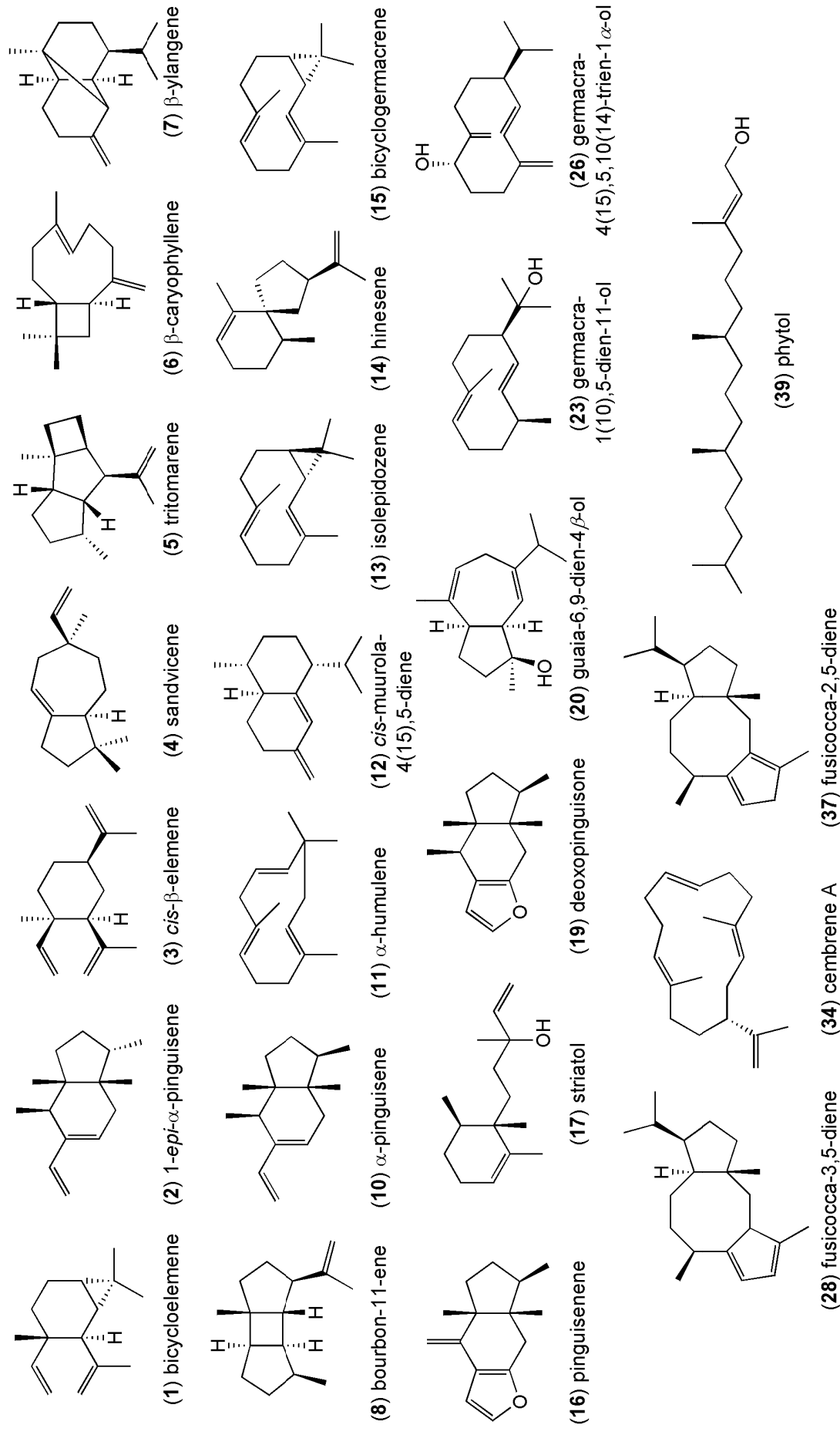


Figure 1. Chemical structure of sesquiterpenoids (1-8, 10-17, 19-20, 23, 26) and diterpenoids (28, 34, 37, 39) identified in selected *Thysananthus* species and *Dendrolejeunea fruticosa*.

Phylogeny, taxon circumscriptions and character evolution in the core Ptychanthoideae (Marchantiophyta: Lejeuneaceae)

Phiangphak Sukkharak¹, S. Robbert Gradstein² & Michael Stech³

¹ *Department of Systematic Botany, Institute of Plant Sciences, University of Göttingen, Untere Karaspüle 2, 37073 Göttingen, Germany*

² *Muséum National d'Histoire Naturelle, Dept. Systématique et Evolution, C.P. 39, 57 rue Cuvier, 75231 Paris cedex 05, France*

³ *Netherlands Centre for Biodiversity Naturalis, section NHN, Leiden University, P.O. Box 9514, 2300 RA Leiden, The Netherlands*

Author for correspondence: *Phiangphak Sukkharak, ppsukk@gmail.com*

Abstract Phylogenetic relationships and character evolution in the core Ptychanthoideae (Lejeuneaceae, Marchantiophyta) are assessed based on molecular (plastid *psbA-trnH*, *trnG*, *trnL-F*, *trnS-rps4*, nrITS), morphological-anatomical and phytochemical data. Generic relationships are molecularly well-resolved and confirm the placement of *Mastigolejeunea pancheri* and the monotypic *Dendrolejeunea fruticosa* in *Thysananthus*. Most morphological characters currently used to distinguish genera in Ptychanthoideae are homoplastic according to ancestral state reconstruction. Molecular (and phytochemical) data suggest the occurrence of polyphyletic species in *Thysananthus* and *Mastigolejeunea*. However, careful study of the polyphyletic taxa revealed morphological differences between some of the intraspecific clades, which correlated with synonymized or novel species. Incongruence between plastid and ITS data in *M. pancheri* indicated the occurrence of a putative hybrid, the first one recorded in Lejeuneaceae and the first in liverworts inferred from phylogenetic data.

Keywords Character evolution; cryptic species; hybrid; Lejeuneaceae; liverworts; molecular phylogeny; Ptychanthoideae; *Thysananthus*

Running head: Phylogeny of the core Ptychanthoideae

Category: Molecular Phylogeny

INTRODUCTION

With about 1200 species in 78 genera (Frey & Stech, 2009, with updates), Lejeuneaceae are by far the largest family of liverworts, and display an amazing

morphological and ecological diversity. Lejeuneaceae are a particularly important floristic component of tropical rain forests and include many species growing epiphyllous on the leaves of rainforest trees. Diversification started in the Mid-Cretaceous according to molecular dating (Wilson & al., 2007b, but see Yang & Wu, 2010) and took place in the shadow of angiosperm evolution, as has also been shown for other lineages of cryptogamic plants such as ferns (Schneider & al., 2004).

Phylogenetic reconstructions resulted in a better understanding of relationships and evolutionary patterns of major lineages within Lejeuneaceae (Gradstein & al., 2003; Wilson & al., 2007a, b). However, very few studies inferred phylogenetic relationships at lower taxonomic levels, aimed at clarifying species circumscriptions (Hartmann & al., 2006; Heinrichs & al., 2009) or the position of morphologically deviant taxa (Gradstein & al., 2006). A particularly pressing problem is the lack of stable morphological diagnostic characters to delimit generic and infrageneric groups, despite the high overall morphological diversity (Wilson & al., 2007a). Comprehensive molecular phylogenetic reconstructions at the inter- and intrageneric level as well as assessments of character evolution, e.g., by ancestral state reconstruction, are thus urgently needed.

This case study infers systematic relationships and character evolution in the molecularly well-supported core group of Lejeuneaceae subfamily Ptychanthoideae (*Dendrolejeunea*, *Lopholejeunea*, *Mastigolejeunea*, *Ptychanthus*, *Spruceanthus*, *Thysananthus*), with a focus on *Thysananthus*. The genus *Thysananthus* comprises eleven species (Sukkharak & Gradstein, 2010a, with updates), all of them epiphytes in tropical rain forests and montane forests. Southeast Asia forms a centre of diversity with five species: *T. aculeatus* Herzog, *T. comosus* Lindenb., *T. convolutus* Lindenb., *T. retusus* (Reinw. & al.) B. Thiers & Gradst. and *T. spathulistipus* (Reinw. & al.) Lindenb., the latter also occurring in tropical Africa. Four species are restricted to Western Melanesia (*T. discretus* Sukkharak & Gradst., *T. mollis* Steph., *T. appendiculatus* Steph., *T. montanus* Gradst. & al.), *T. anguiformis* (Hook.f. & Taylor) Steph. is endemic to New Zealand and *T. amazonicus* (Spruce) Schiffn. is the only species of the genus in the New World.

Thysananthus is morphologically heterogeneous (Gradstein, 1992) and the taxonomic significance of several characters considered diagnostic of the genus is unclear. As a consequence, different generic circumscriptions and intrageneric classifications have been evoked (e.g., Verdoorn, 1934; Thiers & Gradstein, 1989; Gradstein, 1992). For example, relationships between *Thysananthus*, *Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout. and *Mastigolejeunea* remain unclear based on morphology alone. Molecular data support their close relationship (Wilson & al., 2007a) but the limited sampling in the latter

study did not allow a definite conclusion. *Dendrolejeunea* stands out by its dendroid habit but shares with some *Thysananthus* species the prominent character of having a vitta (nerf-like structure of elongate cells) in the leaves. An enlarged dorsal stem epidermis has been utilized to distinguish *Mastigolejeunea* from *Thysananthus* (Thiers & Gradstein, 1989), which, however, does not seem to hold for all species (Hürlimann, 1991). These examples already illustrate the necessity of evaluating the phylogenetic significance of morphological-anatomical characters in Ptychanthoideae. Besides, novel or little known morphological characters such as appendages on leaf lobules or the adnation of underleaves to leaves (Sukkharak & Gradstein, 2010b) may improve taxon circumscriptions but their phylogenetic significance still needs to be tested.

Phylogenetic inference is often hampered by incomplete taxon sampling, caused by the difficulty of obtaining DNA sequences from old herbarium collections. In this study, however, we have been able to generate DNA sequence information from all currently recognized species of *Thysananthus*, covering almost the entire range of morphological variation within the genus, and from a representative species set of related genera. For the first time in Lejeuneaceae we analysed molecular data from five markers (plastid *psbA-trnH*, *trnG*, *trnL-F*, *trnS-rps4*, nrITS), morphological characters of all molecularly analysed specimens as well as phytochemical (terpenoid) data from selected *Thysananthus* species and *Dendrolejeunea fruticosa* comparatively in a phylogenetic framework. The principal objectives of this study are to (i) clarify generic circumscriptions and relationships within the core Ptychanthoideae, (ii) provide the first comprehensive molecular phylogeny of *Thysananthus* and infer inter- and intraspecific variation, and (iii) identify morphological synapomorphies for molecular clades and evaluate the phylogenetic significance and evolution of morphological characters.

MATERIALS AND METHODS

Plant material. — Selection of genera of Ptychanthoideae for molecular analysis was based on the molecular phylogenetic study of Lejeuneaceae by Wilson & al. (2007a). A total of 46 specimens representing 26 species were sequenced, including two of *Dendrolejeunea fruticosa*, two of *Lopholejeunea*, seven of *Mastigolejeunea*, two of *Ptychanthus striatus* (Lehm. & Lindenb.) Nees, three of *Spruceanthus*, 27 of *Thysananthus* and three of *Acrolejeunea* as outgroup representatives. *Mastigolejeunea pancheri* Steph., placed in *Thysananthus* by Hürlimann (1991), was maintained as a member of *Mastigolejeunea* because of its enlarged dorsal stem epidermis. Within *Thysananthus*, all eleven currently recognized species as well as different forms of variable species were sampled to represent the

morphological variation within the genus. Ten *trnL-trnF* and nine nrITS sequences were used from Wilson & al. (2007a), all other sequences were newly generated.

DNA extraction, PCR, and sequencing. — The distal parts of shoots from fresh and herbarium specimens were thoroughly cleaned with distilled water. Total genomic DNA was extracted using the DNeasy[®] Plant Kit (Qiagen). Protocols for PCR were carried out as described in previous publications: *psbA-trnH* spacer (Sang & al., 1997; Stech & Frey, 2008), *trnG* intron (Pacak & Szweykowska-Kulińska, 2000), *trnL-F* (Taberlet & al., 1991), *trnS-rps4* spacer (Nadot & al., 1994; Souza-Chies & al., 1997) and ITS (Stech, 2004; Hartmann & al., 2006). When no PCR product of the whole ITS1-5.8S-ITS2 region could be obtained, ITS1 and ITS2 were amplified and sequenced separately. PCR products were purified using the Wizard[®] DNA Clean-up kit (Promega). Automated sequencing was performed by MacroGen Inc., Amsterdam (www.macrogen.com). Sequencing primers were those used for PCR. Vouchers related to newly sequenced specimens are deposited in BKF and GOET. Voucher information and GenBank accession numbers for all sequences used in this study are given in Appendix 1.

Alignment, sequence analysis and phylogenetic reconstructions. — DNA sequences were manually aligned in PhyDE[®] v0.995 (Müller & al., 2006). Phylogenetic reconstructions according to the maximum parsimony (MP) optimality criterion were performed using PAUP 4.0b10 (Swofford, 2002). The datasets of chloroplast regions and ITS were analysed separately. Heuristic searches under parsimony were implemented using random sequence addition with 1000 replicates and employing the default settings otherwise. Gaps were either treated as missing data or coded as informative by a simple indel coding (SIC) strategy (Simmons & Ochoterena, 2000) as implemented in SeqState (Müller, 2004a). Heuristic bootstrap searches under parsimony were performed with 1000 replicates and 10 random addition cycles per bootstrap replicate with the same options in effect.

Posterior probabilities were calculated using MrBayes v3.1 (Huelsenbeck & Ronquist, 2001). TVM+G was chosen as the model that best fits the data according to the AIC criterion as evaluated by MrModeltest v2.3 (Nylander, 2004) employing MrMTgui (Nuin, 2005). In a second Bayesian analysis the indels coded by SIC were included, with sequence and indel data treated as separate and unlinked partitions, employing the restriction site model ('F81') for the indel matrix. The a priori probabilities supplied were those specified in the default settings of the program. Posterior probability (PP) distributions of trees were created using the Metropolis-coupled Markov chain (MCMC) method. Four runs with four chains (10^6 generations each) were run simultaneously, with the temperature of the single heated chain set to 0.2. Chains were sampled every 10 generations and the respective trees written to a tree

file. Consensus trees and posterior probabilities of clades were calculated by combining the four runs and using the trees sampled after the chains converged. Trace plots generated in Tracer v1.5 (Rambaut & Drummond, 2007) were used to check for convergence of the runs (plateaus of all runs at comparable likelihoods) and to infer the ‘burnin’, which approximately ranged between the first 150,000 and 200,000 generations (first 15,000–20,000 sampled trees). Consequently, the first 25,000 trees (25 %) were deleted by default to be sure that only trees of the stationary phase were included.

Analysis of phytochemical characters. — Sixty-six terpenoids obtained from 20 specimens of *Thysananthus* and *Dendrolejeunea fruticosa* (Sukkharak & al., in press) were included in the present study. A data matrix, which is available on request, was generated based on the presence or absence of the respective compounds in the 21 samples (0 = absent, 1 = present). This matrix was analysed with PAUP 4.0b10 according to the maximum parsimony principle (without outgroup). Heuristic bootstrap searches under parsimony were performed with 1000 replicates and 10 random addition cycles per bootstrap replicate.

Analysis of morphological-anatomical characters and character evolution. — For each of 46 specimens for which phytochemical and/or DNA sequence data was generated, three stems from the main axis were dissected and each stem analysed at 5–10 mm from the apex. Both quantitative and qualitative (discrete) characters were recorded. We used 5 quantitative and 25 qualitative morphological-anatomical characters (Appendices 2–3) for phylogenetic analysis of the respective 46 specimens. Of these, 28 characters were coded as binary characters (0/1) and two as multistate ones (0, 1, and 2). The respective character states for ‘sexual condition’, ‘male bract lobules’, ‘female bract margin’, ‘female bracteole margin’, ‘perianth margin’, ‘number of beak cells’, ‘number of perianth keels’ and ‘subfloral innovation’ could only be recorded from fertile specimens; in sterile specimens missing data was indicated by ‘?’. Maximum parsimony analyses were performed in PAUP 4.0b10 for (i) all 30 characters and (ii) those 22 characters that could be scored from sterile plants and were thus available from all included specimens. Heuristic bootstrap searches under parsimony were performed with 1000 replicates and 10 random addition cycles per bootstrap replicate. To search the trees pace for islands of more parsimonious trees, parsimony ratchet analyses were performed with PRAP2 (Müller, 2004b) in combination with PAUP, employing the default options (200 iterations, 25% of randomly chosen positions upweighted to 2) and superimposed 10 random addition cycles.

To infer patterns of character evolution, we traced the evolution of the 30 morphological characters (Appendices 2–3) over the plastid DNA phylogeny by parsimony-based ancestral state reconstruction, using Mesquite v.2.71 (Maddison & Maddison, 2009).

The plastid dataset was chosen because it resolved the two *Mastigolejeunea pancheri* samples in one clade (cf. results and discussion). The sample of *Thysananthus appendiculatus* was not included in the ancestral state reconstruction as no plastid sequences could be obtained. To account for topological uncertainty we used the ‘trace character history’ option in Mesquite.

RESULTS

Sequence characterization and alignment. — Length ranges of the sequenced markers were 179–194 nucleotides (nt) (186–194 nt within *Thysananthus*) for *psbA-trnH* spacer, 658–684 nt (647–684) for *trnG* intron, 405–435 nt (424–435) for *trnL-F*, 612–658 nt (612–627) for *trnS-rps4* and 950–1130 nt (950–1059) for ITS. For *Mastigolejeunea pancheri* sample 2 and *T. appendiculatus* only ITS1 could be sequenced of the ITS region.

The combined plastid alignment comprised 2077 positions (*trnS-rps4* position 1–668, *trnL-F* 669–1124, *trnG* 1125–1869, *psbA-trnH* 1870–2076). Of the 2077 included characters, 318 (15.3%) were variable, and 218 (10.5%, or 68.6% of the variable positions) were parsimony-informative. Simple indel coding (SIC) yielded another 495 parsimony-informative characters, resulting in 713 informative characters for the plastid markers in total. The ITS alignment comprised 1786 positions. The almost invariable 5.8S gene and 615 ITS positions with ambiguous alignment were excluded from phylogenetic analysis. Of the remaining 1008 included positions, 389 (38.6%) were variable, and 271 (26.9%, or 69.7% of the variable positions) were parsimony-informative. Inclusion of indel characters by SIC yielded another 548 parsimony-informative characters, resulting in 819 informative characters for ITS in total.

Molecular phylogenetic reconstructions. — Separate maximum parsimony analyses of the plastid versus nuclear sequence data (including indels) each retained a single most parsimonious tree (cp: length 482, CI excluding uninformative characters 0.6929, RI 0.8699, RC 0.6587; ITS: length 931, CI excluding uninformative characters 0.4856, RI 0.7428, RC 0.4157). Bayesian analyses of the plastid and ITS data resulted in the same topologies as the respective MP trees. While all trees were generally congruent with respect to well-supported clades, incongruence between the plastid and ITS analyses was observed concerning the position of *Mastigolejeunea pancheri* sample 2. The plastid analyses resolved both *M. pancheri* samples as a well-supported sister clade of *Thysananthus anguiformis* (Fig. 1), whereas in the ITS trees *M. pancheri* sample 2 was placed inside *Thysananthus* s.str. in a clade together with *T. appendiculatus* and *T. discretus* (Fig. 2).

All trees support a basal position of *Lopholejeunea* within the ingroup (Figs. 1, 2), followed by *Ptychanthus striatus* as sister to *Spruceanthus*. These clades (except

Spruceanthus) as well as *Mastigolejeunea* s.str. as sister to the remainder of the ingroup receive significant support in most Bayesian and maximum parsimony analyses. Within *Mastigolejeunea* s.str., the samples of *M. auriculata* (Wils.) Schiffn. are separated into two clades. The species of *Thysananthus* are resolved into two major clades, which also include *Dendrolejeunea fruticosa* and *M. pancheri*. The basal split between the vittate species (*T. mollis*, *T. montanus*, *T. retusus*, *D. fruticosa*) and a clade including *T. anguiformis*-*M. pancheri* (one or both samples, cf. above) as well as the remaining *Thysananthus* species (*T. s.str.*) received significant support, whereas their sistergroup relationship is not supported. Within *Thysananthus* s.str., *T. comosus* sample 4 is resolved as basal with significant support in the ITS analyses, whereas the remaining accessions of *T. comosus*, *T. convolutus* and *T. spathulistipus* are resolved as polyphyletic.

Analysis of phytochemical characters. — The maximum parsimony calculation of the phytochemical matrix (66 characters, of which 52 were parsimony informative) yielded two trees (lengths 167, CI excluding uninformative characters 0.559, RI 0.935, RC 0.560), one of which is shown in Fig. 3. The second tree differs only in the samples *T. retusus* I–III being unresolved as a polytomy. The phytochemical data resolve two clades of *T. convolutus* (samples I–III and IV+V, respectively), two of *T. spathulistipus* (samples I+III and IV+VI+VII, respectively), one clade with two out of four *T. comosus* samples (I+II) and one clade holding all four *T. retusus* samples with bootstrap support >80 %.

Analyses of morphological-anatomical characters and character evolution. — In the maximum parsimony analyses of morphological-anatomical characters, 10,000 trees were retained each with lengths of 100 (all 30 characters) or 77 (22 selected characters), respectively. Applying the parsimony ratchet, 153 or 102 trees were retained, with lengths of 94 (all characters) or 72 (selected characters), respectively. For all most parsimonious reconstructions the CI was <0.4, RI approx. 0.75 and RC <0.3. The trees (not shown) were almost unresolved with a basal polytomy. Only few specimens formed distinct clades (*Lopholejeunea* spp., *Thysananthus mollis*/*T. montanus*, specimens of *Dendrolejeunea*, *Ptychanthus*, *T. anguiformis* and *T. retusus*), and only three of them received bootstrap support >70% (*Dendrolejeunea*, *Ptychanthus*, *T. retusus*).

Parsimony-based ancestral state reconstruction of the 30 morphological-anatomical characters revealed a single state change for five characters (1, 13, 16, 29, 30), viz. branch type (from *Lejeunea*-type to *Frullania*-type in *Ptychanthus striatus*; Fig. 4A), foliar appendages on lobule bases (present in *Thysananthus mollis*, *T. montanus* and *T. retusus*; Fig. 4D), vitta (present in *T. mollis*, *T. montanus*, *T. retusus* and *Dendrolejeunea fruticosa*; Fig. 4E), number of perianth keels (3 in *Dendrolejeunea fruticosa*, *Mastigolejeunea* and

Thysananthus s.l.; Fig. 4I) and subfloral innovations (present in all ingroup taxa except *Lopholejeunea*; Fig. 4J). Three of these characters (1, 13, 30) received individual RC values of 1 in the phylogenetic reconstructions, the other two had values of 0.429 and 0.438, respectively. For character 2, also with an RC of 1, two independent state changes from projecting to dendroid growth are indicated (in *Ptychanthus* and *Dendrolejeunea*; Fig. 4B), and for character 5 (RC 0.615) one change from state 1 (stem hyalodermis present) to states 0 or 2 in the ancestor of all ingroup taxa except *Lopholejeunea* (Fig. 4C) is inferred. For all other 23 characters at least three different state changes, including reversals, are needed to explain the patterns, as exemplarily shown for characters 20 (adnate underleaves; Fig. 4F), 25 (female bracts; Fig. 4 G) and 26 (female bracteoles; Fig. 4H).

DISCUSSION

Phylogenetic relationships, generic circumscriptions and character evolution in the core Ptychanthoideae. — The positions of *Lopholejeunea*, *Ptychanthus striatus*, *Spruceanthus*, *Mastigolejeunea* s.str. (excluding *M. pancheri*) and the remainder of the ingroup in our results are congruent with the molecular phylogenetic reconstructions of Lejeuneaceae by Wilson & al. (2007a). *Lopholejeunea* is resolved at the base of the ingroup. It is distinguished from the other genera by a combination of character states including dark pigmentation of cell walls, a discrete hyalodermis (Fig. 4C), strongly inflated-gibbose lobules, absence of subfloral innovations (Fig. 4J), and perianths with 4–5 sharp, dentate-laciniate (rarely entire) keels (Fig. 4I). Most of these character states, however, occur also in the outgroup (stem hyalodermis, absence of subfloral innovations) or in other clades of the ingroup (e.g., toothed perianth margins in *Thysananthus* s.l.). Synapomorphic character states for *Lopholejeunea* are missing.

Ptychanthus striatus is resolved as sister to *Spruceanthus* from which it differs morphologically by *Frullania*-type branching (Fig. 4A), dendroid habit (Fig. 4B), presence of auricles at underleaf bases, and elongate leaf cells. Similar to *Lopholejeunea*, most of these character states occur in other core Ptychanthoideae taxa as well, except for *Frullania*-type branching. No morphological synapomorphies could be detected for the *Ptychanthus*-*Spruceanthus* clade.

Mastigolejeunea is traditionally characterised by the enlarged dorsal stem epidermis, separating it from *Thysananthus* which has epidermal cells as large as medulla cells (Thiers & Gradstein, 1989). Our results (Fig. 4C) revealed that the enlarged epidermis stem evolved at least twice, in *Mastigolejeunea* s.str. and in the *M. pancheri*-*T. anguiformis* clade.

Mastigolejeunea s.str. can at the moment only be unambiguously characterised based on molecular sequence data.

Thysananthus also includes *Dendrolejeunea fruticosa* and *Mastigolejeunea pancheri* according to the molecular phylogenetic reconstructions (Figs. 1, 2). The frequently changing placement of *D. fruticosa*, either in *Dendrolejeunea* (Spruce, 1884; Lacouture, 1908; Gradstein, 1992) or in *Thysananthus* (Schiffner, 1893; Verdoorn, 1934; Thiers & Gradstein, 1989) reflects an obvious uncertainty about the systematic value of morphological characters, in particular the growth habit. *Thysananthus* shares with most other Ptychanthoideae the ancestral state of projecting growth and irregularly pinnate branches (Fig. 4B), whereas *Dendrolejeunea* stands out by its dendroid habit, having creeping stoloniform stems and upright, regularly pinnate branches. Dendroid growth, however, developed independently in *Ptychanthus striatus* (Fig. 4B). The clade of *D. fruticosa*, *T. mollis*, *T. montanus* and *T. retusus*, in contrast, is easily recognized by the presence of a vitta as a synapomorphic character state (Fig. 4E), and corresponds to one of the three *Thysananthus* sections (sect. *Vittatae*) by Verdoorn (1934). Besides, *D. fruticosa* shares with all *Thysananthus* species the character state of 3 perianth keels (Fig. 4I). Consequently, *D. fruticosa* is treated as a member of *Thysananthus* (*T. fruticosus* (Lindenb. & Gottsche) Schiffn.) in the light of the present molecular data and character state reconstructions. *Thysananthus fruticosus* and the other vittate species in the genus (*T. mollis*, *T. montanus*, *T. retusus*) can be regarded as morphologically advanced, the former due to its dendroid growth and the latter because of the presence of foliar appendages on lobule bases (Fig. 4D).

In contrast to *Thysananthus fruticosus*, *Mastigolejeunea pancheri* has always been separated from *Thysananthus* by its entire female involucre and enlarged dorsal epidermis in stem cross-section (Thiers & Gradstein, 1989; but see Hürlimann, 1991). Our results, however, reveal that these characters are not suitable to separate *M. pancheri* from *Thysananthus*, and confirm the placement of *M. pancheri* in *Thysananthus* by Hürlimann (1991), as *T. pancheri* (Steph.) Hürl. In accordance with traditional usage and Figures 1–4, the species is referred to as *M. pancheri* in this paper. The molecularly well-supported sister-group relationship of the *T. anguiformis*-*M. pancheri* and *Thysananthus* s.str. clades is supported by the presence of adnate underleaves (Fig. 4F). In its current circumscription, synapomorphic character states for *Thysananthus* are missing.

‘Cryptic’ species in *Thysananthus* and *Mastigolejeunea*. — Within *Thysananthus* s.str., *T. comosus*, *T. convolutus* and *T. spathulistipus* were resolved as polyphyletic. This result seems to indicate a higher genetic than morphological variation, resulting in cryptic speciation which is increasingly being demonstrated in bryophytes (e.g., Shaw, 2000; Shaw &

Allen, 2000; Feldberg & al., 2004, 2010; Stech & Dohrmann, 2004; Stech & Wagner, 2005; Heinrichs & al., 2009, 2010; Kreier & al., 2010). However, morphological scrutiny of the samples of the “polyphyletic” species revealed that some of the intraspecific molecular clades fitted with formerly recognized species treated as synonyms, or with novel taxa. For example, *T. convolutus* samples 2 and 5 were resolved in a well-supported clade separate from other *T. convolutus* samples. This separation is reflected in the morphology, samples 2 and 5 having entire instead of toothed leaves. Plants of *T. convolutus* with entire or toothed leaves are also separated phytochemically (Fig. 3). The samples with entire leaves fit with the formerly recognized *T. gottschei* (Jack & Steph.) Steph., which was reduced to synonymy under *T. convolutus* and considered the edentate form of the latter (Grolle & Piippo, 1984). Our molecular results, however, indicate that *T. gottschei* should be re-instated at the species level.

A similar case is seen in the sister genus *Mastigolejeunea*. Accessions of *M. auriculata* (Wils.) Schiffn. from Malaysia (sample 1) and southern USA (sample 2) were not in the same clade, which was also observed by Wilson & al. (2007a) based on specimens from Indonesia and Bolivia. The molecular evidence of Wilson & al. (2007a) and the present study suggests that the Asiatic and neotropical populations of *M. auriculata* represent different taxa. The plants from Malaysia and Indonesia have rather short, broad and flat leaves, a transverse lobule apex not or shortly continuing into the ventral lobe margin, and curved flagelliform branches on the older portions of the stem. Leaves of the plants from USA and Bolivia, in contrast, are much more elongate and strongly convex to subsquarrose, the lobule apex is oblique and longly continuing into the ventral lobe margin, and flagelliform branches are absent. In addition, perianths of Asiatic plants are large and the ventral keels are as large as the lateral keels, in contrast to much smaller perianths with ventral keels much less pronounced than the lateral ones in the neotropical plants. The Asian populations of *M. auriculata* were originally described as *M. humilis* (Gottsche) Schiffn.; later taxonomic work (e.g., Gradstein & Inoue, 1980) suggested that *M. humilis* cannot be sharply separated morphologically from *M. auriculata*, described from the Neotropics. Our molecular results, however, clearly support the recognition of the Asiatic *M. humilis* as a separate species.

Thysananthus comosus sample 4, which was also sequenced by Wilson & al. (2007a), is separated from other accessions of *T. comosus* in the present analyses. Morphological re-examination of this specimen shows that it differs from typical *T. comosus* by its enlarged dorsal epidermis, entire leaves and underleaves, elongate lobule teeth 4–6 cells long (0–2 cells long in typical *T. comosus*), and underleaf bases only occasionally connate with leaves. *Thysananthus comosus* sample 4 shares several characters with the other *Thysananthus* s.str. taxa (toothed female involucre and perianths) and with the *T. anguiformis*-*M. pancheri* clade

(stem with enlarged dorsal epidermis), which supports its position in the molecular trees as an evolutionary link between these two groups. Elongate lobule teeth 4–6 cells long, in contrast, possibly evolved independently in *T. comosus* sample 4 and in *T. retusus* according to the phylogenetic reconstructions. The unique combination of morphological character states of *T. comosus* sample 4 clearly supports its separation from the remaining specimens in the molecular phylogenetic reconstructions. Consequently, this specimen should be described as a new species (Sukkharak, submitted).

The phytochemical data indicate further intraspecific variation in *T. comosus*, since samples I+II are resolved in a well-supported clade separated from samples III+IV (Fig. 3). Samples I+II originate from inland forest habitats, whereas sample III was collected from rock in coastal forest, and sample IV grew near a torrential waterfall. The different chemical composition of samples III+IV might thus possibly be due to stress induced by salt spray or the harsh aquatic environment, respectively. Similar environmental effects on chemical composition have been reported from other liverwort species (cf. Asakawa, 1995; Harinantenaina & Asakawa, 2004). Whether the two phytochemical and ecological types of *T. comosus* groups represent different genotypes needs to be tested with molecular data.

Hybridization in bryophytes and the first example in Lejeuneaceae. — Phylogenies constructed from the nuclear ribosomal ITS and plastid sequence data were incongruent concerning the placement of *Mastigolejeunea pancheri* sample 2. In the cpDNA phylogeny (Fig. 1), *M. pancheri* sample 2 is sister to *M. pancheri* sample 1, and both samples are placed in a well-supported clade with *T. anguiformis*. In contrast, in the nuclear ITS tree (Fig. 2), *M. pancheri* sample 2 is sister to the *T. appendiculatus*-*T. discretus* clade with significant support. As *M. pancheri* is morphologically well separated from *T. appendiculatus* and *T. discretus* (e.g., by the enlarged stem epidermis; Fig. 4C), the ITS phylogeny is probably the deviating one, whereas the plastid phylogeny concurs with the current species circumscription. *Mastigolejeunea pancheri* sample 2 is morphologically most similar to *M. pancheri* sample 1, but differs from the latter by larger plants (70–75 mm wide in contrast to 48–57 mm in *M. pancheri* sample 1).

Incongruent gene phylogenies can either reflect complex phylogenetic patterns or simply highlight methodological or stochastic errors, or poorly supported data (Wendel & Doyle, 1998; McBreen & Lockhart, 2006; Frajman & al., 2007; Harris, 2008; Rautenberg & al., 2008). Sequencing errors can be rejected as a cause of the incongruence in *M. pancheri*, as the sequences were verified by repeated DNA extractions as well as multiple PCR and sequencing reactions. Besides, the incongruence is obviously not a result of different analysis

methods, since the same pattern was found with significant support in both MP and Bayesian reconstructions.

Biological processes leading to incongruent gene phylogenies are manifold and include both intra-lineage (e.g., mistaken orthology due to gene duplications) and inter-lineage events, such as incomplete lineage sorting of alleles, or homo- or polyploid hybridization (e.g., Wendel & Doyle, 1998; Rautenberg & al., 2008). Distinguishing between these phenomena is difficult based on phylogenetic evidence alone (e.g., Gómez-Zurita & Vogler, 2006; Harris, 2008). One way to decide between incomplete lineage sorting or hybridization is to compare the divergence times of the conflicting nodes (Rautenberg & al., 2008). If the age of the respective node is older in the organismal tree than in the deviating one, incomplete lineage sorting can be rejected and hybridization accepted. The single dated phylogeny of Lejeuneaceae (Wilson & al., 2007b) includes only few representatives of *Thysananthus* and *Mastigolejeunea*, however, we can hypothesize that the position of *M. pancheri* sample 2 in the plastid tree concerns an older node than its position in the ITS tree. The split of *T. anguiformis* and *Thysananthus* s.str. was dated c. 17 Mya (Wilson & al., 2007b), whereas the common ancestor of *T. convolutus* and *T. spathulistipus* in their study (corresponding to *T. convolutus* sample 4 and *T. spathulistipus* sample 5 in the present study) is dated c. 3 Mya. The clade of *T. appendiculatus* and *T. discretus* must then be even younger, which would also hold for *M. pancheri* sample 2 if the ITS tree would represent the organismal phylogeny. Together with the larger plant size, these considerations provide first evidence that *M. pancheri* sample 2 is probably of hybrid origin. Given the maternal inheritance of plastids in bryophytes, *M. pancheri* should be considered the maternal parent of *M. pancheri* sample 2, whereas either *T. appendiculatus* or *T. discretus* is probably the paternal parent of the hybrid. However, further analyses including chromosome counts are necessary to test the hybridization hypothesis and to determine possible polyploidy of *M. pancheri* sample 2. Inference from a more detailed dated phylogeny of Ptychanthoideae may confirm the putative young age of the hybridization event.

Hybridization is a major factor leading to phylogenetic incongruence among different datasets in angiosperms (Mason-Gamer & Kellogg, 1996; Nishimoto & al., 2003; Winkworth & Donoghue, 2005; McBreen & Lockhart, 2006; Kim & Donoghue, 2008). In bryophytes, several molecular studies based on allozyme data reported (putative) hybridization in mixed populations of related species, and hybrid speciation via allopolyploidy. Most cases were observed in the moss families Sphagnaceae (peatmosses) (e.g., Cronberg, 1996; Cronberg & Natcheva, 2002; Sæstad & al., 1999, 2000), Bryaceae (Shaw, 1994), Mniaceae (e.g., Wyatt & al., 1992, 1993a, 1993b) and Polytrichaceae (Derda & Wyatt, 2000), but there are also reports

from liverwort families, viz. Pelliaceae (Odrzykoski & al., 1996), Aytoniaceae (Boisselier-Dubayle & al., 1996), Plagiochilaceae (Newton, 1986) and Porellaceae (Boisselier-Dubayle & al., 1998).

Incongruence between phylogenies based on DNA sequences have been observed much more rarely in bryophytes, and usually concern plastid versus nuclear ribosomal DNA. Again, cases were found in the moss families Sphagnaceae (Shaw & Goffinet, 2000; Shaw & al., 2005), and Mniaceae (Harris, 2008), but also in Funariaceae (McDaniel & al., 2009). The case of *Plagiomnium medium* (B.S.G.) Kop. (Harris, 2008; Wyatt & al., 1988) might be comparable with *M. pancheri*: the hybrid origin of *P. medium* was reflected by its incongruent placement as sister to *P. insigne* (Mitt.) Kop. (plastid data) versus *P. ellipticum* (Brid.) Kop. (nuclear data), the former species probably representing the maternal parent of *P. medium*, based on plastid DNA restriction fragment patterns (Wyatt & al., 1988).

Our findings in *Mastigolejeunea pancheri* constitute the first report of a putative hybrid in Lejeuneaceae, the largest liverwort family, and the first case of putative hybridization in the liverworts inferred from incongruence of plastid versus nuclear data.

CONCLUSIONS

The new molecular evidence has provided a solid basis for inferring systematic relationships and taxon circumscriptions in the core Ptychanthoideae, and for determining the phylogenetic significance of morphological-anatomical characters in this group. The generally high molecular variability of non-coding DNA markers in liverworts (e.g., Quandt & Stech, 2005) provides sufficient variation for well-resolved and supported phylogenetic reconstructions, which are generally congruent between the employed plastid markers and nrITS except in the putative hybrid specimen of *M. pancheri*. As a general pattern, the genera of the core Ptychanthoideae are characterised more clearly by molecular data than by morphological characters. Only five character states were resolved as synapomorphic for single clades by ancestral state reconstruction (*Frullania*-type branching, appendages on lobule bases, presence of a vitta, 3-keeled perianths, presence of subfloral innovations; Fig. 4). In contrast, the majority of morphological characters traditionally used to distinguish between genera in Ptychanthoideae (Gradstein, 1994), including leaf characters such as leaf position, leaf shape and dentation of leaf margins, are homoplastic to different degrees. Our results indicate that genera within Ptychanthoideae may be distinguished by a combination of molecular data and non-exclusive morphological-anatomical character states. Recent evidence, furthermore, indicates that a search for new morphological characters may be worthwhile. For example, adnate underleaves are very rare in the order Porellales

(Frullaniaceae, Lejeuneaceae, Porellaceae, etc.) but were recently shown to be a common feature in *Thysananthus* (Sukkharak & Gradstein, 2010b; Fig. 4F). The presence of appendages at lobule bases is another example of a phylogenetically significant new morphological characters (Sukkharak & Gradstein, 2010b), being resolved as synapomorphic for the *T. mollis*-*T. montanus*-*T. retusus* clade (Fig. 4D).

At the intraspecific level, the present study revealed high molecular diversity within *Thysananthus*, which is in accordance with the results of a growing number of molecular studies of liverworts and mosses (see above). In *Thysananthus*, however, this intraspecific diversity appeared to be less ‘cryptic’ than in other bryophyte taxa, as some molecular clades fitted quite well with novel or synonymized taxa recognized previously as separate species. The molecular evidence was effective in the resurrection of these synonyms as separate species. Again, a combination of molecular and morphological data appears most effective to clearly delimit such taxa. Similar to the liverwort genera *Plagiochila* (e.g., Heinrichs & al., 2000, 2004; Rycroft & al., 2004) and *Radula* (Figueiredo & al., 2009; Stech & al., 2010), phytochemical data also appear to be of some taxonomic value in Lejeuneaceae and may contribute as a third independent dataset, which needs to be further evaluated.

ACKNOWLEDGEMENTS

The research of the first author was supported by a Royal Thai government scholarship in cooperation with the German Academic Exchange Service (DAAD). We thank C. Gehrig-Downie and S. Chantanaorrapint for additional fresh material. Thanks are also due to M.C.M. Eurlings and the staff of DNAMarkerpoint (Leiden University) for technical assistance and to J.-P. Frahm, I. Haerida, T. Hallingbäck, B.C. Ho, S. Kornochalart, T. Peng, R.P. Shi, Y.M. Wei and R.-L. Zhu for photographs.

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Fig. 1. Majority rule Bayesian phylogram inferred from the combined chloroplast dataset including differences in sequence lengths (indels). Branch thickness and color indicate bootstrap support and posterior probability values. BPP = posterior probability values from Bayesian analysis, in which gaps treated as missing data; BPPSIC = posterior probability values from Bayesian analysis, in which gaps treated as informative by a simple indel coding strategy; MPB = bootstrap support values from the maximum parsimony optimality criterion, in which gaps treated as missing data; MPBSIC = bootstrap support values from the maximum parsimony optimality criterion, in which gaps treated as informative by a simple indel coding strategy. For further explanation see text.

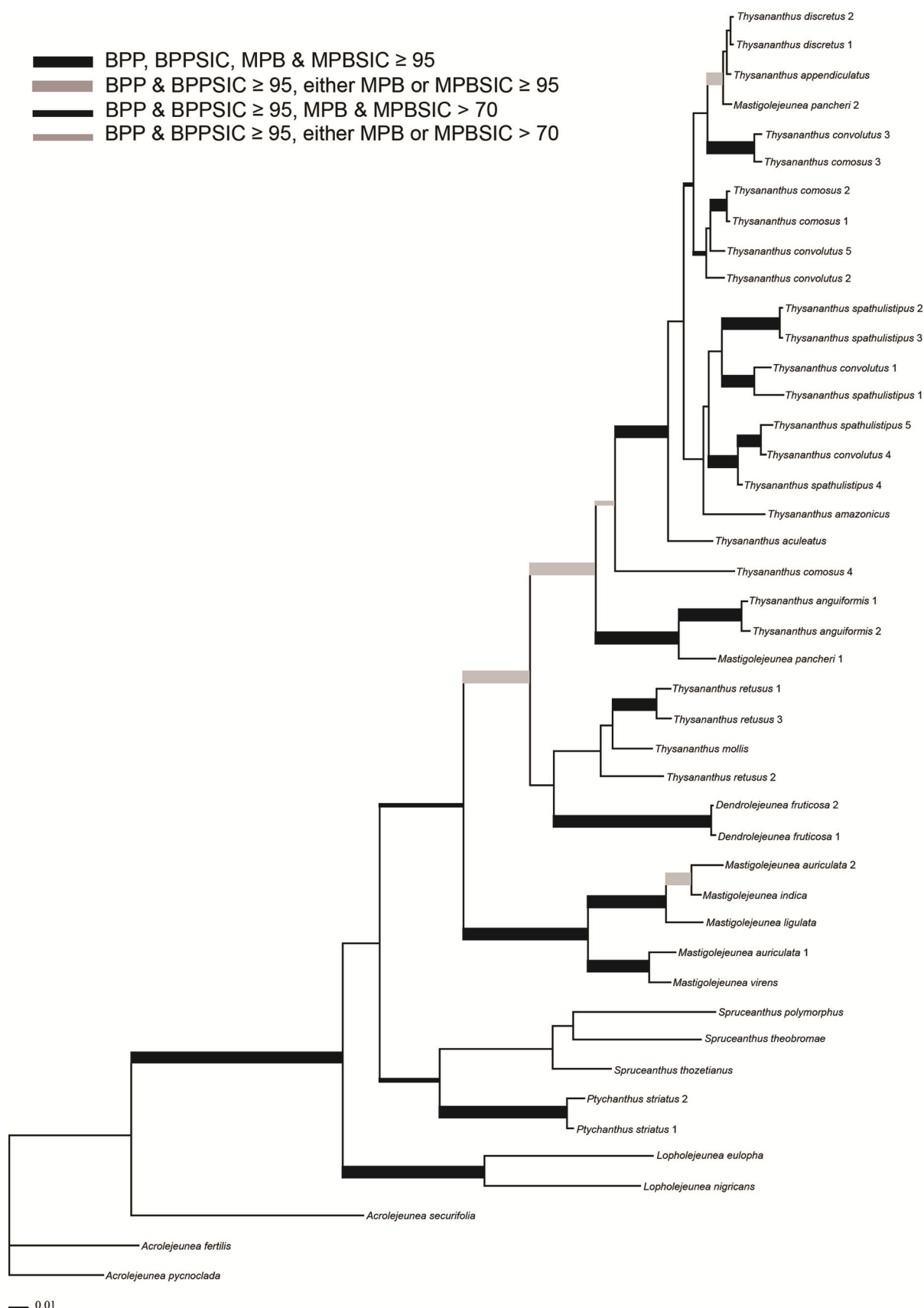


Fig. 2. Majority rule Bayesian phylogram inferred from the ITS dataset. For further explanation see Fig. 1.

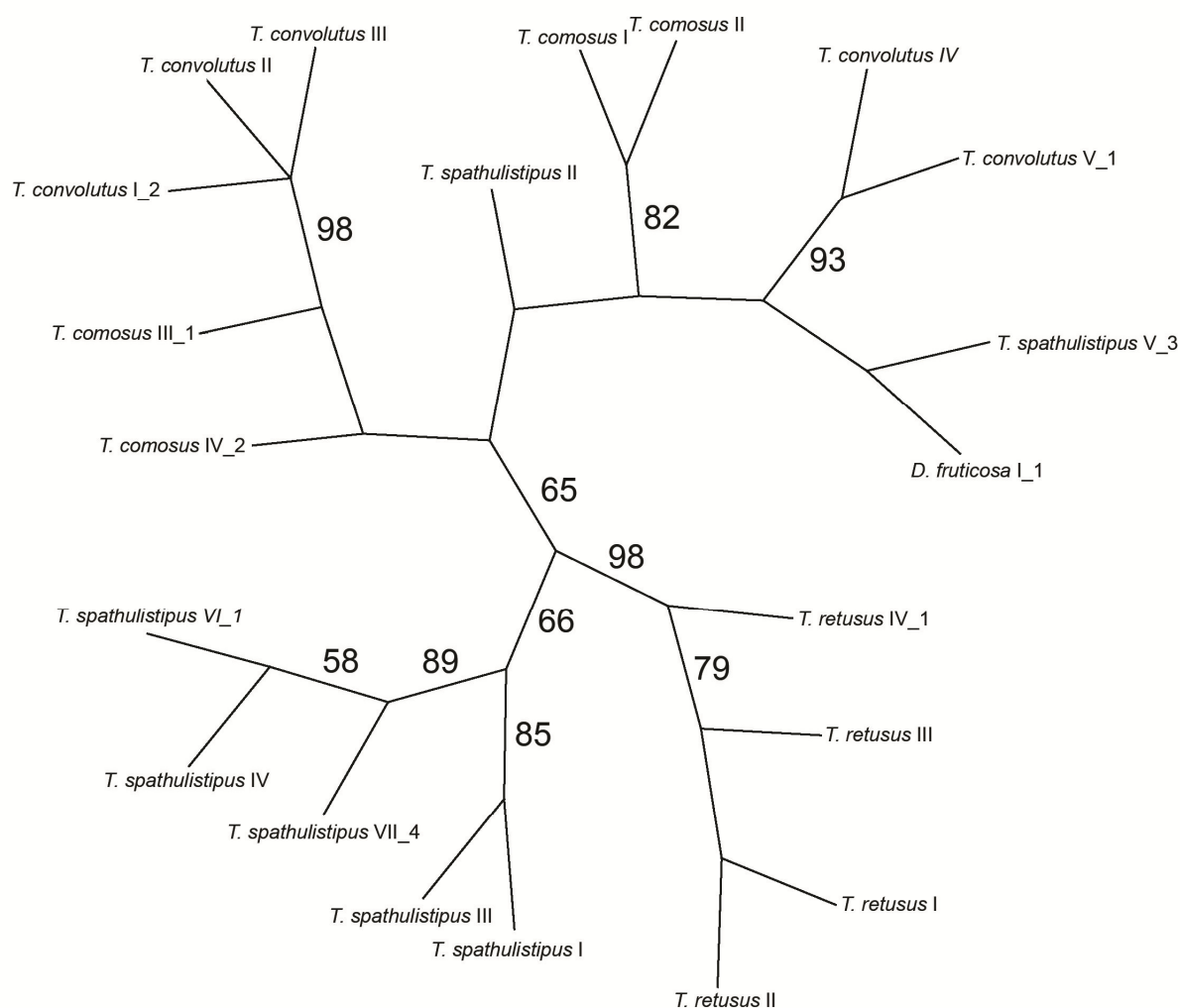


Fig. 3. Strict consensus maximum parsimony tree inferred from phytochemical (terpenoid) characters of *Dendrolejeunea fruticosa* and four species of *Thysananthus*, without outgroup. The Roman numerals after the taxon name refers to the phytochemistry voucher (Sukkharak et al., in press) and the arabic ones refers to the molecular voucher (this study). Bootstrap support values $\geq 50\%$ are given at the branches.

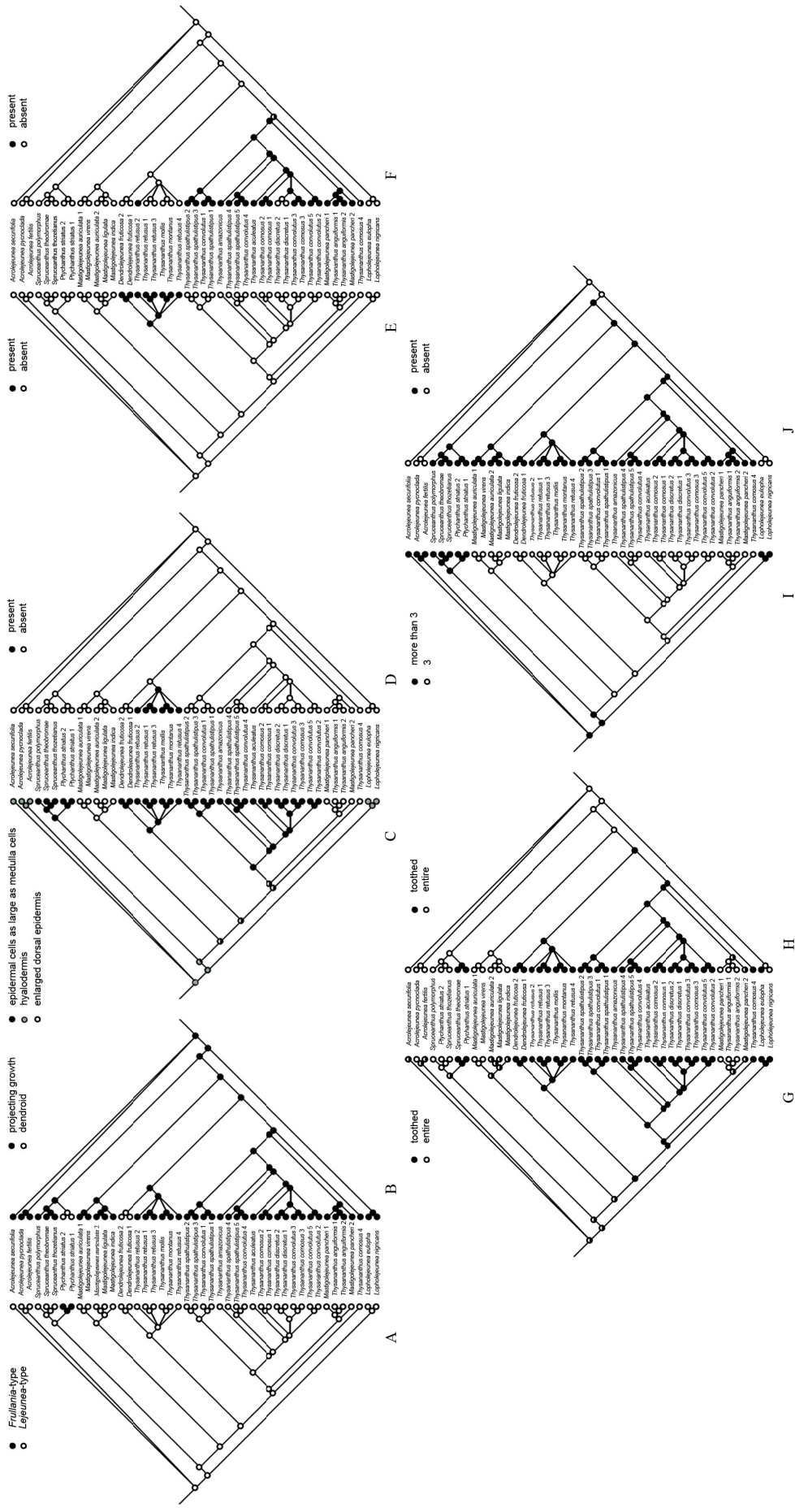


Fig. 4. Parsimony-based ancestral state reconstruction of ten selected morphological-anatomical characters. **A**, branch type; **B**, growth habit; **C**, stem type; **D**, appendages on lobule bases; **E**, vitta; **F**, adnate underleaves; **G**, female bracts; **H**, female bracteoles; **I**, number of perianth keels; **J**, subfloral innovation. For description of character states see Appendix 2.

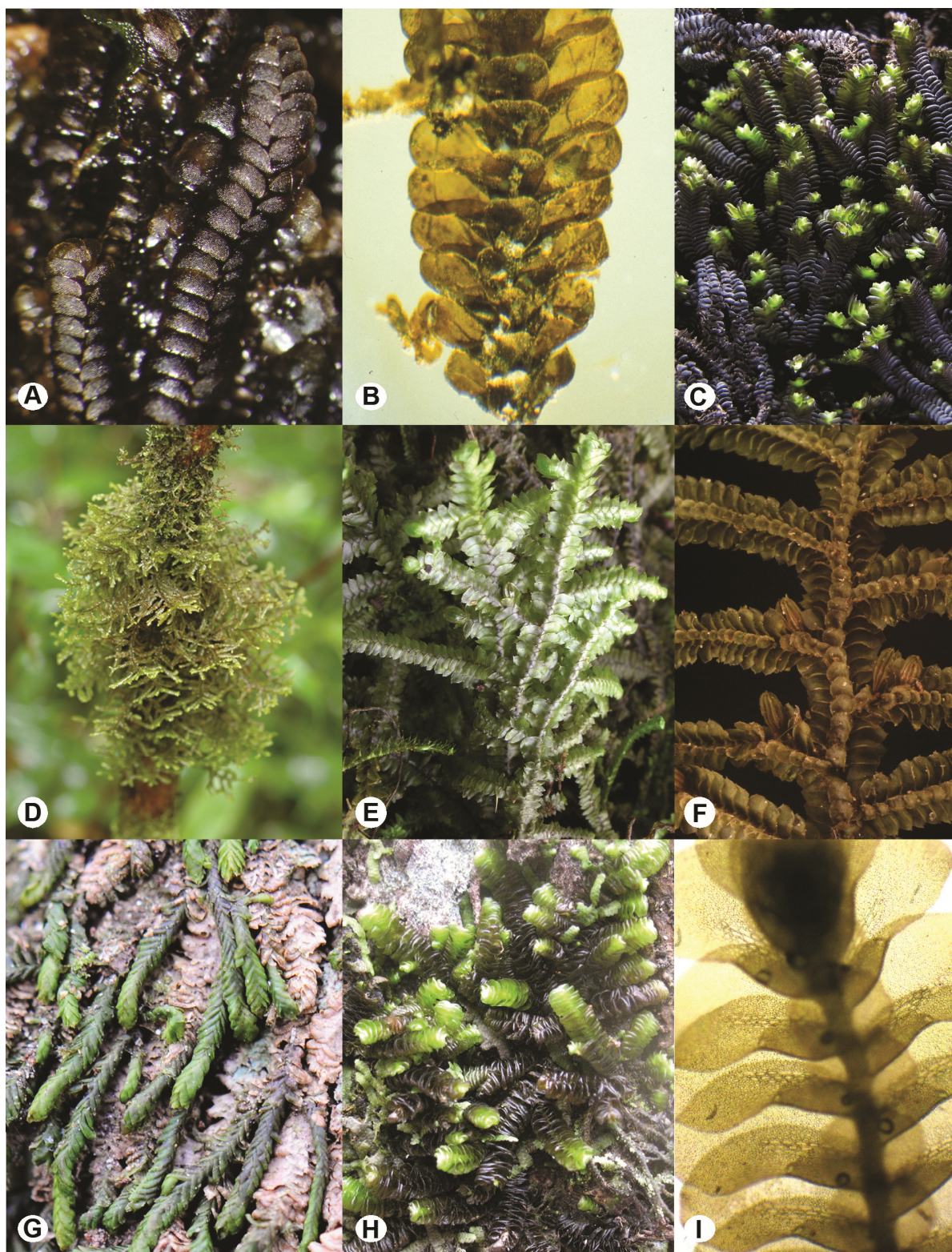


Fig. 5. Representatives of the core Ptychanthoideae. **A**, *Lopholejeunea subfusca* (Nees) Schiffn.; **B**, *Mastigolejeunea bidentula* Gradst., fossil species in Dominican amber, ca. 20 Mya, ventral view; **C**, *Mastigolejeunea repleta* (Tayl.) A. Evans; **D**, *Ptychanthus striatus* (Lehm. & Lindenb.) Nees, growth habit; **E**, *Ptychanthus striatus*, dorsal view; **F**, *Ptychanthus striatus*, ventral view; **G**, *Thysananthus comosus* Lindenb.; **H**, *Thysananthus gottschei* (Jack & Steph.) Steph.; **I**, *Thysananthus retusus* (Reinw. & al.) B. Thiers & Gradst., showing the vitta. Plants sizes: stems with leaves ca. 1.5–3 mm wide. Photographs A: R.-L. Zhu & R.P. Shi; B: S.R. Gradstein; C: Y.M. Wei & T. Peng; D: S. Kornochalart; E: T. Hallingbäck; F: J.-P. Frahm; G–H: P. Sukkharak; I: I. Haerida.

Appendix 1. List of taxa studied. Accession numbers in bold are new for this study. Other sequences are from Wilson & al. (2007a).

Taxon; DNA no.; geographic origin; herbarium voucher; GenBank accession numbers (*psbA-trnH*, *trnG*, *trnL-F*, *trnS-rps4*, ITS).

Acrolejeunea fertilis (Reinw. & al.) Schiffn.; Indonesia; Schäfer-Verwimp 17009 (GOET); **PS, PS**, DQ987391, **PS**, DQ987281. *A. pycnoclada* (Tayl.) Schiffn.; Malaysia; Gradstein 10360 (GOET); **PS, PS, PS, PS, PS**. *A. securifolia* (Endlicher) Steph.; Australia, Pócs 99101/B (GOET); **PS, PS, PS, PS, PS**. *Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout.; 1; Thailand; Chantanaorrapint 2112 (PSU); **PS, PS, PS, PS, PS**. *Dendrolejeunea fruticosa*; 2; Malaysia; Ilkiu-Borges & Yong 3026 (GOET); **PS, PS**, DQ987420, **PS**, DQ987316. *Lopholejeunea eulopha* (Tayl.) Schiffn.; Malaysia; Gradstein 10367 (GOET); **PS, PS, PS, PS, PS**. *L. nigricans* (Lindenb.) Schiffn.; Malaysia; Gradstein 10357 (GOET); **PS, PS, PS, PS, PS**. *Mastigolejeunea auriculata* (Wils.) Schiffn.; 1; Malaysia; Gradstein 10383 (GOET); **PS, PS, PS, PS, PS**. *M. auriculata*; 2; USA; Davidson 7686 (GOET); **PS, PS, PS, PS, PS**. *M. indica* Steph.; Thailand; Sukkharak 825 (BKF, GOET); **PS, PS, PS, PS, PS**. *M. ligulata* (Lehm. & Lindenb.) Schiffn.; Thailand; Schäfer-Verwimp 16246 (GOET); **PS, PS**, DQ987465, **PS, PS**. *Mastigolejeunea pancheri* Steph.; 1; New Caledonia; Guillaumin & Baumann 9343 (GOET); **PS, PS, PS, PS, PS**. *M. pancheri*; 2; New Caledonia; Hürlimann 2624 (GOET); **PS, PS, PS, PS, PS**. *M. virens* (Ångstr.) Steph.; Thailand; Sukkharak 838 (BKF, GOET); **PS, PS, PS, PS, PS**. *Ptychanthus striatus* (Lehm. & Lindenb.) Nees; 1; Thailand; Sukkharak 755 (BKF, GOET); **PS, PS, PS, PS, PS**. *P. Striatus*; 2; India; Schäfer-Verwimp 27974 (GOET); **PS, PS, PS, PS, PS**. *Spruceanthus polymorphus* (Sande Lac.) Verd.; Indonesia; Gradstein 10207 (GOET); **PS, PS, PS, PS, PS**. *S. theobromae* (Spruce) Gradst. Ecuador; Andersson & Kautz AK 10 (GOET)**PS, PS**, DQ987407, **PS**, DQ987301. *S. thozetianus* (Gottsche & F. v. Müll) B. Thiers; Australia; Pócs 01107/M (GOET); **PS, PS**, DQ987460, **PS**, DQ987362. *Thysananthus aculeatus* Herzog; Japan; Inoue s.n. (L); **PS, PS, PS, PS, PS**. *T. amazonicus* (Spruce) Schiffn.; French Guiana; Gehrig s.n. (GOET); **PS, PS, PS, PS, PS**. *T. anguiformis* (Hook.f. & Taylor) Steph.; 1; New Zealand; Schäfer-Verwimp & Verwimp 14058 (GOET); **PS, PS, PS, PS, PS**. *T. anguiformis*; 2; New Zealand; Frahm 20-10 (GOET); **PS, PS**, DQ987455, **PS**, DQ987355. *T. appendiculatus* Steph.; Papua New Guinea; Streimann & Bellamy 18093 (JE); **PS, —, —, —, PS**. *T. comosus* Lindenb.; 1; Malaysia; Sukkharak 730 (BKF, GOET); **PS, PS, PS, PS, PS**. *T. comosus*; 2;

Thailand; Inuthai s.n. (PSU); **PS, PS, PS, PS, PS. *T. comosus***; 3; Papua New Guinea; Streimann 41608 (JE); **PS, PS, PS, PS, PS. *T. comosus***; 4; Malaysia; Gradstein & al. 10366 (GOET); **PS, PS, DQ987425, PS, DQ987321. *T. convolutus*** Lindenb.;1 ;Thailand; Sukkharak 803 (BKF, GOET); **PS, PS, PS, PS, PS. *T. convolutus***; 2; Malaysia; Sukkharak 717 (BKF, GOET); **PS, PS, PS, PS, PS. *T. convolutus***; 3; Papua New Guinea; Streimann 41088 (JE); **PS, PS, PS, PS, PS. *T. convolutus***; 4; Indonesia; Gradstein 10205 (GOET); **PS, PS, DQ987414, PS, DQ987310. *T. convolutus***; 5; Malaysia; Gradstein & al. 10324 (GOET); **PS, PS, DQ987431, PS, DQ3987327. *T. discretus*** Sukkharak & Gradst.; 1; Papua New Guinea; Gradstein 3856 (GOET); **PS, PS, PS, PS, PS. *T. discretus***; 2; Papua New Guinea; Gradstein 3894 (GOET); **PS, PS, PS, PS, PS. *T. mollis*** Steph. Papua New Guinea; Gradstein 3792 (GOET); **PS, PS, PS, PS, PS. *T. montanus*** Gradst., X.-L. He & Piippo; Koponen 33958b (H); **PS, PS, PS, –, –, *T. retusus*** (Reinw. & al.) B. Thiers & Gradst.; 1; Thailand; Sukkharak 743 (BKF, GOET); **PS, PS, PS, PS, PS. *T. retusus***; 2; Australia; Renner 1514 (NSW); **PS, PS, PS, PS, PS. *T. retusus***; 3; Papua New Guinea; Gradstein 3963 (GOET); **PS, PS, PS, PS. *T. retusus***; 4; New Caledonia; Mürlimann 2111 (G); **PS, –, PS, –, –, *T.spathulistipus*** (Reinw. & al.) Lindenb.; 1; Thailand; Sukkharak 788 (BKF, GOET); **PS, PS, PS, PS, PS. *T. spathulistipus***; 2; Thailand; Sukkharak 784 (BKF, GOET); **PS, PS, PS, PS, PS. *T. spathulistipus***; 3; Thailand; Sukkharak 768 (BKF, GOET); **PS, PS, PS, PS, PS. *T. spathulistipus***; 4; Thailand; Sukkharak 793 (BKF, GOET); **PS, PS, PS, PS, PS. *T. spathulistipus***; 5; Indonesia; Schäfer-Verwimp 20790 (GOET); **PS, PS, DQ987392, PS, DQ987282.**

Appendix 2. Morphological-anatomical scored for phylogenetic analysis of the 46 specimens of Lejeuneaceae-Ptychanthoideae.

1. Branch: *Lejeunea*-type (0), *Frullania*-type (1); **2.** Growth habit: dendroid (0), projecting growth (1); **3.** Flagellae: lacking (0), present (1); **4.** stem: rigid (0), rather fragile (1); **5.** Stem types: enlarged dorsal epidermis (0), hyalodermis (1), epidermal cells as large as medulla cells (2); **6.** Subepidermis: lacking (0), present (1); **7.** Leaf position: suberect when dry and moving outwards when wetted (becoming wide spreading) (0), at a wide angle with the stem when dry and (thus) not moving outwards when wetted (1); **8.** Leaf lobes: symmetric (0), asymmetric (1); **9.** Leaf shapes: lanceolate to oblong (0), ovate (1); **10.** Leaf margin: entire (0), toothed (1); **11.** Ventral leaf teeth: entire (0), 1-7 (1), more than 7 (2); **12.** Foliar appendages on keels of leaves: lacking (0), present (1); **13.** Foliar appendages on lobule bases: lacking (0), present (1); **14.** Auricles at dorsal bases of leaves: lacking (0), present (1); **15.** Leaf areolation: cells \pm elongate and basically with cordate trigones (0), cells isodiametrical and trigones not cordate (1); **16.** Vitta: absent (0), present (1); **17.** Lobule shape: rectangular (0), ovate (1); **18.** Lobule length: width: 1:1-2:1 (0), more than 2:1 (1); **19.** Number of first tooth apex cells: 0-3 cells long (0), more than 3 cells long (1); **20.** Adnate underleaves: absent (0), present (1); **21.** Underleaf shape: spatulate (0), obovate or reniform (1); **22.** Auricles at bases of underleaves: lacking (0), present (1); **23.** Sexual condition: autoicous or paroicous (0), dioicous (1); **24.** Male bract lobules: hypostatic (0), epistatic (1); **25.** Female bract margin: entire (0), toothed (1); **26.** Female bracteole margin: entire (0), toothed (1); **27.** Perianth margin: entire (0), toothed (1); **28.** Number of beak cells: 3-5 (0), more than 5 (1); **29.** Number of perianth keels: 3 (0), more than 3 (1); **30.** Subfloral innovation: absent (0), present (1).

Appendix 3. Morphological-anatomical data matrix of the 46 specimens of Lejeuneaceae-Ptychanthoideae. Columns correspond to the numbers in

Appendix 2.

Taxon	Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>A. fertilis</i>		0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	?	?	?	?	?	?	?	?
<i>A. pycnoclada</i>		0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	?	?	0	0	0	1	1	0
<i>A. securifolia</i>		0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	?	1	?	?	?	?	?	?
<i>D. fruticosa</i>	1	0	0	0	0	2	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?
<i>D. fruticosa</i>	2	0	0	0	0	2	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	?	0	?	?	?	?	?	?
<i>L. eulopha</i>		0	1	0	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0
<i>L. nigricans</i>		0	1	0	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
<i>M. auriculata</i>	1	0	1	1	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>M. auriculata</i>	2	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?
<i>M. indica</i>		0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	?	?	?	?	?	?	?
<i>M. ligulata</i>		0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?
<i>M. pancheri</i>	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	?	?	0	0	1	1	0	1
<i>M. pancheri</i>	2	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?
<i>M. virens</i>		0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	(01)	0	0	0	0	0	1
<i>P. striatus</i>	1	1	0	0	0	2	1	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1
<i>P. striatus</i>	2	1	0	0	0	2	1	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1
<i>S. polymorphus</i>		0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1
<i>S. theobromae</i>		0	1	1	0	2	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1
<i>S. thozetianus</i>		0	1	1	0	2	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?
<i>T. aculeatus</i>		0	1	1	0	2	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?

<i>T. amazonicus</i>		0	1	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	?	?	?	?		
<i>T. anguiformis</i>	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	?	?	0	0	1	1	0	1	
<i>T. anguiformis</i>	2	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	?	1	?	?	?	?	?	?	
<i>T. appendiculatus</i>		0	1	1	0	2	0	0	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1	0	?	?	?	?	?	?	?	?	
<i>T. comosus</i>	1	0	1	1	0	2	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?	
<i>T. comosus</i>	2	0	1	1	0	2	0	0	1	1	(01)	0	0	1	0	0	0	0	0	0	1	1	0	?	?	1	1	1	1	0	0	1	
<i>T. comosus</i>	3	0	1	1	0	2	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	
<i>T. comosus</i>	4	0	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	(01)	1	0	?	?	1	1	1	1	0	0	1	
<i>T. convolutus</i>	1	0	1	1	0	2	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	
<i>T. convolutus</i>	2	0	1	1	0	2	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	?	0	?	?	?	?	?	?	?	
<i>T. convolutus</i>	3	0	1	1	0	2	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	
<i>T. convolutus</i>	4	0	1	1	0	2	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	1
<i>T. convolutus</i>	5	0	1	1	0	2	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	
<i>T. discretus</i>	1	0	1	1	0	2	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	
<i>T. discretus</i>	2	0	1	1	0	2	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	
<i>T. mollis</i>		0	1	1	0	2	0	0	0	0	1	1	0	1	1	0	1	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	
<i>T. montanus</i>		0	1	1	0	2	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	
<i>T. retusus</i>	1	0	1	1	1	2	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	
<i>T. retusus</i>	2	0	1	1	1	2	0	1	0	1	0	0	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	
<i>T. retusus</i>	3	0	1	1	1	2	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	?	0	?	?	?	?	?	?	?	
<i>T. retusus</i>	4	0	1	1	1	2	0	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	0	?	?	?	?	?	?	?	?	
<i>T. spathulistipus</i>	1	0	1	1	0	2	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	
<i>T. spathulistipus</i>	2	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	
<i>T. spathulistipus</i>	3	0	1	1	0	2	0	0	0	1	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	

<i>T. spathulistipus</i>	4	0	1	1	0	2	0	0	0	1	(01)	0	0	0	0	0	0	0	1	0	0	?	?	1	1	1	0	0	1
<i>T. spathulistipus</i>	5	0	1	1	0	2	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?

Monograph of *Thysananthus* subgenus *Thysananthus* (Lejeuneaceae, Marchantiophyta)

Phiangphak Sukkharak

Department of Systematic Botany, Institute of Plant Sciences, University of Göttingen, Untere
Karspüle 2, 37073 Göttingen, Germany

* Department of Biology, Faculty of Science, Burapha University, 169 Long-Hard Bangsaen
Road, Saen Sook Sub- district, Mueang District, 20131 Chonburi, Thailand.

E-mail: ppsukk@gmail.com

ABSTRACT. A world-wide revision of subgenus *Thysananthus* of the liverwort genus *Thysananthus* (Marchantiophyta: Lejeuneaceae) leads to the recognition of fifteen species, in two sections: sect. *Thysananthus* (eleven species) and sect. *Dendrolejeunea* (Spruce) comb. nov. (four species). The two sections are characterized by the absence resp. presence of a vitta in the leaves. Species are defined by the presence of two or more independent, diagnostic morphological characters. The results of a molecular phylogenetic analysis confirm the placement of *Mastigolejeunea pancheri* and *M. sellingii* in *Thysananthus* and support combining the genus *Mastigolejeunea* (fourteen spp.) with *Thysananthus*, as *T.* subg. *Mastigolejeunea* (Spruce) comb. nov. Moreover, *Dendrolejeunea* is returned to *Thysananthus* based on the molecular results and *T. gottschei*, previously considered a synonym of *T. convolutus*, is resurrected as a separate species. One species, *T. combinatus* sp. nov., and one variety are newly described, and numerous new combinations are proposed. An artificial key to the species of the genus *Thysananthus* is provided and each species of subg. *Thysananthus* is fully described and illustrated, with extensive synonymy and detailed data on habitat and distribution. An annotated list of the species in subg. *Mastigolejeunea* is also provided; a monograph of the latter subgenus should be the subject of future work. The subg. *Thysananthus* is pantropical in distribution, with four species ranging into warm temperate regions; the centre of diversity is in Southeast Asia. The species grow as epiphytes in rain forests and montane forests, and include ecological specialists (shade epiphytes, sun epiphytes) as well as generalists. A comparison of sexuality and range size in the genus shows that the endemic species are dioicous and the most widespread ones monoicous, which

* New address after 1 July 2011.

suggests that dispersal has played an important role in shaping the distribution of the species of subg. *Thysananthus*.

INTRODUCTION

The genus *Thysananthus* was first described by Lindenberg in 1844 based on the sharply 3-keeled, dentate-lacinate perianth. Further differential characters have been added by later authors, viz. toothed leaves (Spruce, 1884), elongate leaf cells (Stephani, 1912), purely presence of *Lejeunea*-type branches, epidermal cells not larger than medullary cells, leaves convolute when dry and cordate trigones, often become coalesced (Gradstein, 1975), and lejeuneoid leaf sequence of innovations (Thiers & Gradstein, 1989).

Spruce (1884) published *Thysano-Lejeunea* as one of his 37 subgenera of *Lejeunea* Lib., a genus which was almost equivalent to the present family Lejeuneaceae. The subgenus *Thysano-Lejeunea* was more or less equivalent to *Thysananthus* and was classified in the “Holostipae” Spruce due to its undivided underleaves. Spruce included 7 species in *Lejeunea* subg. *Thysano-Lejeunea*: *L. amazonica* Spruce, *L. dissoptera* Spruce and *L. pterobryoides* Spruce from tropical America, and *L. comosa* (Lindenb.) Spruce, *L. convoluta* (Lindenb.) Spruce, *L. reniloba* (Gottsche) Spruce and *L. spathulistipa* (Lindenb.) Spruce from Southeast Asia.

In the Species Hepaticarum, Stephani (1912) listed 34 species of *Thysananthus*, which had been restored at generic rank by Schiffner (1893), replacing “*Thysano-Lejeunea*”. Fourteen species of *Thysananthus* were newly described in his treatment from which only two survived subsequent revisions (including this revision), *T. appendiculatus* Steph. and *T. mollis* Steph.

Verdoorn (1934) revised the Asiatic species of *Thysananthus* and classified them into three sections on the basis of leaf characters: (1) *T. sect. Spathulistipae* Verd. with six species (*T. aculeatus* Herzog, *T. appendiculatus*, *T. comosus* Lindenb., *T. minor* Verd., *T. richardsianus* Verd., *T. spathulistipus* (Reinw. et al.) Lindenb.) characterized by symmetric and rather plane leaves without vitta; (2) *T. sect. Convolutae* Verd. with two species (*T. convolutus* Lindenb., *T. gottschei* (Jack & Steph.) Steph.) characterized by asymmetric and deeply concave leaves without vitta; and (3) *T. sect. Vittatae* Verd. with three species (*T. fruticosus* (Lindenb. & Gottsche) Schiffn., *T. mollis*, *T. planus* Sande Lac.) characterized by symmetric, vittate leaves.

Fulford (1941) recognized four species of *Thysananthus* in tropical America including *T. amazonicus* (Spruce) Schiffn., *T. comosus*, *T. evansii* Fulford and *T. pterobryoides* (Spruce) Schiffn., and reduced *Lejeunea dissoptera* to a synonym of *T. comosus*. However, in his revision of neotropical *Thysananthus*, Gradstein (1994) accepted only one species in tropical America, *T. amazonicus*.

Vanden Berghen (1950) studied *Thysananthus* in Africa and accepted one species in this continent (*T. spathulistipus*). Mizutani (1961, 1969, 1977, 1987) and Mizutani and Piippo (1986) published updated descriptions and keys for various Asiatic species, and Hürlimann (1989) treated the species of *Thysananthus* from New Caledonia, and transferred two New Caledonian species of *Mastigolejeunea* (Spruce) Schiffn. (*M. pancheri* Steph., *M. sellingii* Herzog) to *Thysananthus*. Thiers and Gradstein (1989) studied the Australian species of *Thysananthus* and classified the species from that area into two subgenera, subg. *Thysananthus* (*T. fruticosus*, *T. spathulistipus*) and subg. *Sandeanthus* B. Thiers & Gradst. (*T. australis* (Steph.) B. Thiers & Gradst., *T. retusus* (Reinw. et al.) B. Thiers & Gradst.), based on differences in leaf position and areolation.

Gradstein (1992a) proposed a new classification of the species assigned to *Thysananthus* based on characters of the dried as well as the living plants. He removed the two deviating New World species, *T. evansii* and *T. pterobryoides*, from *Thysananthus* and erected for them the new genus *Fulfordianthus* Gradst., based on the dendroid habit, the isodiametric leaf cells with evenly thickened walls, lacking any trace of trigones, the lack of oil bodies, etc. The genus *Dendrolejeunea* (Spruce) Lacout., which is also dendroid like *Fulfordianthus*, was reinstated for the Asiatic *T. fruticosus*. The remaining species of *Thysananthus* were attributed to the two subgenera recognized by Thiers and Gradstein (1989).

Sukkharak & Gradstein (2010a) described the new species *T. discretus* Sukkharak & Gradst. based on hitherto neglected morphological characters of the underleaves, and recognized 10 species in the genus *Thysananthus*.

As to the systematic placement of the genus *Thysananthus*, Mizutani (1961) in his taxonomic treatment of the Japanese Lejeuneaceae classified the genus in the subfamily Ptychanthoideae Mizut. and this has been followed and confirmed by all subsequent authors. Morphological phylogenetic analysis of the Ptychanthoideae (Gradstein, 1994; Gradstein et al., 2003) recovered *Thysananthus* as a member of the Ptychanthinae clade together with *Bryopteris* (Nees) Lindenb., *Mastigolejeunea*, *Ptychanthus* Nees and *Schiffneriolejeunea* Verd. *Dendrolejeunea* was not included in the analysis because sporophytes were unknown. Wilson et al. (2007a) in a molecular phylogenetic analysis of the family based on four

markers recovered *Thysananthus* (4 species sampled) in a robust clade together with *Dendrolejeunea* and *Mastigolejeunea*, being sister to a clade containing *Ptychanthus* and *Spruceanthus* Verd. *Bryopteris* and *Schiffneriolejeunea* appeared to be more distantly related to *Thysananthus*. All studies revealed *Thysananthus* as monophyletic.

Recent molecular data (Sukkharak et al., submitted) based on a complete sampling of all species of *Thysananthus* confirmed the monophyly of the genus with the inclusion of *Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout. *Thysananthus gottschei*, considered a synonym of *T. convolutus* (Grolle & Piippo, 1984) and called the edentate form of the latter, was recovered as a separate species. In addition, evidence for an undescribed species, *T. combinatus* sp. nov., was found based on an accession identified as *T. comosus*. Finally, the placement of the New Caledonian *Mastigolejeunea pancheri* and *M. sellingii* in *Thysananthus* (Hürlimann, 1989) was confirmed and the inclusion in *Thysananthus* of the genus *Mastigolejeunea*, long considered very closely related to *Thysananthus*, appeared necessary.

The purpose of the present treatment is the presentation of a world-wide revision of *Thysananthus* subg. *Thysananthus* based on morphological and anatomical study of the types and other available herbarium materials, as well as using phytochemical and molecular evidence (Sukkharak et al., in press; Sukkharak et al., submitted).

MATERIAL AND METHODS

About 1600 herbarium specimens from BCU, BKF, BM, BM-K, BR, BZ, C, FH, G, GOET, H, HIRO, JE, L, LAE, NICH, NSW, NY, PC, PSU, S, SING, STR, U and W were examined in the present study. Fresh specimens of subg. *Thysananthus* were studied from Suriname and French Guiana (*T. amazonicus*), Thailand (*T. comosus*, *T. convolutus* var. *convolutus*, *T. fruticosus*, *T. retusus* subsp. *retusus*, *T. spathulistipus*), and Malaysia (*T. comosus*, *T. convolutus* var. *convolutus*, *T. spathulistipus*). The fresh materials have also been used for chemical and molecular studies.

Specimens were examined in the dry state for determining the habit of the leaves. For the description of all other aspects, the specimens were observed, measured, and illustrated with a Leica DMLS microscope after fully moistening with tap water. Measures always represent the complete observed morphological variation of the plants. Shoots, leaves, underleaves, bracts, bracteoles, and perianths were illustrated without cover slips while cells, spores and elaters were studied under cover slips. Bracketed measurements, e.g., in ventral merophyte, stem epidermal and medullary cells, and series of male bracts, indicate that these

are rare for that taxon when taken as the sum of the component populations, and not that these numbers are uncommon in individual populations.

Shoot width is the width between opposite leaf apices. Leaf length is measured as the distance from the basal insertion of the leaf on the stem to the apex of the leaf lobe. Leaf width is measured parallel to the stem and is the distance from the apical insertion of the free margin of the lobule on the ventral lobe margin to the dorsal margin of the lobe. The ventral margin was carefully compressed before measurement, when the free margin continues into the ventral margin. Lobule length is the distance from the basal insertion of leaf on the stem to the base of first tooth. Lobule width is the widest distance from keel to free margin measured parallel to the stem (Fig. 1A). Underleaf length is the distance from the mid-basal insertion of underleaf to the stem to the middle of apex. The underleaf width is arbitrarily chosen as the widest distance of the underleaves (Fig. 1B). The length of the cells is defined as the longest distance between the trigones, present in the angles. Width is measured perpendicularly to length. Female bracts were measured as leaves while bracteoles were measured as underleaves. Perianth length is the distance from the mid-basal insertion of perianth to the innovation to the basal of the beak. Perianth width is arbitrarily chosen as the widest distance of the perianth (Fig. 1C). Characteristics of capsule valves and size of elaters were taken from dehiscent capsules while the number of elaters per valve (or capsule) and spore characteristics were taken from mature, undehiscent ones. Elaters and spores were observed in fully hydrated condition in water, at 1000× magnification. The total number of rosettes per spore was difficult to determine, therefore, in this treatment number of rosettes per spore facet is given.

MORPHOLOGY AND ANATOMY

Growth Habit. Species of subg. *Thysananthus* usually grow in dense mats over bark or rock. Most species have projecting growth, turning upwards and becoming ascending to erect or projecting downwards and becoming pendent (*T. amazonicus*). Only *T. fruticosus* has a dendroid or fan-shaped like habit.

Color and size. Plants are pale green to dull green in the field, becoming brownish green to black in older portions. Dried herbarium specimens are pale yellow to dark brown. Most species of subg. *Thysananthus* are rather robust plants, measuring up to 6.5 cm long and to 5 mm wide.

Branching. Branches are always gyrothecal and of the *Lejeunea*-type (Crandall 1969; Fig. 1D) except for innovations (= branches originating directly below the perianths and

associated with the inner bracts) which are of the *Radula*-type (Fig. 1E). Leaf sequence of innovations is lejeuneoid, with the sequence of leaf production begin with a lateral leaf. Consequently, the leaf spiral is dextrorse on innovations originating from the right-hand side of the stem and sinistrorse on innovations on the left-hand side (if viewed from the ventral surface of the plant). Thiers (1985) recognized four patterns of spatial arrangement of the gynoecia in Ptychanthoideae: (1) Simple (innovations lacking or short sterile), (2) monochasial (innovations single and frequently fertile), (3) dichasial (innovations in pairs and repeatedly fertile), and (4) diffuse (innovations variable). A monochasial pattern is particularly characteristic of *T. amazonicus*, *T. comosus*, *T. convolutus*, *T. gottschei*, *T. pancheri* (Steph.) Hürl. whereas a dichasial pattern is found in *T. aculeatus*, *T. anguiformis*, *T. appendiculatus*, *T. combinatus*, *T. discretus* and *T. montanus* Gradst. et al. Both monochasial and dichasial pattern are found in the remaining species.

The presence of flagelliform branches (“flagellae”) along the older portions of the stems is common in this subgenus (Fig. 1F). These branches are always curved backwards, towards the stem base, and bear leaves which are much smaller than ordinary branch leaves. Gradstein (1994) suggested that these flagellae may serve as a specialized means of attachment, additional to rhizoids.

Stem structure. The stems are rather rigid except in *T. retusus*, which are rather small plant with rather fragile stems. The lateral merophytes always meet dorsally on the stem along a straight longitudinal line and the ventral merophyte surface is 6–18 cells wide, being narrowest in *T. retusus* and widest in *T. discretus*. The width of the ventral merophyte in subg. *Thysananthus* is not a very stable taxonomic character. For the present study, transverse stem sections were made in all species. The stem measures 0.1–0.3(–0.5) mm high \times 0.1–0.3(–0.45) mm wide. In transverse section the stem is round-orbicular to subelliptic in shape. The total number of epidermal cells varies between 25 and 57 but may be up to 80 in *T. discretus* and only 18–21 in *T. retusus*. The number of medullary cells varies between 27 and 225 but may be up to 381 in *T. discretus* and no more than 27–34 in *T. retusus*. Epidermal cells are usually large as medullary cells except in *T. anguiformis* (Hook. f. & Taylor) Steph., *T. combinatus* and *T. pancheri* which have dorsally enlarged epidermal cells. The stem cell walls are always strongly thickened, and are colourless to brown.

Leaves. The leaves in *Thysananthus* (both subgenera) are inserted incubously and imbricate (rarely contiguous), and divided into a dorsal lobe and a smaller, inflated ventral lobule (Fig. 1A). The leaves are attached to the stems along a J-shaped insertion line which covers the whole length of the straight lateral merophytes (Fig. 1G). When dry the leaves are suberect, strongly convolute and wrapped around the stem. An exception is found in *T.*

retusus, in which the leaves are spread out widely, loosely reflexed or plane. When moistened, the leaves are weakly to strongly concave, with the apical parts plane or (in *T. anguiformis*, *T. combinatus*, *T. convolutus*, *T. gottschei*, *T. pancheri*) ventrad (turned to ventral side) and recurved. In *T. discretus* the leaves are clasping the stem when moistened.

The leaf lobes of *Thysananthus appendiculatus*, *T. mollis*, *T. montanus*, *T. retusus* and *T. spathulistipus* are symmetrical whereas those of the remaining species are asymmetrical, with the apex positioned towards the ventral side of the leaves. The dorsal bases are cordate or auriculate and the ventral margin is usually upcurved ca. $1/2 \times$ leaf length except in *T. anguiformis*, *T. fruticosus* and *T. retusus* in which it is plane. The leaf margins are usually toothed except in *T. amazonicus*, *T. anguiformis*, *T. combinatus*, *T. gottschei*, *T. montanus*, *T. pancheri* and *T. retusus*. In *T. comosus*, *T. discretus*, *T. mollis* and *T. spathulistipus* leaf dentation is variable and leaves may be toothed or entire. The variation in leaf dentation observed in the latter species is not uncommon in Lejeuneaceae and also occurs in, e.g., *Bryopteris filicina* (Sw.) Nees (Gradstein, 1994), *Archilejeunea planiuscula* (Mitt.) Steph. (Thiers & Gradstein, 1989; Gradstein et al., 2002), and in some species of *Lejeunea* (Reiner-Drehwald & Goda, 2000).

The leaf has three hyaline papillae (“slime papillae”) as also seen in other species of Lejeuneaceae (Gradstein, 1994). The hyaline papilla is pyriform. Two of them are associated with the outer ends of the insertion line of the leaf, the third one is located at or near the proximal base of the first tooth on the inner surface of the lobule.

The lobule in subg. *Thysananthus* is oblong-rectangular and $1/4$ – $1/3 \times$ lobe length (Fig. 1A) except in *T. mollis*, which has $1/8$ – $1/10 \times$ lobe length lobule. In *T. retusus* subsp. *sellingii* comb. nov. the lobule is $5 \times$ longer than wide whereas in the others it is $2 \times$ longer than wide.

The keel, which connects the lobule with the lobe, is smooth and gradually curved or almost straight. The free margin is plane. The number of teeth on the free margin varies between one and two or lacking. In this treatment, I follow the terminology of Mizutani (1961) and Gradstein (1975) in using “first tooth” and “second tooth” in numerical sense and not in connection with the location of the hyaline papilla. At the apex of the lobule the free margin and the keel mostly meet at an oblique angle, rarely a straight angle. When oblique, the free margin usually continues into the ventral margin of the lobe, rendering it difficult to determine where the free margin ends and the ventral margin of the lobe begins. In *T. gottschei* var. *continuus* var. nov. the free margin continues over almost the entire length of the ventral margin and sometimes into the dorsal margin of the lobe (Fig. 17B). When straight the free margin ends abruptly at the junction of the keel and the ventral margin of the lobe (Figs. 7B–C; 8A, F; 22B; 23B, E).

Underleaves. The underleaves in subg. *Thysananthus* are imbricate and slightly squarrose except in *T. aculeatus* and *T. comosus*, where they are channeled/hollow or flat respectively. They are obovate, spatulate or oblong-rectangular in shape and always undivided (Fig. 1B). In some species the underleaf apex is emarginate but bifid underleaves are lacking in this genus. In *T. convolutus* var. *laceratus* comb. nov. and *T. gottschei* var. *continuus* the apex is recurved or incurved whereas in the other species it is plane. The central region of the underleaf is gibbous. Well-developed auricles at the underleaf bases are always present in *T. discretus* and sometimes in *T. appendiculatus*. The base of the underleaf at the place of attachment to the stem, as seen in longitudinal stem section, is always bistratose, lacking an intermediate cell layer, and belongs to Winkler's *Stictolejeunea*-type (Fig. 1H). The rhizoids are mostly brown, originating from the base of the underleaves. Rhizoid discs are absent.

An unusual feature of subg. *Thysananthus* is the common presence of adnate underleaves that are connected to leaf bases (Fig. 2A–B) (Sukkharak & Gradstein, 2010b). The presence of adnate underleaves appears to be a stable and taxonomically relevant feature of *T. aculeatus*, *T. amazonicus*, *T. anguiformis*, *T. appendiculatus*, *T. comosus*, *T. convolutus*, *T. gottschei*, *T. pancheri* and *T. spathulistipus*; in the other species of the subgenus underleaf bases are usually free. Interestingly, it appeared that the adnation of underleaves on branches occurs in a distinct left-right symmetry pattern, on right-hand branches being connected to leaves on the left side and on left-hand branches on the right-hand side.

Appendages of leaves, bracts and perianths. Sukkharak & Gradstein (2010b) observed further morphological features in subg. *Thysananthus*, relative to leaf bases. In all species of subg. *Thysananthus* a small “appendage” may be developed on leaves, female bracts and perianths (Fig. 2A, C–J). In *T. anguiformis*, *T. appendiculatus*, *T. convolutus* var. *laceratus*, *T. discretus*, *T. fruticosus* and *T. gottschei* var. *continuus* the appendages are found on the keel of leaves and inserted partially on the stems. In *T. fruticosus*, the appendages are found on both sides of the stem. In *T. appendiculatus*, *T. convolutus* var. *laceratus* and *T. gottschei* var. *continuus* they are always found on one side of the stem only, on the side where underleaves are free and being opposite to the adnate ones, whereas in *T. anguiformis* they are sometimes found on one side of the stem (Fig. 2A). In species with free underleaves such as *T. discretus*, however, the position of the appendages is variable and may be on one or both sides of the stems (or lacking). These observations are further evidence for the left-right symmetry on branches in subg. *Thysananthus*. In all species of subg. *Thysananthus* wing-like appendages occur on the keels of the female bracts, on one or both sides of the stem (or lacking) and partially inserted on the associated innovation. In addition, a small appendage may be found

on the mid-basal portion of the bract lobules and on the base of the keels of the perianth (Fig. 2D–F, I). Moreover, an appendage which is attached to the lobule bases and the stem epidermis cells on both sides of the stem was observed in *T. mollis*, *T. montanus* and *T. retusus* (Fig. 2K–L).

Cells. The cells in the leaf lobe are elongate-hexagonal and arranged in diverging rows. An exception is found in *T. retusus*, in which the cells are (sub)isodiametric (except for the vittate cells). Along the margin of the lobe a row of subquadrate cells is always present. Towards the base of the lobe the cells become slightly larger. The presence of a marked vitta is the special feature of *T. fruticosus*, *T. mollis*, *T. montanus* and *T. retusus* (Figs. 22K, 27K). Ocelli are lacking in all species of subg. *Thysananthus*.

The cell walls are smooth and colorless. They consist of a thin middle lamella, with collenchymatic thickenings (“trigones”) and intermediate thickenings 1–2(–3) per cell wall. The trigones are heart-shaped (“cordate”) possessing two convex sides and one concave side. Often they tend to become large and confluent (“coalesced”), except in *Thysananthus retusus*, in which trigones and intermediate thickening are indistinct (except for the vittate cells). The cells of underleaves and leaf lobules are smaller than those of the leaf lobes.

Oil bodies are present in all cells of leaves, underleaves, involucre, and perianth. They were described previously in *Thysananthus aculeatus* (Mizutani, 1961), *T. spathulistipus* (Mizutani, 1969), *T. retusus* (Thiers & Gradstein, 1989), *T. amazonicus* and *T. discretus* (Gradstein, in sh) and are newly described here for *T. comosus* and *T. convolutus*. The oil bodies of all species of *Thysananthus* are coarsely segmented granulose (*Calypogeia*-type) and narrow ellipsoid to subglobose in shape (Figs. 12P, 13N, 18N, 27N–O). The granules are distinctly protruding beyond the outer membrane, the oil body thus resembling a “grape-cluster” (Schuster, 1966). In margin and median leaf cells their number varies from 2 to 6, reaching to 8 in vitta cells. The oil bodies may appear to be spherical when laying in transverse position in the cells.

Gametoecia. *Thysananthus amazonicus* is paroicous, having sexual branches with male bracts below the female bracts, *T. aculeatus*, *T. fruticosus*, *T. retusus* subsp. *retusus* and *T. spathulistipus* are autoicous with gynoecia and androecia on separate branches, and the remaining species of subg. *Thysananthus* are dioicous. The androecium consists of a slightly modified leaf (bract) enveloping two antheridia (Fig. 3B), rarely only one (Gradstein, 1994). The androecia are produced on terminal or intercalary branches except for those of *T. amazonicus*, which are below the gynoecium. The androecial spike in subg. *Thysananthus* is composed of 2–13 pairs of bracts but may be up to 23 in *T. mollis*. The bract lobe is similar to the lobe of the vegetative leaf, but smaller in size. The male lobules are strongly inflated and

teeth are more numerous than in the vegetative leaves. Mostly male bract lobules of subg. *Thysananthus* are mostly hypostatic (free margin-in ventral view-distinctly overlapping the younger bract) except in *T. amazonicus*, in which epistatic (free margin curving behind the lobule of the younger bract) and hypostatic bracts can be observed (Fig. 3A). Bracteoles are similar to underleaves or slightly smaller. The mature antheridium is globose and 78–115 μm in diameter, and has a unistratose wall of thin-walled and colorless cells. The antheridium is attached to the lateral side of the stem by a straight to curved, uniseriate stalk 11–13 μm in diameter and 24–27 cells long (Fig. 3C).

The gynoecium is produced terminal on elongate branches, and consists of a single archegonium surrounded by a perianth and one series of bracts and bracteoles. The bracts are obliquely spreading to subsquarrose and divided into a large dorsal lobe and a plane ventral lobule. The lobes are ovate with margins toothed or entire, and the lobules are broadly ovate and $2/3$ – $1/2\times$ lobe length. The bracteoles are spatulate in shape, with emarginate to bifid apex and plane or recurved margins which are toothed or entire. The central region of the bracteoles is gibbous.

The juvenile perianth consists of three portions: (1) a basal portion, surrounding the venter of the archegonium; (2) a central portion, soon becoming triplicate; and (3) a beak, which has completed its development (Fig. 3D). The base of the archegonial neck is surrounded by the beak. The archegonium is flask-shaped and has a long neck of cells extending beyond the beak of the juvenile perianth (Fig. 3E–F). After fertilization, the expanding archegonial venter develops into the calyptra, which surrounds the developing sporophyte (Fig. 3G, J). The rapidly growing, trigonous perianth encloses the calyptra and the developing sporophyte. The mature perianth is emergent and obovate or oblong-cylindrical in shape, and has three sharp keels (two laterals and one ventral). The upper $1/3$ of the keels of all species of subg. *Thysananthus* are toothed except in *T. montanus*. The teeth are triangular (usually) or long lacinate (in *T. appendiculatus*, *T. combinatus*, *T. comosus*, *T. convolutus* var. *laceratus*, *T. discretus*, *T. fruticosus*, *T. gottschei*, *T. pancheri*). The beak is normally 3–5 cells long, reaching to 7 cells long in *T. discretus*.

Sporophytes. The development of the sporophyte takes place entirely within the 1–2-layered calyptras as is usual in Lejeuneaceae. The outer cells of the calyptra are larger than the inner cells. At its base, the calyptra is slightly narrowed into a stalk. I found in subg. *Thysananthus* a conical foot with 5–6 transversal rings of cells. Weis (2001) reported 4–5 transversal cell rings in this subgenus. The foot gradually continues into seta, which is 22–25 cells long, articulate (evenly tiered) (Fig. 3H–I), and in cross section made up of 16 outer cells and 4 inner cells (Fig. 3K). The fully elongate seta is to 2.5 mm long.

The mature capsule is dark-brown, globose, and 0.2–0.3 mm in diameter. Upon dehiscence the capsule splits from apex downward 3/4 of its length into four valves. The valves are 0.6–0.8 mm long and 0.3–0.5 mm wide at middle, and widely spread backwards, to 60–90°. The outer valve cells have asymmetrically nodulose trigones and intermediate thickenings which tend to become confluent (Fig. 4B–D). In all species of subg. *Thysananthus* the shape of hinge (= group of differentiated cells in the lower half of the outer valve surface where the free part of the valve curves outwards upon dehiscence; Weis, 2001), is rectangular (Fig. 4A, D). The inner surface of the valves has 6–7 longitudinal ridges or lamellae (= “elateroids”; Gradstein et al., 2003), which are about 200–230 µm long × 30–40 µm wide with the tip is strongly tapering (Fig. 4E). The inner cells of the valves are slightly smaller than the outer cells and are covered by fenestrate sheet of thickening, being monofenestrate (one, large pore per cell) or plurifenestrate (several pores per cell), or both (Fig. 4F). The capsule base (inner view) consists of over 96–100 thin-walled quadrate cells, forming a round to slightly quadrate pattern (Fig. 4E).

Mature, but unopened capsules members of subg. *Thysananthus* have 66 elaters, which are vertical in position and attached to the capsule base and the apical region of the valves. The number and arrangement of elaters are identical in opposite valves, each valve bearing either 15 or 18 elaters (as shown after dehiscence), in a 1+3+5+6 or 2+4+6+6 pattern (Fig. 4G). The elaters are linear, 350–550 × 12–20 µm, with a single brown spiral which is 5–8 µm wide. The tip of the elaters is obtuse but the end is rounded and dilated (Fig. 4H).

The mature spores have undergone precocious germination inside the capsules as is usual in the Lejeuneaceae, and consequently they are green and subisodiametric to oblong. The outer surface of the spores is covered by numerous bluntish papillae and 1–4 rosettes per facet. The rosettes are 8–12 µm in diameter and consist of one circle of 5–8 sharp and smooth papillae (Fig. 4I). The sporeling of subg. *Thysananthus* is of the *Lopholejeunea*-type (Nehira, 1983).

Asexual reproduction. Special means for asexual reproduction have not been observed in subg. *Thysananthus*.

KARYOLOGY

Chromosome numbers and morphology have been reported only for *Thysananthus aculeatus* and *T. spathulistipus* (see Fritsch, 1991). These two species have a haploid number

of $n = 9$, which is characteristic of the Lejeuneaceae and many other liverwort families (Fritsch, l.c.).

CHEMISTRY

Ten species of subg. *Thysananthus*: *T. amazonicus*, *T. appendiculatus*, *T. comosus*, *T. convolutus* var. *convolutus*, *T. discretus*, *T. fruticosus*, *T. gottschei* var. *gottschei*, *T. mollis*, *T. retusus* subsp. *retusus*, *T. spathulistipus* have been investigated for the occurrence of terpenoids, flavonoids, sterols, and aromatic compounds, which are usually stored in the oil bodies (Gradstein et al., 1985; Kruijt et al., 1986; Harinantenaina et al., 2006, Sukkharak et al., in press). The chemical substances not only show strong biological activity but may play an important role in the defence of the plants against environmental hazards (Gradstein, 1994) or predators (Harinantenaina et al., 2006).

Terpenoids. Gradstein et al. (1985) studied the occurrence of terpenoids in *Thysananthus amazonicus*, *T. convolutus* var. *convolutus*, *T. discretus* (under *T. convolutus* sample nr. 49), *T. mollis* and *T. retusus* subsp. *retusus* (under *T. fruticosus*). Later, *T. comosus*, *T. convolutus* var. *convolutus*, *T. fruticosus* (under *Dendrolejeunea fruticosa*), *T. gottschei* var. *gottschei* (under *T. convolutus* sample nr. 1–3), *T. retusus* subsp. *retusus* and *T. spathulistipus* were studied by Sukkharak et al. (in press). Cadinane sesquiterpenoids and diterpene acetates are main components in *T. amazonicus* and aromadendrene sesquiterpenoids has been reported from *T. discretus* (Gradstein et al., 1985). Isolepidozene is detected as a major component in *T. comosus*, *T. convolutus* var. *convolutus* and *T. spathulistipus*, the unidentified (M^+)302, 190(100), 81(95) as the most abundant component in *T. gottschei* var. *gottschei*, pinguisane sesquiterpenoids as major components in *T. retusus* subsp. *retusus*, and the unidentified (M^+)304, 271(100), 105(90) as the most abundant component of *T. fruticosus* (Sukkharak et al., in press).

It appears that most members of subg. *Thysananthus* elaborate large amounts of unidentified diterpenoids and diterpene acetates (Gradstein et al., 1985; Sukkharak et al., in press). Harinantenaina et al. (2006) isolated two clerodane diterpenoids: 3 β ,4 β :15,16-diepoxy-13(16),14-clerodadiene and thysaspathone from *T. spathulistipus*. Clerodane diterpenoids are very rare among Lejeuneaceae. To evaluate their biological activity, the compounds were examined for inhibition of nitric oxide production in culture media of lipopolysaccharide-stimulated RAW 264.7 cells. Thysaspathone exhibited moderate inhibition while 3 β ,4 β :15,16-diepoxy-13(16),14-clerodadiene showed weak activity. Finding new agents that inhibit nitric

oxide production from natural sources is important in drug discovery, since over-production of nitric oxide by inducible nitric oxide synthase is involved in inflammatory disease.

Flavonoids. At least six different flavonoids in *Thysananthus appendiculatus* are detected by Kruijt et al. (1986).

Sterols. Stigmasterol reported from *Thysananthus amazonicus*, *T. convolutus* var. *convolutus*, *T. discretus*, *T. mollis* and *T. retusus* subsp. *retusus* is not uncommon in Lejeuneaceae (Gradstein et al., 1985).

Aromatic compounds. *Thysananthus appendiculatus* produces at least six aromatic hydroxy acids (Kruijt et al., 1986), whereas no trace of aromatic compounds can be detected in *T. amazonicus*, *T. convolutus* var. *convolutus*, *T. discretus*, *T. mollis* and *T. retusus* subsp. *retusus* (Gradstein et al., 1985).

PHYTOGEOGRAPHY

The subg. *Thysananthus* is pantropical in distribution with *T. aculeatus* (Japan, Taiwan), *T. anguiformis* (New Zealand), *T. fruticosus* (Australia, Pacific) and *T. retusus* subsp. *retusus* (Japan, Australia, Pacific) ranging into warm temperate regions (Fig. 29). The centre of diversity is in Southeast Asia with eight species occurring in the area (*T. aculeatus*, *T. combinatus*, *T. comosus*, *T. convolutus*, *T. fruticosus*, *T. gottschei*, *T. retusus*, *T. spathulistipus*), the latter reaching tropical Africa. Four further species are restricted to Western Melanesia, viz. *T. appendiculatus*, *T. discretus*, *T. mollis*, *T. montanus* (Papua New Guinea only). *Thysananthus anguiformis* is endemic to New Zealand and *T. pancheri* and *T. retusus* subsp. *sellingii* to New Caledonia. *Thysananthus amazonicus* is the only species of the subgenus occurring in the New World.

The distribution of the species and subspecies is summarized as follows (sexuality added as in Gradstein, 1975):

1. Pluriregional

a. Africa–Indochina–Malesia–Australia–Pacific

T. spathulistipus (autoicous)

b. Indochina–Malesia–Australia–Pacific

T. fruticosus (autoicous)

c. Japan–Malesia–Australia–Pacific

T. retusus subsp. *retusus* (autoicous)

- d. India–Indochina–Malesia–Australia
 - T. convolutus* (dioicous)
- e. East African Islands (Seychelles)–India (Andaman and Nicobar Islands)–Malesia
 - T. comosus* (dioicous)
- f. Japan–Taiwan–Malesia
 - T. aculeatus* (autoicous)
- 2. Tropical America
 - T. amazonicus* (paroicous and autoicous)
- 3. Malesia
 - T. combinatus* (dioicous)
 - T. gottschei* (dioicous)
- 4. Endemic
 - a. Western Melanesia
 - T. appendiculatus* (dioicous)
 - T. discretus* (dioicous)
 - T. mollis* (dioicous)
 - b. Papua New Guinea
 - T. montanus* (dioicous)
 - c. New Caledonia
 - T. pancheri* (dioicous)
 - T. retusus* subsp. *sellingii* (sexuality? sterile)
 - d. New Zealand
 - T. anguiformis* (dioicous)

The above data show that all seven endemic species and subspecies of subg. *Thysananthus* are dioicous where the three most widespread species (*T. fruticosus*, *T. retusus*, *T. spathulistipus*) of the subgenus are monoicous (autoicous). This data may indicate that dispersal plays an important role in the distribution of the species of subg. *Thysananthus*, as has also been postulated for other liverwort groups (e.g., van Zanten & Gradstein, 1988; Heinrichs et al., 2009).

ECOLOGY

The species of subg. *Thysananthus* usually grow as epiphytes on bark of trees and shrubs, twigs or logs in various stages of decay; *T. aculeatus* and *T. comosus* may also occur on rocks. Epiphyllous growth has not been observed in this subgenus. The species have been recorded from sea level to 3100 m (Table 1), with highest records from Papua New Guinea. The members of subg. *Thysananthus* occur in rain forests and montane forests, with *T. aculeatus*, *T. appendiculatus*, *T. mollis* and *T. retusus* subsp. *retusus* being restricted to the understory of the forest and being specialized shade epiphytes, while *T. amazonicus* and *T. convolutus* var. *convolutus* are sun epiphytes occurring in the canopy. The latter species can be found also in plantations. The remaining species are generalists, having rather broad vertical ranges and occurring in the understory as well as in the canopy, in open or more shaded areas, in particular *T. spathulistipus* which is a very common and variable species. *Thysananthus comosus* and *T. spathulistipus* are salt-spray tolerant taxa and may occur in coastal forests and mangrove forests.

Table 1. Habitat and elevational range of subg. *Thysananthus* species.

Species	Alt/m	Main habitat
<i>T. aculeatus</i>	200–2350	along stream, rain forests, montane forests (understory)
<i>T. amazonicus</i>	0–1000	marsh forest, swamp forest, scrub, savanna, rain forests (canopy)
<i>T. anguiformis</i>	50–150	rain forests
<i>T. appendiculatus</i>	400–2600	old gardens with regrowth species, grassland with regrowth species, rain forests, montane forests (understory)
<i>T. combinatus</i>	50	park with old planted trees
<i>T. comosus</i>	0–500	coastal forest, mangrove forest, rain forests
<i>T. convolutus</i> var. <i>convolutus</i>	10–2100	plantation, old garden site with regrowth species, swamp forest, rain forests, montane forests (canopy)
<i>T. convolutus</i> var. <i>laceratus</i>	–	–
<i>T. discretus</i>	760–2700	rain forests, montane forests
<i>T. fruticosus</i>	25–2000	rain forests, montane forests

Species	Alt/m	Main habitat
<i>T. gottschei</i> var. <i>gottschei</i>	20–2100	rain forests, montane forests
<i>T. gottschei</i> var. <i>continuus</i>	–	–
<i>T. mollis</i>	1200–3100	montane forests (understory)
<i>T. montanus</i>	1900–2300	montane forests
<i>T. pancheri</i>	40–1100	rain forests
<i>T. retusus</i> subsp. <i>retusus</i>	125–1700	grassland, rain forests, montane forests (understory)
<i>T. retusus</i> subsp. <i>sellingii</i>	400–700	rain forests
<i>T. spathulistipus</i>	85–2800	plantation, swamp forest, mangrove forest, rain forests, montane forests

CONSERVATION

No subg. *Thysananthus* species has yet been reported as extinct or endangered. However, four species including *T. aculeatus*, *T. appendiculatus*, *T. mollis* and *T. retusus* subsp. *retusus* are shade epiphytes, which are often limited to undisturbed forest and most seriously affected by disturbance (Gradstein, 1992b; Gradstein et al., 2001; Gradstein & Sporn, 2010). Sun epiphytes, however, may also be limited to undisturbed forest as is shown by the example of *T. amazonicus* (Gradstein, 1994). As advocated by conservation organizations such as IUCN (Hallingbäck & Hodgetts, 2000), protection of as much as possible of the remaining natural rain forest area may be the best approach to the conservation of the bryophyte flora.

GENERIC RELATIONSHIPS

Based on the molecular phylogenetic analysis (Sukkharak et al., submitted) *Thysananthus* is monophyletic and also includes *Dendrolejeunea* and *Mastigolejeunea*. *Dendrolejeunea*, containing only *D. fruticosa*, first described by Spruce (1884) as a subgenus of *Lejeunea*. *Dendrolejeunea* was long included in *Thysananthus* but was resurrected as a separate genus by Gradstein (1992a). Morphologically, *Dendrolejeunea* stands out by its dendroid habit, having creeping stoloniform stems and upright, regularly pinnate branches. *Mastigolejeunea* also first described by Spruce (1884) as a subgenus *Mastigolejeunea* sect.

Trigonolejeunea of *Lejeunea* and had been restored at generic rank by Schiffner (1893). Traditionally, *Thysananthus* and *Mastigolejeunea* are separated based on the different stem types and the possession of entire versus toothed involucre (Bischler, 1964; Thiers & Gradstein, 1989). Spruce (1884) was inclined to combine these two groups in single subgenus *Mastigolejeunea* but for remaining the name *Thysananthus*, he preferred to regard each group subgeneric. However, Schuster (1980) and Gradstein (1985) advocated to combine the two genera into one single genus because of the existence of intermediate taxa. In addition, Sukkharak et al. (submitted) found that *T. anguiformis* and *T. pancheri* are intermediate between *Thysananthus* and *Mastigolejeunea*, having adnate underleaves and toothed perianth like in *Thysananthus* and enlarged dorsal epidermis and entire female involucre of *Mastigolejeunea*. In addition, *T. combinatus* has toothed female involucre and perianth like in *Thysananthus* but its dorsal epidermis is enlarged like the members of *Mastigolejeunea*. Thiers & Gradstein (1989) found that *M. florea* (Mitt.) Paris has undifferentiated dorsal epidermis cells. Finally, entire perianths occur in *T. montanus*, a species recently described by Gradstein et al. (2002). The latter authors failed to observe the perianth but based on examination of the type specimen I found that this species has entire perianths, being the character of *Mastigolejeunea*. All these findings indicate that *Mastigolejeunea* is not sharply separate from *Thysananthus* and should be included in the latter genus.

Spruceanthus and *Ptychanthus* are the sister group of *Thysananthus* (Sukkharak et al., submitted). The differences among the three genera are given below.

Table 2. A comparison of *Thysananthus*, *Spruceanthus* and *Ptychanthus*.

genus character	<i>Thysananthus</i>	<i>Spruceanthus</i>	<i>Ptychanthus</i>
growth habit	projecting	projecting	dendroid
branching	<i>Lejeunea</i> -type	<i>Lejeunea</i> -type	<i>Frullania</i> -type
stem structure	epidermal cells as large as medullary cells or enlarged dorsal stem epidermal cells	epidermal cells as large as medullary cells	epidermal cells as large as medullary cells
subepidermis	absence	absence	presence
leaf cells	elongate (isodiametric in <i>T. retusus</i>)	isodiametric	elongate
oil bodies	segmented	homogeneous	segmented

number of keels	3(–10)	(3–)5–12	8–10
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CLASSIFICATION

Based on the molecular phylogenetic analysis (Sukkharak et al., submitted), the genus *Thysananthus* is divided in this monograph into 2 subgenera: subg. *Thysananthus* (15 spp., 4 varieties, 2 subspecies) and subg. *Mastigolejeunea* (Spruce) comb. nov. (14 spp.). The subgenera are characterized by the toothed resp. entire perianth and possibly by the different numbers of elaters in the capsule (66 resp. 72). Subgenus *Thysananthus* is divided into two sections: sect. *Thysananthus* and sect. *Dendrolejeunea* (Spruce) comb. nov. Each section is divided into two series: ser. *Thysananthus* and ser. *Anguiformes* ser. nov. in sect. *Thysananthus*, and ser. *Dendrolejeunea* and ser. *Sandeanthus* (B. Thiers & Gradst.) comb. nov. in sect. *Dendrolejeunea*. A synopsis of the classification is shown below.

The species concept applied in this monograph is similar to the one used by Gradstein (1975, 1994). The concept is based on the assumption that the more differences can be found among groups of populations, the more likely it is that a biological species is at hand. Accordingly, species are defined here by the presence of two or more independent, diagnostic characters. When clear-cut intraspecific discontinuities were found, two categories were applied: subspecies and varieties. The difference between both categories is geographical. Varieties are sympatric forms, whereas subspecies are allopatric forms with geographic distributions of their own which are distinct from the area occupied by the other subspecies of the same species (Gradstein, 1975).

In its current circumscription, subg. *Thysananthus* is mainly characterized by (1) *Lejeunea*-type vegetative branches, (2) stem epidermal cells large as medullary cells (dorsal epidermal cells enlarged in *T. combinatus*, *T. anguiformis*, *T. pancheri*), (3) leaves convolute when dry (spread out widely in *T. retusus*), (4) Leaf cells elongate and trigones cordate (isodiametric and trigones faint in *T. retusus*), (5) adnate underleaves present (absent in *T. discretus*, *T. fruticosus*, *T. mollis*, *T. montanus*), (6) gynoecial innovations present and with lejeuneoid leaf sequence, (7) toothed female involucre (entire in *T. anguiformis*, *T. pancheri*), and (8) perianth sharply 3-keeled and toothed (entire in *T. montanus*).

The distinction of species and infraspecific taxa in subg. *Thysananthus* is mainly based on character states of growth habit, leaf, lobule, auricle, foliar appendage, leaf cell, underleaf, adnation of leaf and underleaf, and androecium.

a. Growth habit. Growth habit separates the series *Dendrolejeunea* (*Thysananthus fruticosus*) from the rest of subg. *Thysananthus*.

b. Leaf. Particularly important is the appearance of the leaf when dry, which separates *Thysananthus retusus* from the rest of subg. *Thysananthus*, whereas *T. convolutus* separates from *T. discretus* by the appearance of the leaf when wet. In addition, *T. mollis* and *T. montanus* are distinguished by the shape of the leaf lobe.

c. Lobule. The length of the lobule can be used for distinguishing the subspecies of *Thysananthus retusus*.

d. Auricle. The presence of an auricle at the base of the underleaf separates *Thysananthus discretus* from *T. convolutus*.

e. Foliar appendage. An appendage on the leaf keel is found only in *Thysananthus appendiculatus*, *T. convolutus* var. *laceratus*, *T. discretus* and *T. gottschei* var. *continuus* but may be present on the keels of bracts and perianths, and on the mid-basal portion of bract lobules in all *Thysananthus* species. Moreover, the appendage which is attached to the lobule bases and the stem epidermis cells separates the series *Sandeanthus* (*T. mollis*, *T. montanus*, *T. retusus*) from the rest of subg. *Thysananthus*.

f. Leaf cell. The presence or absence of a vitta is the principal morphological character for distinguishing the sections of subg. *Thysananthus*. In addition, *T. retusus* is separated from the rest of subg. *Thysananthus* by its (iso)diametric leaf cells.

g. Underleaf. *Thysananthus aculeatus* and *T. comosus* are separated by the shape and appearance of underleaves. In addition, the varieties of *T. convolutus* and *T. gottschei* are distinguished by the recurved underleaves.

h. Adnation of leaf and underleaf. The presence of adnate leaves and underleaves is a stable and characteristic feature of *Thysananthus aculeatus*, *T. amazonicus*, *T. anguiformis*, *T. appendiculatus*, *T. comosus*, *T. convolutus*, *T. gottschei*, *T. pancheri* and *T. spathulistipus*. In *T. combinatus* and *T. retusus*, the underleaves and leaves may be adnate or free.

i. Androecium. Mostly male bract lobules of subg. *Thysananthus* are hypostatic, except in *T. amazonicus*, in which epistatic and hypostatic can be found. Moreover, *T. amazonicus* is the only paroicous species, all other species are autoicous or dioicous.

The classification of *Thysananthus* in this monograph is as follows:

Thysananthus subg. *Thysananthus*

sect. *Thysananthus*

ser. *Thysananthus*

1. *T. aculeatus* Herzog

2. *T. amazonicus* (Spruce) Schiffn.
 3. *T. appendiculatus* Steph.
 4. *T. combinatus* sp. nov.
 5. *T. comosus* Lindenb.
 6. *T. convolutus* Lindenb.
 var. *convolutus*
 var. *laceratus* (Steph.) comb. nov.
 7. *T. discretus* Sukkharak & Gradst.
 8. *T. gottschei* (Jack & Steph.) Steph.
 var. *gottschei*
 var. *continuus* var. nov.
 9. *T. spathulistipus* (Reinw. et al.) Lindenb.
- ser. *Anguiformes* ser. nov.
10. *T. anguiformis* (Hook. f. & Taylor) Steph.
 11. *T. pancheri* (Steph.) Hürl.
- sect. *Dendrolejeunea* (Spruce) comb. nov.
- ser. *Dendrolejeunea*
12. *T. fruticosus* (Lindenb. & Gottsche) Schiffn.
- ser. *Sandeanthus* (B. Thiers & Gradst.) comb. nov.
13. *T. mollis* Steph.
 14. *T. montanus* Gradst. et al.
 15. *T. retusus* (Reinw. et al.) B. Thiers & Gradst.
 subsp. *retusus*
 subsp. *sellingii* (Hürl.) comb. nov.
- Thysananthus* subg. *Mastigolejeunea* (Spruce) comb. nov.
16. *T. auriculatus* (Wils.) comb. nov.
 17. *T. calcaratus* (Steph.) comb. nov.
 18. *T. floreus* (Mitt.) comb. nov.
 19. *T. humilis* (Gottsche) comb. nov.
 20. *T. integrifolius* Steph.
 21. *T. innovans* (Spruce) comb. nov.
 22. *T. ligulatus* (Lehm. & Lindenb.) comb. nov.
 23. *T. plicatiflorus* (Spruce) comb. nov.
 24. *T. reconditus* (Steph.) comb. nov.
 25. *T. recurvifolius* (Mizut.) comb. nov.

26. *T. repletus* (Taylor) comb. nov.
27. *T. truncatus* (Mizut.) comb. nov.
28. *T. undulatus* (Gradst. & Grolle) comb. nov.
29. *T. virens* Ångstr.

In this monograph an artificial key to the species of the genus *Thysananthus* is provided and each species of subg. *Thysananthus* is fully described and illustrated, with extensive synonymy and detailed data on habitat and distribution. In addition, an annotated list of the species in subg. *Mastigolejeunea* is provided. A monograph of the latter subgenus should be the subject of future work.

TAXONOMIC TREATMENT

***Thysananthus* Lindenb.**, in Lehmann, Nov. Stirp. Pug 8: 24. 1844; Mizutani (1961: 152); Arnell (1963: 235); Thiers & Gradstein (1989: 66); Gradstein (1992a: 44); Gradstein (1994: 83); Gradstein et al. (2002: 70); Wigginton (2004: 282). *Lejeunea* subg. *Thysanolejeunea* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 105. 1884. *Lejeunea* subg. *Mastigolejeunea* sect. *Thysanolejeunea* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 100. 1884. *Thysanolejeunea* (Spruce) Steph., Hedwigia 28: 263. 1889, nom. inval. fide Zijlstra (1982, 1983).—Type: *Thysananthus comosus* Lindenb. Genus named for its brush-like shoots.

Plants dioicous, autoicous, or paroicous, growing in dense mats, habit deliquescent with dendroid growth, having creeping stoloniform stems and upright, regularly pinnate branches (*T. fruticosus*) or with projecting growth and irregularly (1)-pinnate, becoming ascending to erect or projecting downwards and becoming pendent (*T. amazonicus*), pale green to dull green, becoming brownish green, dark brown to black in older portions, when dry pale yellow, yellowish brown, reddish or dark brown, to 6.5 cm long × 1–5 mm wide, branches *Lejeunea*-type, flagellae present on the older portions of stems. **Stems** rather rigid (strongly rigid in *T. discretus*, rather fragile in *T. reconditus* and *T. retusus*); lateral merophyte straight longitudinal line, ventral merophyte 6–18 cells wide; in cross section round-orbicular to subelliptic in shape, 0.1–0.3(–0.5) mm high × 0.1–0.3(–0.45) mm wide, composed of (18–)25–57(–80) epidermal cells surrounding (27–)49–225(–381) medullary cells in 8–18(–22) layers, epidermal cells usually not larger than medullary cells, occasionally dorsal epidermal cells larger and somewhat thinner-walled than medulla and ventral epidermal cells (in *T.*

anguiformis, *T. combinatus* and *T. pancheri*), all cells with thickened walls, walls of epidermal cells brownish, those of medullary cells hyaline, pale brownish or yellowish brown. **Leaves** incubous, with a dorsal lobe and a smaller ventral lobule, imbricate, rarely contiguous (*T. retusus*), attached to the axis along a J-shaped insertion line which covers the whole length of the straight lateral merophytes, merophytes not interlocking; leaves when dry suberect and convolute (wide spreading and flat in *T. retusus*), when moist weakly concave with apical part plane and not recurved, to strongly concave with apical part turned to ventral side and recurved (in *T. anguiformis*, *T. combinatus*, *T. convolutus*, *T. gottschei* and *T. pancheri*); dorsal lobes symmetrically ovate to ligulate, lanceolate, oblong to falcate or asymmetrically ovate to oblong-falcate, apex round to acute, mucronate or apiculate, dorsal base cordate or auriculate, dorsal margin entire or with triangular teeth (serrate in *T. comosus*), ventral margin usually upcurved $1/2 \times$ leaf length to over most of its length (plane in *T. anguiformis*, *T. fruticosus* and *T. retusus*), becoming flat near the apex, entire or with triangular teeth; cells arranged in diverging rows, elongate-hexagonal with acute ends (subisodiametric to isodiametric in *T. retusus*), vitta cells absent or present in midportion of lobe, extending to base, $2/3 \times$ lobe length, median cells $12-35(-45) \times 5-15 \mu\text{m}$, at leaf base slightly larger, towards the margins becoming gradually smaller, at margins subquadrate, cell walls thin, trigones cordate, often coalesced, intermediate thickenings 1-2(-3) per cell wall (cell walls evenly thickened, trigones and intermediate thickening faint in *T. retusus*); cuticle smooth; oil bodies *Calypogeia*-type, 2-6(-8) per cell. **Lobules** oblong-rectangular, usually $1/5-1/3 \times$ lobe length ($1/10-1/8 \times$ in *T. mollis*), inflated, occasionally with a tiny appendage on the surface at the base; keel gradually curved, the surface smooth, sometimes with an orbicular to oblong appendage; lobule apex usually oblique and longly continuing into the ventral lobe margin, occasionally transverse and not or shortly continuing into the ventral lobe margin (in *T. aculeatus*, *T. anguiformis*, *T. fruticosus* and *T. retusus*), free margin plane, apex with 1 narrow-elongate tooth, with 1(-2) triangular teeth, or without teeth; hyaline papilla pyriform-oblong, $27-37 \times 7-12 \mu\text{m}$, at or near the proximal base of the tooth on the inner surface of the lobule. **Underleaves** imbricate, slightly squarrose (channeled or hollow in *T. aculeatus*, flat in *T. comosus*), broadly obovate, ovate or spatulate, apex rounded or truncate to emarginate, entire to serrate or toothed, plane, recurved or incurved, margins entire, recurved, central region gibbous, bases cuneate or auriculate, underleaf bases free or adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches (underleaf bases free or adnate with leaves on one side in *T. combinatus* and *T. retusus*), insertion line slightly arched; cells becoming longer towards the base of the underleaf; underleaf attachment bistratose; rhizoids brown; rhizoid discs absent. **Androecia** terminal-intercalary on *Lejeunea-*

type branches (below the gynoeceium in *T. amazonicus*), bracts and bracteoles in 2–13(–23) pairs, bracts hypostatic (epistatic in *T. ligulatus*, occasionally epistatic in *T. amazonicus*), ovate, apex acute to apiculate or mucronate, margins entire or with 1–2 teeth, lobules strongly inflated; bracteoles similar to underleaves; antheridia (1–)2 per bract. **Gynoecea** terminal on elongate branches, with 1–2 lejeuneoid innovations, innovations repeatedly fertile, forming a monochasial or dichasial pattern or both; bracts in one pair, obliquely spreading to subsquarrose, lobe ovate, ligulate or lanceolate, apex acute-apiculate, entire or with triangular or lacinate teeth; appendages sometimes present on keel on one or both sides, orbicular-oblong; lobules broadly ovate, $2/3$ – $1/2 \times$ lobe length, apex apiculate to bifid; appendages sometimes present at the middle of basal part, orbicular-oblong; bracteoles spatulate, apex emarginate to bifid, $1/2 \times$ bracteole length with triangular teeth, the teeth consisting of 3–7 cells, 2–3 cells wide at base and ending in a row of 1–2 cells, margins plane or recurved, central region gibbous. **Perianths** exerted to $1/2$, obovate or oblong-cylindrical, 2.5 – 2.6×1.1 – 1.3 mm, apex truncate, surface sharply 3-keeled, keels in upper $1/3$ with numerous lacinate or triangular teeth (entire in *T. montanus* and subg. *Mastigolejeunea*); appendages on basal part of keel or not developed; beak 3–5(–7) cells long. **Calyptra** entirely enveloping the young sporophyte, 1–2 stratose, outer cells larger than inner cells. **Sporophyte** exerted up to 2.5 mm above the perianth; foot 5–6 transversal cell rings; setae 22–25 cells long, non-articulate, with 16 outer rows of cells and 4 inner row; capsules globose, dark-brown, 0.2–0.3 mm in diameter, dehiscing from the apex downward into 4 valves, valves recurved $3/4$ of their length, with a rectangular-shaped hinge, inner valve surfaces covered by a yellow-brown, monofenestrate or plurifenestrate layer of thickening; elaters linear, 350 – 550×12 – 20 μm , with one brown spiral band, 66 (in subg. *Thysananthus*) or 72 (in subg. *Mastigolejeunea*) per capsule, attached to both surface and margins of valve in “1+3+5+6” or “2+4+6+6” pattern (in subg. *Thysananthus*, unknown in subg. *Mastigolejeunea*), elateroids absent; spores subisodiametric to oblong, surface with numerous bluntish papillae, 1–4 rosettes per facet, rosettes with 5–8 sharp, smooth papillae, 8–12 μm in diameter. **Sporelings** of the *Lopholejeunea*-type. **Vegetative reproduction** absent.

Chromosome number. $n = 9$ (in *Thysananthus aculeatus* and *T. spathulistipus*), $n = 8 + m$ (in *T. floreus*) (Fritsch, 1991).

Chemistry. Sesquiterpenoids, unidentified diterpenoids, flavonoids, stigmasterol and aromatic hydroxy acids (Gradstein et al. 1985, Kruijt et al. 1986, Harinantenaina et al. 2006, Sukkharak et al., in press).

Distribution and ecology. Pantropical, ranging in altitude from sea level up to 3100 m in Papua New Guinea. The centre of diversity is in Southeast Asia. All species are epiphytes

(not epiphyllous), growing on stems or twigs of living trees or decaying wood in logging areas, along roadsides, in cultivated areas (plantations, gardens, etc), savannas, rain forests and montane forests. Occurrence on rock along stream, coastal forests and in mangrove forests is very rare.

KEY TO THE SUBGENERA, SECTIONS AND SECTIONS OF *THYSANANTHUS*

1. Perianth toothed (except *T. montanus*).....subg. *Thysananthus* 2
2. Leaf lobe without vitta.....sect. *Thysananthus* 3
3. Stem with epidermal cells as large as medulla cells (except *T. combinatus*). Underleaf bases free or adnate with leaves on one side. Margins of female bracts and bracteoles and bracteoles toothed..... ser. *Thysananthus*
3. Dorsal epidermis cells of stem larger than inner cells. Underleaf bases adnate with leaves on one side. Margins of female bracts and bracteoles entire..... ser. *Anguiformes*
2. Leaf lobe with vitta.....sect. *Dendrolejeunea* 4
4. Plants dendroid, with creeping stoloniform stems and ascending leafy stems. Branching of leafy stems regularly pinnate. Lobule bases without appendage..... ser. *Dendrolejeunea*
4. Plants with projecting growth and irregularly pinnate branching. Lobule bases with appendages..... ser. *Sandeanthus*
1. Perianth entire.....subg. *Mastigolejeunea*

ARTIFICIAL KEY TO THE SPECIES OF THE GENUS *THYSANANTHUS*

1. Leaf lobe without vitta.
2. Leaf margins entire.
3. Underleaf bases with well-developed auricles..... *T. discretus*
3. Underleaf bases without well-developed auricles.

4. Leaves when moist weakly concave, apical parts plane, not recurved.
5. Underleaves toothed.
6. Dorsal base of leaves auriculate. Underleaves obovate. Perianth teeth laciniate, 4–5 cells long. Paleotropical..... *T. comosus*
6. Dorsal base of leaves not auriculate. Underleaves spatulate. Perianth teeth triangular, 1–3 cells long. Neotropical..... *T. amazonicus*
5. Underleaves entire.
7. Dorsal epidermis cells of stem not larger than inner cells. Female bracteole apex bifid. Tropical Africa..... *T. floreus*
7. Dorsal epidermis cells of stem larger than inner cells. Female bracteole apex rounded-truncate. Tropical America, Asia.
8. Lobules with (2–)3–5 teeth.
9. Male bracts at base of spike larger than at apex. Paleotropical..... *T. integrifolius*
9. Male bracts small throughout spike. Neotropical, rare..... *T. innovans*
8. Lobules with (0–)1 tooth.
10. Lobule teeth elongate, 3–6 cells long.
11. Lobules $1/2 \times$ leaf length..... *T. calcaratus*
11. Lobules $1/4$ – $1/3 \times$ leaf length.
12. Leaves oblong, leaf apex acute-apiculate..... *T. undulatus*
12. Leaves ovate, leaf apex rounded..... *T. virens*
10. Lobule teeth triangular, 1–2 cells long.
13. Leaf margins recurved
14. Leaf margins undulate..... *T. truncatus*

14. Leaf margins not undulate..... *T. recurvifolius*
13. Leaf margins not recurved.
15. Leaf apex acute-apiculate..... *T. repletus*
15. Leaf apex rounded or obtuse
16. Leaves rounded-ovate, less than 1.5× longer than wide
17. Stem rigid, stem epidermal cells thick-walled. Perianths 3-keeled..... *T. humilis*
17. Stem fragile, stem epidermal cells thin-walled. Perianths 10-keeled in upper half
..... *T. reconditus*
16. Leaves oblong, more than 1.5× longer than wide
18. Male bract lobules epistatic, distant from each other. Paleotropical..... *T. ligulatus*
18. Male bract lobules hypostatic, imbricate. Neotropical
19. Underleaves squarrose. Perianth with a sharp ventral keel, subsidiary folds lacking. South America except Amazonia..... *T. auriculatus*
19. Underleaves flat. Perianth with swollen ventral keel and subsidiary folds. Northern South America..... *T. plicatiflorus*
4. Leaves when moist strongly concave, apical parts turn to ventral side, recurved.
20. Underleaves spatulate, entire or slightly toothed. Dorsal epidermis cells of stem not larger than inner cells..... *T. gottschei*
20. Underleaves obovate, entire. Dorsal epidermis cells of stem larger than inner cells.
21. Dorsal base of leaves not auriculate. Perianth teeth triangular, 1–2 cells long..... *T. anguiformis*
21. Dorsal base of leaves auriculate. Perianth teeth laciniate, 2–7 cells long.
22. Lobule teeth triangular, 1–3 cells long. New Caledonia..... *T. pancheri*

22. Lobule teeth elongate, 4–5(–6) cells long. Malesia..... *T. combinatus*
2. Leaf margins toothed.
23. Leaves symmetric.
24. Lobule keel on one side of the stem with a foliar appendage (on the side where leaves and underleaves are free)..... *T. appendiculatus*
24. Lobule keel without foliar appendage..... *T. spathulistipus*
23. Leaves asymmetric.
25. Underleaf bases with well-developed auricles..... *T. discretus*
25. Underleaf bases without well-developed auricles.
26. Leaves when moist strongly concave, apical parts turn to ventral side, recurved. Underleaves spatulate..... *T. convolutus*
26. Leaves when moist weakly concave, apical parts plane. Underleaves obovate.
27. Dorsal base of leaves auriculate. Underleaves flat. Perianth teeth laciniate, 4–5 cells long..... *T. comosus*
27. Dorsal base of leaves not auriculate. Underleaves channeled/hollow. Perianth teeth triangular, 1–2 cells long..... *T. aculeatus*
1. Leaf lobe with vitta.
28. Branching regularly pinnate. Stoloniform creeping stems present..... *T. fruticosus*
28. Branching irregularly pinnate or branches lacking. Stoloniform creeping stems lacking.
29. Leaves when dry widely spreading, loosely reflexed or plane. Leaf cells (except for vitta) subisodiametric..... *T. retusus*
29. Leaves when dry convolute. Leaf cells elongate.
30. Leaves lanceolate, toothed (rarely entire). Leaves when dry laterally appressed to the stem or convolute. Perianth teeth triangular, 1–2 cells long *T. mollis*

30. Leaves oblong, entire. Leaves when dry convolute. Perianth entire..... *T. montanus*

Thysananthus* subgenus *Thysananthus

Perianth toothed (except *T. montanus*).

Type species: *Thysananthus comosus* Lindenb.

Distribution: tropical America, Africa, Indochina, Malesia, Australia, Pacific.

Thysananthus* section *Thysananthus

Leaves without vitta.

For distribution see under subg. *Thysananthus*.

Thysananthus* series *Thysananthus

Stem with epidermal cells as large as medulla cells (except *T. combinatus*). Underleaf bases free or adnate with leaves on one side. Margins of female bracts and bracteoles toothed.

For distribution see under subg. *Thysananthus*.

1. *Thysananthus aculeatus* Herzog (Figs. 7–8)

Ann. Bryol. 4: 89. 1931; Verdoorn (1934: 174); Mizutani (1961: 153; 1969: 137; 1977: 135).—Type: PHILIPPINES. Luzon: Mt. Banahao, 20 XII 1913, *Baker 7079*, (lectotype, here designated: JE!; isoelectotypes: PC!, U!). PHILIPPINES. Luzon: Mt. Banahao, 20 XII 1913, *Baker 7083* (paralectotype: JE!).

Thysananthus formosanus Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 252. 1934.—Type: TAIWAN. Taito: between Shinsuiei and Shucho-kyokai, 3 I 1933, *Y. Horikawa 10622* (holotype: HIRO!).

Thysananthus richardsianus Verd., Ann. Bryol. Suppl. 4: 173. 1934.—Type: MALAYSIA. Sarawak: “G. Balapau, Ulu Tinjar, in silvis et ad arb. truncos, 750 m, XI 1932”, *P. Richards s.n.*, Hep. Sel. Crit. Verdoorn 398 (holotype: FH!; isotypes: BM!, BM-K!, BR!, C!, G! 2 packets, JE!, L! 2 packets, NY!, PC!, S!, U!, W!).

Plants autoicous, with projecting growth, turning upwards and becoming ascending to erect, yellowish brown to dark brown in herbarium specimens, up to 3.5 cm long × 1–1.8 mm wide. **Stems** rather rigid; ventral merophyte 9–10 cell rows wide; in cross section round-orbicular in shape, 200–211 µm high × 160–180 µm wide, composed of 38–42 epidermal

cells surrounding 103–121 medullary cells in 10–14 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute, when moist weakly concave, apical parts plane, not recurved; dorsal lobe asymmetrically ovate, $0.8\text{--}1 \times 0.5\text{--}0.7$ mm, apex obliquely acute, dorsal base cordate, dorsal margin with 4–7 triangular teeth, the teeth consisting of 3–4 cells, being 2–3 cells wide at base, apex of one cell, ventral margin slightly upcurved, with 12–13 triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base, apex of one cell; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells $7\text{--}12 \times 7\text{--}10\text{ }\mu\text{m}$, median cells $22\text{--}35 \times 7\text{--}10\text{ }\mu\text{m}$, basal cells $25\text{--}50 \times 10\text{--}22\text{ }\mu\text{m}$, trigones cordate, often coalesced, intermediate thickenings 0–2 per cell wall; oil bodies 3–4 per cell (Mizutani, 1961). **Lobules** oblong-rectangular, $0.2\text{--}0.3 \times 0.1\text{--}0.2$ mm, $1/4\text{--}1/3 \times$ lobe length; appendage on surface of lobule base not developed; keel without appendage; lobule apex transverse, not or shortly continuing into the ventral lobe margin, apex with one triangular tooth, the teeth consisting of 4–6(–36 in *Baker 7083*) cells, being 2–6 cells wide at base and ending in a row of (1–)2–3 cells. **Underleaves** imbricate, channeled or hollow, obovate, $0.5\text{--}0.6 \times 0.4\text{--}0.5$ mm, $3\text{--}4 \times$ stem width, apex truncate, plane, with 8–15 triangular teeth, the teeth consisting of 3–4 cells, being 2 cells wide at base, apex of one cell, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells $13\text{--}20 \times 7\text{--}10\text{ }\mu\text{m}$. **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 3–12 pairs, bracts hypostatic, $0.7\text{--}0.8 \times 0.5\text{--}0.6$ mm, apex acute, margins entire; antheridia 2 per bract. **Gynoecia** with 2 lejeuneoid innovations forming a dichasial pattern; lobe ovate, $0.5\text{--}1.4 \times 0.3\text{--}0.7$ mm, apex apiculate, margins in upper $1/3$ with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base, apex of one cell; lobules broadly ovate, $1/2\text{--}2/3 \times$ lobe length, apex apiculate, margins with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in row of 1–2 cells; bracteoles spatulate, $1.2\text{--}1.3 \times 0.7\text{--}0.8$ mm, apex emarginate, $1/3 \times$ bracteole length with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base, apex of one cell, margins plane. **Perianths** oblong-cylindrical, $1.7\text{--}1.8 \times 0.7\text{--}0.8$ mm, keels in upper $1/3$ with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; beak $53\text{--}71\text{ }\mu\text{m}$ with 3 cells long.

Chromosome number. $n = 9$ (Fritsch, 1991).

Chemistry. Unknown.

Additional illustrations. Herzog (1931, p. 88, Fig. 3); Horikawa (1934, p. 20, Figs. 1–10 as *Thysananthus formosanus*); Mizutani (1961, p. 154, Fig. VI. 1–23).

Distribution and ecology. Southern Japan, Taiwan, Malaysia and Philippines; 200–2350 m; on moist rocks along streams and on bark of trees in the understory of rain forests and montane forests.

REPRESENTATIVE SPECIMENS. **Japan.** KAGOSHIMA: Amami Ōshima, Kawauchi River, 1 Dec 1988, *Inoue s.n.* (BR, C, G, L, PC, S, U); Suzukawa near Onoaida, *Mizutani 10313, 10372* (L, S); Miyanoura, Jul 1951, *Amakawa s.n.* (C, L, S, W); along Hana-age river, *Tagawa & Kitagawa 561* (S, W); along Odagumi river, *Tagawa & Kitagawa 939* (S, W); Yakushima, *Faurie 750* (BM, G); Yakushima, Jul 1900, *Faurie s.n.* (PC).—OKINAWA: Ryukyu Islands, Oogimi, 28 Jan 1955, *Amano s.n.* (BM, BR, C, G, L, S, W). **Taiwan.** the type of *Thysananthus formosanus*, *Horikawa 10642* (HSNU) (J. Wang, pers. comm.).

Malaysia. SARAWAK: the type of *Thysananthus richardsianus*. **Philippines.** BENGUET: Baguio, Mt. Santo Tomas, *Onraedt 84.P.10959* (BR, JE), *Aptroot 20370a* (U).—LAGUNA AND QUEZON: the type.—ORIENTAL MINDORO: Mt. Halcon, “*Dhenill 5709a*” (G), *Salgado 88.P.12142* (BR).—ZAMBALES: without location, Dec 1907, *Curran & Merrit s.n.* (G).

Gradstein et al. (2002) treated *Thysananthus aculeatus* as a synonym of *T. spathulistipus* whereas Verdoorn (1934) treated the two taxa as separate species. The difference between both taxa was discussed by Verdoorn (l.c.). Based on examination of a number of collections, I found that the asymmetrical leaves (symmetrical in *T. spathulistipus*), lobule apex transverse, not or shortly continuing into the ventral lobe margin (lobule apex oblique, longly continuing into the ventral lobe margin in *T. spathulistipus*) and channeled/hollow obovate underleaves (spathulate in *T. spathulistipus*) in *T. aculeatus* are sufficiently distinct to keep both taxa separate.

Thysananthus aculeatus was described by Herzog in 1931 based on two specimens, *Baker 7079* and *7083*. The two specimens are different in the number lobule tooth cells (4–6 cells in specimen nr. 7079 while 12–36 cells in nr. 7083). In the original description, the variation in lobule teeth was not mentioned, however, the original figure of the lobule teeth was drawn from specimen nr. 7079 only. I have chosen the latter specimen as the lectotype of this species because it is good material with perianths.

Mizutani (1961) considered *Thysananthus formosanus* and *T. richardsianus* as a synonym of *T. aculeatus*. In addition, he showed that the difference between *T. aculeatus* and *T. richardsianus* is only the size of the first tooth of the leaf-lobule. Variation in shape and size of the teeth of the leaf-lobule is common and is also seen in, e.g., *Spruceanthus semirepandus* (Nees) Verd., *Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) A. Evans,

Cheilolejeunea imbricate (Nees) Steph., etc. In the present study it appeared that *T. formosanus* is somewhat intermediate between *T. aculeatus* and *T. richardsianus*, having the appearance and innovation pattern like in *T. aculeatus* and the curved, elongate lobule teeth of *T. richardsianus*. I, therefore, treat them all as one species and reduce *T. formosanus* and *T. richardsianus* to a synonym of *T. aculeatus*. The type of *T. richardsianus* was distributed by Verdoorn in his exsiccata series (F. Verdoorn (ed.), Hep. Sel. Crit. VIII: 398) and the label data of the exsiccata are slightly different from the specimen data in the original publication.

2. *Thysananthus amazonicus* (Spruce) Schiffn. (Fig. 9)

in Engler & Prantl, Nat. Pflanzenfam. 1, 3:130. 1893; Stephani (1912: 784); Fulford (1941: 37); Gradstein (1994: 84). *Lejeunea* (subg. *Thysanolejeunea*) *amazonica* Spruce, Trans. & Proc. Bot. Soc. Edinburgh. 15: 106. 1884.—Type: BRAZIL. Pará: Spruce s.n. (lectotype, designated by Fulford, 1941: MANCH; isoelectotypes: G, MANCH, NY, fide Gradstein, 1994).

Plants paroicous and autoicous, with projecting growth, turning upwards and becoming ascending to erect, or project downwards and becoming pendent, green to dull brown in the field, yellowish to reddish brown in herbarium specimens, up to 1.6 cm long \times 2–2.9 mm wide. **Stems** rather rigid; ventral merophyte 7–9 cell rows wide; in cross section round-orbicular in shape, 175–188 μm high \times 161–167 μm wide, composed of 29–32 epidermal cells surrounding 63–73 medullary cells in 12–14 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute, when moist weakly concave, apical parts plane, not recurved; dorsal lobe asymmetrically oblong-falcate, 1.2–1.7 \times 0.6–1 mm, apex apiculate, margin entire, dorsal base cordate, ventral margin upcurved $1/2 \times$ leaf length; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 5–7.5 \times 7.5–12.5 μm , median cells 15–27.5 \times 7.5–10 μm , basal cells 50–70 \times 10–22 μm , trigones cordate, often coalesced, intermediate thickenings 0–2(–3) per cell wall; oil bodies (3–)4–6 per cell. **Lobules** oblong-rectangular, 0.2–0.5 \times 0.1–0.2 mm, $1/5$ – $1/3 \times$ lobe length; appendage on surface of lobule base not developed; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex entire or with 1(–2) triangular teeth, the first tooth consisting of 3–6 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, the second tooth consisting of 3–5 cells, being 1–2 cells wide at base and ending in a row of 1–2 cells, often obsolete. **Underleaves** imbricate, slightly squarrose, broadly spatulate, 0.7–1 \times 0.5–0.9 mm, 3–4 \times stem width, apex emarginate-lunulate, plane,

with 8–12 triangular teeth, the teeth consisting of 7–9 cells, being 2–3 cells wide at base, apex of one cell, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells $15\text{--}20 \times 5\text{--}8 \mu\text{m}$. **Androecia** below the gynoecium or terminal-intercalary on lateral branches, bracts and bracteoles in 2–8 pairs, bracts epistatic or hypostatic, $0.8\text{--}1 \times 0.3\text{--}0.5 \text{ mm}$, apex acute, margins entire; antheridia 2 per bract (Gradstein, 1994: 1–2 antheridia). **Gynoecia** with one lejeuneoid innovation forming a monochasial pattern; lobe ovate, $1.3\text{--}1.5 \times 0.6\text{--}0.8 \text{ mm}$, apex apiculate, margins in upper 1/3 with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; lobules broadly ovate, $1/2\text{--}2/3 \times$ lobe length, apex apiculate to slightly bifid, margin with triangular teeth, the teeth consisting 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; bracteoles spatulate, $1.1\text{--}1.4 \times 0.5\text{--}0.7 \text{ mm}$, apex emarginate to short bifid, $1/3 \times$ bracteole length with 12–14 triangular teeth, the teeth consisting of 3–7 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells long at apex, margins recurved. **Perianths** oblong-cylindrical, $1.4\text{--}1.7 \times 0.6\text{--}0.8 \text{ mm}$, keels in upper 1/3 with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells at base and ending in a row of 1–3 cells; beak 300–600 μm with 3–4 cells long.

Chromosome number. Unknown.

Chemistry. Cadinane sesquiterpenoids, diterpene acetates as major components and sterols (Gradstein et al., 1985).

Additional illustrations. Fulford (1941, p. 38, Figs. 28–40); Gradstein (1994, p. 85, Fig. 23).

Distribution and ecology. Tropical America (Colombia, Amazonian part of Brazil, Venezuela, Trinidad and Guianas; disjunct in Costa Rica and eastern Cuba); from sea level to about 1000 m; on branches, twigs, trunks or lianas, occasionally on logs, in marsh forest, swamp forest, evergreen forests on white sand, and savannas; usually in the forest canopy.

REPRESENTATIVE SPECIMENS. **Martinique**. LA TRINITÉ: Basse Comté, *Cremers 5557* (BR). **Costa Rica**. LIMÓN: Tortuguero, *Cleef & Kapelle s.n.* (GOET), *Timme 11158* (GOET). **Colombia**. AMAZONAS: Rio Caqueta TRA 12 km, *Mohr & Sosa 20* (U). **Venezuela**. BOLÍVAR: Cerro Guaiquinima, *Sipman 26654, 26678* (U). **Guyana**. CUYUNI-MAZARUNI: Essequibo river, *Richards 510* (BM-K, GOET), *188* (BM-K).—DEMERARA-MAHAICA: Timehri, Thomson's farm, *Gradstein 4709* (G, GOET), *Cornelissen & ter Steege C017* (U).—UPPER DEMERARA-BERBICE: Mabura hill, *Cornelissen & ter Steege C111, C679, C680, C681, C682, C743, C744, C761, C762, C829, C860, C861* (U).—UPPER MAZARUNI: North slope of Mt. Roraima, *Gradstein 5151* (G, U); Waruma river, *Gradstein 4993* (G, U); Mt. Latipu,

Gradstein 5560, 5650 (U); Waramadan, trail to Mt. Pwipwi, *Gradstein* 5693 (BR, G, U); Jawalla, at confluence of Kukui river and Mazaruni river, *Gradstein* 4835, 4911 (U), 4857 (G, U). **Suriname.** NICKERIE: Nickerie, area of Kabalebo dam project, *Bekker* 1086a, 1090, 1160b, 1164b, 1166, 1174, 1176, 1177, 1195, 1296, 1343, 1346b, 1361a, 1375, 1387, 1427b, 1459, 1471, 1475, 1483b, 1494b, 1514, 1522b, 1526b, 1530, 1554, 1555, 1749c, 1756a (U), *Florschütz-de Waard & Zielman* 5187A, 5189A, 5529A (U); Jodensavanne-Mapane kreek area, *Lindeman* 3937 (GOET; PC); Marchal creek, *Gradstein* s.n. (GOET).—SIPALIWINI: Blanche Marie valley, *Muñoz* 98–19 (GOET). **French Guiana.** CAYENNE: Trésor reservation, *Hartmann & al.* 04–052 (GOET); Montagne de Kaw, *Hartmann & al.* 04–117, 04–118 (GOET), *Cornelissen & ter Steege* C0265, C0311 (U), *Gradstein* 5900 (U); forest between savanna one and “petit savanna”, *Hartmann & al.* 04–120, 04–121, 04–123 (GOET); Emerald Jungle village, *Holz* FG00–51A, FG00–55 (GOET); bridge over Comté river, *Gradstein* 6658 (U); Montsinery, along “Risque tout” forest track, *Gradstein* 5793 (U); Saül, along La Fumée trail, *Gradstein* 6131 (U), *Aptroot* 15381, 15447 (U), *Montfoort & Ek* 1164, 1165, 1166, 1167, 1168, 1169 (U).—SAINT-LAURENT-DU-MARONI: Charvein, 20 Jan 1914, *Benoist* s.n. (PC); along trail from St. Laurent to Apatoa, *Cornelissen & ter Steege* C0270 (U). **Brazil.** AMAZONAS: Lages river, *Vital & Yano* 718 (U); Manaus, Reserve Experimental do INPA, *Prance & al.* 18714 (U); Tarumã Fülle, *Schäfer-Verwimp & Verwimp* 9815 (BR); along Manaus-Caracaraí road, 8 Jul 1974, *Vital & al.* s.n. (U); *ibid.*, 13 Nov 1973, *Berg & al.* P19514 (U); Caqueta river, *Mohr & Sosa* 20 (GOET); Trombetas river, *Campbell & al.* P22268 (U), *Prance & al.* 22208 (U); Madeira river, *Ule* 585 (G); Juruú river, *Ule* 338 (G); Rio Negro, *Ule* 571 (G).—PARÁ: the type.

Reported from Cuba (Holguin and Guantánamo), Trinidad (East of Sangre Grande) and Venezuela (Amazonas) by *Gradstein* (1994).

Thysananthus amazonicus often grows more or less pendent, especially when occurring on small branches or twigs (*Gradstein*, 1994). The leaf lobules of *T. amazonicus* may have one or two teeth and sometimes there is no tooth at all. According to *Gradstein* (1994) the leaf lobule is usually 1/4 or less the length of the leaf but in some Cuban specimens the lobules may be slightly larger, up to 1/3× leaf length.

Thysananthus amazonicus is morphologically most closely related to the Asiatic *T. comosus*, from which it is readily distinguished by (1) slightly squarrose spatulate and emarginate-lunulate underleaves (flat obovate and truncate in *T. comosus*), (2) monoicous (dioicous in *T. comosus*), (3) epistatic or hypostatic male bract lobules (hypostatic in *T. comosus*), and (4) triangular perianth teeths, 1–3 cells long (laciniate, 3–6 cells long in *T.*

comosus). *Thysananthus amazonicus* may also be confused with *T. spathulistipus*. However, *T. spathulistipus* differs by toothed (sometimes entire) leaf margin, truncate underleaves, hypostatic male bract lobules and occurrence in paleotropics.

Along the Rio Caqueta, Colombia, *Thysananthus amazonicus* is called “lama” and is used as a painkiller against snake and scorpion poisoning (Mohr & Sosa, in sched.; fide Gradstein, 1994).

3. *Thysananthus appendiculatus* Steph. (Fig. 10)

Sp. Hepat. 4: 794. 1912; Mizutani & Piippo (1986: 484); Gradstein et al. (2002: 70). *Thysanolejeunea appendiculata* Steph., Hedwigia 35: 138. 1896, nom. inval.—Type: PAPUA NEW GUINEA. Western: Fly River Branch, *Bäuerlein* 85 (lectotype, designated by Verdoorn, 1934: G!); Icon. Steph. nr. 10166.

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, yellowish brown in herbarium specimens, up to 2.5 cm long \times 2–2.2 mm wide. **Stems** rather rigid; ventral merophyte 9–12 cell rows wide; in cross section round-orbicular in shape, 228–260 μm high \times 188–250 μm wide, composed of 41–55 epidermal cells surrounding 95–118 medullary cells in 13–14 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute, when moist weakly concave, apical parts plane, not recurved; dorsal lobe symmetrically oblong-falcate, 1.1–2.5 \times 0.8–1.4 mm, apex apiculate, dorsal base auriculate, auricle 77–225 \times 75–250 μm , dorsal margin with 3–5 triangular teeth, the teeth consisting of 3–7 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, ventral margin upcurved $1/2 \times$ leaf length with 8–10 triangular teeth, the teeth consisting of 3–8 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 7–13 \times 5–8 μm , median cells 17–35 \times 5–10 μm , basal cells 30–57 \times 12–15 μm , trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies unknown. **Lobules** oblong-rectangular, 0.4–0.5 \times 0.1–0.2 mm, $1/5$ – $1/3 \times$ lobe length; appendage on surface of lobule base not developed; keels with appendages on one side where leaves and underleaves are free and opposite to adnate ones; lobule apex oblique, longly continuing into the ventral lobe margin, apex with 1(–2) triangular teeth, the first tooth consisting of 3–6 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, the second tooth of one cell only, often obsolete. **Underleaves** imbricate, slightly squarrose, broadly spatulate, 0.9–2.2 \times 0.5–0.9 mm, $3\text{--}4 \times$ stem width, apex truncate to emarginate, plane, with 9–11 triangular teeth, the teeth consisting

of 3–6 cells, being 2–3 cells wide at base, apex of one cell, bases cuneate or auriculate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells $15\text{--}20 \times 5\text{--}7 \mu\text{m}$. **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 4–13 pairs, bracts hypostatic, $0.6\text{--}0.9 \times 0.4\text{--}0.6 \text{ mm}$, apex acute, margins entire; antheridia 2 per bract. **Gynoeceia** with 2 lejeuneoid innovation forming a dichasial pattern; lobe ovate, $2.2\text{--}2.4 \times 1\text{--}1.1 \text{ mm}$, apex apiculate, margins in upper 1/3 with triangular teeth, the teeth consisting of 3–8 cells, being 2–3 cells wide at base and ending in a row of 1–3 cells; lobules broadly ovate, $1/2 \times$ lobe length, apex apiculate, margin with triangular teeth, the teeth consisting 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; bracteoles spatulate, $1.8\text{--}1.9 \times 0.9\text{--}1.1 \text{ mm}$, apex emarginate, $1/3 \times$ bracteole length with triangular teeth, the teeth consisting of 3–7 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, margins slightly recurved. **Perianths** oblong-cylindrical, $1.9\text{--}2.1 \times 0.8\text{--}0.9 \text{ mm}$, keels in upper 1/3 with numerous lacinate teeth, with 2–4 cells long at apex; beak $62\text{--}65 \mu\text{m}$ with 5 cells long.

Chromosome number. Unknown.

Chemistry. Six flavonoids and six aromatic hydroxy acids (Kruijt et al., 1986).

Distribution and ecology. Endemic to Western Melanesia: Western New Guinea (Indonesia) and Papua New Guinea; 400–2600 m; on trunks, branches, large vines, stems of treelets in old garden sites, grasslands with regrowth species, understory of rain forests (secondary forests) and montane forests.

REPRESENTATIVE SPECIMENS. **Indonesia.** WESTERN NEW GUINEA: Papua, Cycloop Mts., *Royen & Sleumer 6006* (JE, L); West Papua, Arfak Mts., *Beccari s.n.* (JE, L). **Papua New Guinea.** CENTRAL: K. B. Sawmill, *Streimann & Naoni 16567* (JE).—EASTERN HIGHLAND: Daulo Pass, *Streimann 18124* (JE), *Streimann & Bellamy 18093* (JE), *Streimann & Kairo 18138* (LAE); track to Mt. Michael, *Streimann 18807* (JE).—GULF: Bema-Kaintiba road, *Streimann 33647* (JE).—MOROBE: Wau, Mt. Kaindi, *Gradstein 3875* (U), *Streimann 22497* (LAE); Kunai Creek, *Gradstein 3962* (G); Ogeramnang, *Clemens 5414* (JE, PC, S, W); Slate creek & Gumi creek divide, *Streimann 13829, 13834* (JE), *13826, 13838* (LAE), *13859* (JE, LAE); Bulolo-Watut divide, *Streimann 25022* (JE); Kaisenik logging area, *Shea 6336* (JE); Upper Watut river, *Streimann 23092* (JE); Aseki-Bulolo road, *Streimann 23191, 26124* (JE, LAE), *23195* (LAE); Pouyu village, *Streimann & Tamba 12674* (JE, LAE); Oomsis logging area, *Streimann 25836* (JE); Aiuwa-Bakia track, *Streimann & Tamba 12358* (JE, LAE), *12276, 12362, 12377, 12413* (LAE).—SIMBU: Dirima mission, *Toia 171* (LAE).—SOUTHERN HIGHLANDS: Margarima-Tari road, *Streimann 24378, 24388* (JE, LAE, W); Onim

forestry station, *Streimann* 24628, 24740 (JE); Komo-Tari road, *Streimann* 32618, 32631 (JE); Kengaput, *Streimann* 26902 (JE), 23702 (LAE); Lama Sawmill logging area, *Streimann* 26422, 26562 (JE); Tari gap, *Streimann* 32730 (JE).—WESTERN: the type.—WESTERN HIGHLAND: Kum Magei Mts., *Streimann* 20679 (JE, LAE).

The most outstanding character of *Thysananthus appendiculatus* is the foliar appendage which is developed on the keels of leaves on one side of the stem only, on the side where leaves and underleaves are free and opposite to adnate ones. This character is otherwise only found in *T. anguiformis*, *T. convolutus* var. *laceratus*, *T. discretus*, *T. fruticosus* and *T. gottschei* var. *continuus*. Differences are discussed under *T. discretus*. *Thysananthus appendiculatus* is closely related to *T. spathulistipus*; the latter species differs essentially by the absence of the appendage and by the triangular perianth teeth with 1–2 cells long.

The epithet “*appendiculatus*” is derived from the foliar appendage which is found on the keels of leaves as described by Stephani in the original description. The original drawing of *Thysananthus appendiculatus* in Stephani’s “*Icones Hepaticarum Ineditae*” is erroneous in showing a foliar appendage on both sides of stems. The shown left-hand side appendages are probably parts of the dissected underleaves. Note that the illustration of the species in Gradstein et al. (2002: Fig. 44) does not show the foliar appendage.

4. *Thysananthus combinatus* sp. nov. (Fig. 11)

Type. MALAYSIA. Perak: Taiping, on old planted trees in park around Taiping lake at the foot of Maxwell Hill, ca 50 m, on tree buttress, 9 Mar 2004, *Gradstein et al.* 10366 (holotype: GOET!). The epithet *combinatus* refers to the occurrence of characters of ser. *Thysananthus* and ser. *Anguiformes* in this species.

Cellulae epidermales dorsales dilatatae. Amphigastria integra. Lobuli dentis elongatis 4–6 cellulis longibus.

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, dark brown in herbarium specimens, up to 1.4 cm long × 0.8–1.5 mm wide. **Stems** strongly rigid; ventral merophyte 8–9 cell rows wide; in cross section orbicular-subelliptic in shape, 137–200 µm high × 112–190 µm wide, composed of 20–37 epidermal cells surrounding 31–93 medullary cells in 16–22 layers high, dorsal epidermal cells larger and somewhat thinner-walled than medulla and ventral epidermal cells. **Leaves** imbricate, when dry suberect and convolute, when moist concave, apical parts turn to ventral side, recurved;

dorsal lobes asymmetrically ovate, $0.6\text{--}0.7 \times 0.5\text{--}0.6$ mm, apex apiculate, margin entire, dorsal base auriculate, ventral margin upcurved $1/2 \times$ leaf length; cells elongate-hexagonal with acute ends, vitta cells absent, marginal lobe cells $12\text{--}17 \times 10\text{--}12$ μm , median cells $20\text{--}25 \times 7\text{--}12$ μm , basal cells $30\text{--}37 \times 15\text{--}22$ μm , trigones cordate, often coalesced, intermediate thickenings 0–1(–2) per cell wall; oil bodies unknown. **Lobules** rectangular, $0.2\text{--}0.3 \times 0.1\text{--}0.2$ mm, $1/3 \times$ lobe length; appendage on surface of lobule base not developed, keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex with one elongate tooth, the tooth consisting of 6 cells, being 2–3 cells wide at base and ending in a row of 4–5(–6) cells. **Underleaves** imbricate, slightly squarrose, broadly obovate, $0.4\text{--}0.5 \times 0.5\text{--}0.6$ mm, $3\text{--}4 \times$ stem width, apex broadly rounded to truncate, plane, entire, bases cuneate, underleaf bases free or adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells $17\text{--}20 \times 7\text{--}10$ μm . **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 8–10 pairs, bracts hypostatic, $0.6\text{--}0.7 \times 0.3\text{--}0.4$ mm, apex acute, margins entire; antheridia 2 per bract. **Gynoeceia** with 2 lejeuneoid innovations forming a dichasial pattern; lobe ovate, $0.9\text{--}1 \times 0.6\text{--}0.8$ mm, apex apiculate, margins in upper $2/3$ with lacinate teeth, the teeth consisting of 3–13 cells, being 2–3 cells wide at base and ending in a row of 2–5 cells; lobules broadly ovate, $2/3 \times$ lobe length, apex apiculate, margins with lacinate teeth, the teeth consisting of 3–10 cells, being 2–3 cells wide at base and ending in a row of 2–5 cells; bracteoles spatulate, $0.9\text{--}1 \times 0.7\text{--}0.8$ mm, apex emarginate, $2/3 \times$ bracteole length with lacinate teeth, the teeth consisting of 4–9 cells, being 2–3 cells wide at base and ending in a row of 2–6 cells, margins slightly recurved. **Perianths** oblong, $0.9\text{--}1 \times 0.6\text{--}0.7$ mm, keels in upper $1/3$ with numerous lacinate teeth, the teeth consisting of 5–11 cells, being 2–3 cells wide at base and ending in a row of 3–7 cells long; beak $30\text{--}50$ μm with 3–4 cells long.

Chromosome number. Unknown.

Chemistry. Unknown.

Distribution and ecology. Known only from the type.

Thysananthus combinatus was previously identified as *T. comosus* and included in the molecular phylogenic analysis of Lejeuneaceae by Wilson et al. (2007a). It differs from typical *T. comosus* by its enlarged dorsal epidermis (epidermal cells as large as medulla cells in *T. comosus*), entire leaves and underleaves (sometimes toothed in *T. comosus*), elongate lobule teeth 4–6 cells long (0–1(–2) cells long in *T. comosus*), and underleaf bases only sometimes adnate with leaves (always adnate in *T. comosus*). The new species shares several characters with the member of ser. *Thysananthus* (toothed female involucre and perianths)

and ser. *Anguiformes* (dorsal epidermal cells larger and somewhat thinner-walled than medulla and ventral epidermal cells), which suggests that it could represent an evolutionary link between these series. Moreover, *T. combinatus* may also be confused with *T. retusus*, which possesses elongate lobule teeth (4–6 cells long) as well. However, *T. retusus* differs by epidermal cells as large as medullary cells, isodiametric leaf cells, and presence of a vitta.

5. *Thysananthus comosus* Lindenb. (Fig. 12)

in Lehmann, Nov. Stirp. Pug 8: 25. 1844; Gottsche et al. (1845: 288); Stephani (1912: 787); Verdoorn (1934: 175); Fulford (1941: 39); Gradstein (1994: 87). *Lejeunea comosa* (Lindenb.) Mitt., J. Linn. Soc. Bot. 5: 109. 1861; Spruce (1884: 108, in subg. *Thysanolejeunea*).—Type: MALAYSIA. Penang: Pulo Penang, Wallich s.n. (lectotype, designated by Verdoorn, 1934: W; isoelectotypes: BM!, U!).

Lejeunea (subg. *Thysanolejeunea*) *dissoptera* Spruce, Trans. & Proc. Bot. Soc.

Edinburgh 15: 108. 1884. *Thysananthus dissopterus* (Spruce) Steph., Hedwigia 29: 4. 1890.—Type: “Guiana” ex hb. Hooker (holotype: MANCH; isotypes: BM, G, fide Gradstein, 1994).

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, pale green, becoming dark brown in the older portion in the field, reddish brown in herbarium specimens, up to 2.8 cm long × 2 mm wide. **Stems** rather rigid; ventral merophyte 8–9 cell rows wide; in cross section round-orbicular in shape, 167–180 µm high × 130–148 µm wide, composed of 25–27 epidermal cells surrounding 49–55 medullary cells in 8–12 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute, when moist weakly concave, apical parts plane, not recurved; dorsal lobe asymmetrically ovate, 0.9–1 × 0.7–0.9 mm, apex obliquely mucronate, margins entire or serrate (*Schiffner s.n.*), dorsal base auriculate, auricle 112–137 × 75–88 µm, ventral margin upcurved 1/2× leaf length; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 10–20 × 7.5–15 µm, median cells 22.5–30 × 10–15 µm, basal cells 32.5–40 × 15–22.5 µm, trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies 2–4(–5) per cell. **Lobules** oblong, 0.3–0.4 × 0.1–0.2 mm, 1/4–1/3× lobe length; appendage on surface of lobule base not developed; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex entire or with 1(–2) triangular tooth, the first tooth consisting of 3 cells, being 2 cells wide at base, apex of one cell; the

second tooth consisting of 3 cells, being 2 cells wide at base, apex of one cell, often obsolete. **Underleaves** imbricate, flat, broadly obovate, $0.5\text{--}0.6 \times 0.6\text{--}0.7$ mm, $2\text{--}3\times$ stem width, apex truncate, plane, entire to serrate, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells $17\text{--}22 \times 7.5\text{--}10$ μm . **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 4–7 pairs (15–21 in *Wood 1380*), bracts hypostatic, $0.8\text{--}0.9 \times 0.6\text{--}0.7$ mm, apex mucronate, margins entire; antheridia 2 per bract. **Gynoecia** with one lejeuneoid innovations forming a monochasial pattern; lobe ovate, $1.1\text{--}1.3 \times 0.7\text{--}1$ mm, apex apiculate, margin in upper $1/3$ with triangular teeth, the teeth consisting 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; lobules broadly ovate, $1/2\times$ lobe length, apex apiculate to obscurely bifid, margin with triangular teeth, the teeth consisting of 5–6 cells, being 2–3 cells wide at base and ending in row of 2–3 cells; bracteoles spatulate, $1.1\text{--}1.2 \times 0.7\text{--}0.8$ mm, apex emarginate, margin with triangular teeth, the teeth consisting 5–9 cells, being 2–3 cells wide at base and ending in a row of 2–3 cells, margins recurved. **Perianths** obovate, $0.9\text{--}1 \times 1.3\text{--}1.4$ mm long, keels in upper $1/2$ with numerous lacinate teeth with 3–6 cells long at apex; beak 2.5×3 μm with 4–5 cells long.

Chromosome number. Unknown.

Chemistry. *Cis*- β -elemene, isolepidozene and unidentified sesquiterpenoid (M^+)220, 107(100), 43(80) (Sukkharak et al., in press).

Additional illustrations. Fulford (1941, p. 41, Figs. 41–51).

Distribution and ecology. Indomalesia; sea level up to 500 m; on bark of living and fallen trees in the mangrove forests, rain forests (secondary forest), also on rock in coastal forests.

REPRESENTATIVE SPECIMENS. **Seychelles.** BEAU VALLON: Dans Iles cliff walk, *Norkett 18167* (BM); forest above Le Niol reservoir, *Norkett 16584* (BM, JE).—GRAND' ANSE PRASLIN: Vallee de Mai Nature Reserve, *Norkett 18426* (BM, JE), *Pócs 9358/B* (GOET).

India. ANDAMAN AND NICOBAR ISLANDS: Andaman islands, Port Blair, 1893, *Man s.n.*, ex hb. Levier 740 (G); Nicobar Island, Katschall, 10 Feb 1975, *Kurz s.n.* (W 3 packets). **Thailand.** PANG NGA: Khao Luk National Park, *Porn-Sook-Sawang 15* (BCU); Sri Pang Nga National Park, *Chantanaorrapint 2121* (PSU); mangrove forest site 3, *Boonkerd 5* (BCU); mangrove forest site 6, *Thaithong 1130* (BCU).—NAKHON SI THAMMARAT: Mt. Khao Luang, *Chantanaorrapint s.n.* (PSU); Mt. Khao Nan Yai, *Sukkharak 334* (BCU).—SONGKLA: Ton Nga Chang, *Inuthai s.n.* (PSU). **Vietname.** KHANH HOA: Nha trang, 11 Apr 1958, *Tixier s.n.* (PC). **Malaysia.** PENANG: without location, *Hooker s.n.* (G).—PERAK: Pangkor Island,

Sukkharak 730 (BKF, GOET).—SABAH: Kalabakan, *Wood* 1380 (L).—SARAWAK: Mt. Dulit, Aug 1932, *Richards s.n.*, Hep. Sel. Crit. Verdoorn 400 (G, W); Banting, “*Beccari* 1867” (PC). **Singapore**. Boekit Timah, Nov 1893, *Schiffner s.n.*, Hep. Sel. Crit. Verdoorn 280 (BR, C, G 2 packets, PC, SING). **Indonesia**. KALIMANTAN: East Kalimantan, along Bongan river, *Meijer B.1197c* (L).—JAVA: Bogor (“Buitenzorg”), 1893–1894, *Schiffner s.n.*, Hep. Sel. Crit. Verdoorn 281 (BR, C, G 2 packets, GOET, L 2 packets, PC, S, SING, U).—SUMATRA: West Sumatra, Padang, *Pieper s.n.* (S), *Schild* 117 (W). **Philippines**. BUKIDNON: Impalutao B. F. D. reforestation project, *Onraedt* 85.P.11043 (BR).—ZAMBALES: without location, *Curran & Merritt* 8192 (G); without location, *Curning* 1488, 2110 (BM). **Federated States of Micronesia**. POHNPEI: Mt. Nanlaut, 28 Jun 1949, *Glassman s.n.* (G). **Papua New Guinea**. EAST NEW BRITAIN: Nakanai Mts., *Streimann* 40422 (JE).—MILNE BAY: near Mita, *Micholitz s.n.* (G).—MOROBE: Labutali village, *Bellamy* 178 (U).

Thysananthus comosus varies in the dentation of leaves and underleaves, which is entire to strongly serrate, and the number of leaf lobule teeth as seen in *T. amazonicus*.

Thysananthus comosus is closely related to *T. gottschei*, from which it differs mainly by the leaves, which weakly concave when moist (strongly concave in *T. gottschei*) and underleaves, which are flat obovate and truncate (slightly squarrose, broadly spatulate and rounded in *T. gottschei*).

Thysananthus comosus was described by Lindenberg in 1844 based on two specimens, one from Asia (“Pulo Penang”) and one from South America (“Guiana”). Spruce (1884) considered the two specimens different and named the South American plant *Lejeunea dissoptera* (= *T. dissopterus*). Fulford (1941), however, considered *T. dissopterus* as a synonym of *T. comosus*. Gradstein (1994) found that the two specimens are identical except that the material from Pulo Penang is male whereas the plants from Guiana are female; he proposed that *T. comosus* is excluded from the neotropical flora. I have found both male and female plants in the type collection from Pulo Penang and agree with Gradstein to exclude *T. comosus* from the neotropical flora. Reasons for the exclusion were discussed by Gradstein (l.c.).

6. *Thysananthus convolutus* Lindenb. (Figs. 13–14)

Syn. Hepat. 288. 1845; Stephani (1912: 795); Verdoorn (1933: 230; 1934: 178); Mizutani (1969: 138; 1977: 135); Gradstein et al. (2002: 72). *Jungermannia spathulistipa* var. γ Nees, Enum. Pl. Crypt. Jav.: 38. 1830. *Lejeunea* (subg.

Thysanolejeunea convoluta Lindenb., Trans. & Proc. Bot. Soc. Edinburgh. 15: 106. 1884. *Thysanolejeunea convoluta* (Lindenb.) Steph., Hedwigia 29: 142. 1890, nom. inval.—Type: INDONESIA. Java: “Habitat in Javae montosis, v.c. in monte Leback Provinciae Bantam, frequens”, *Blume s.n.* (lectotype, here designated: STR!; isoelectotypes: BM!).

Thysananthus subreversus Steph., Sp. Hepat. 4: 791. 1912.—Type: PAPUA NEW GUINEA. Morobe: “Kaiser Wilhelmsland: Sattelberg”, *Nyman s.n.* (isotype, S!); Icon. Steph. nr. 10218.

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, pale green, becoming dark brown to blackish in the older portion in the field, reddish brown in herbarium specimens, up to 2.3 cm long \times 1.5–2.2 mm wide. **Stems** rather rigid; ventral merophyte 8–10 cell rows wide; in cross section round-orbicular in shape, 278–297 μm high \times 230–262 μm wide, composed of 37–49 epidermal cells surrounding 107–156 medullary cells in 13–16 layers high, epidermal cells not larger than medullary cells. **Leaves** strongly imbricate, when dry suberect and strongly convolute, when moist strongly concave, apical parts turn to ventral side, recurved; dorsal lobe asymmetrically ovate, 1–1.3 \times 0.8–0.9(–1.1) mm, apex mucronate-apiculate, dorsal base auriculate, auricle 130–165 \times 75–100 μm , dorsal margin with 4–6 triangular teeth, the teeth consisting of 3–5 cells, being 2 cells wide at base and ending in a row of 1–2 cells, ventral margin upcurved $2/3 \times$ leaf length with 4–5 triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 7–10 \times 5–7 μm , median cells 20–25 \times 5–7 μm , basal cells 25–37 \times 12–20 μm , trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies 2–4 per cell. **Lobules** rectangular, 0.3–0.4 \times 0.1–0.2 mm, $1/4$ – $1/3 \times$ lobe length; appendage on surface of lobule base not developed; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex with 1(–2) triangular teeth, the first tooth consisting of 3–6 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, the second tooth of one cell only, often obsolete. **Underleaves** imbricate, slightly squarrose, broadly spatulate, 0.5–0.6(–1.0) \times 0.4–0.6 mm, 3 – $4 \times$ stem width, apex truncate to rounded, plane to incurved, with 17–20 triangular teeth, the teeth consisting of 3–4 cells, being 2 cells wide at base and ending in a row of 1–2 cells, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells 12–15 \times 5–7 μm . **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 3–4 pairs, bracts hypostatic, 0.9–1 \times 0.7–0.8 mm, apex acute, margins entire; antheridia 2 per bract. **Gynoeceia**

with one lejeuneoid innovation forming a monochasial pattern; lobe widely ovate, $1.7\text{--}1.9 \times 9\text{--}10$ mm, apex apiculate, margin in upper 1/3 with 8–9 triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells at base, apex of one cell; lobules broadly ovate, $1/2 \times$ lobe length, apex apiculate to obscurely bifid, margins with triangular teeth, the teeth consisting of 5–9 cells, being 2–3 cells at base and ending in a row of 1–2 cells; bracteoles spatulate, $1.3\text{--}1.4 \times 0.7\text{--}0.8$ mm, apex slightly emarginate, $1/3 \times$ bracteole length with triangular teeth, the teeth consisting of 3–6 cells, being 2–3 cells wide at base, apex of one cell, margins recurved. **Perianths** oblong-cylindrical, $2.3\text{--}2.5 \times 0.8\text{--}1$ mm long, keels in upper 1/3 with triangular teeth, the teeth consisting of 7–8 cells, being 2–3 cells at base and ending in a row of 1–2 cells; beak 38–60 μm with 3–4 cells long or obsolete.

Chromosome number. Unknown.

Chemistry. Isolepidozene, bicyclogermacrene and aromadendrene sesquiterpenoids, diterpenoids, and sterols (Gradstein et al., 1985; Sukkharak et al., in press).

Distribution and ecology. Indomalesia; 10–1900 m; on stems of treelets in old cocoa plantations with leguminous shaded trees and old garden sites with regrowth species, bark of living trees and fallen trees in rain forests (primary and secondary forests), and montane forest canopy.

REPRESENTATIVE SPECIMENS. **India.** ANDAMAN AND NICOBAR ISLANDS: Andaman Islands, Port Blair, Jul 1890, *Man s.n.*, ex hb. Levier “302” (G, W); *ibid.*, 12 Apr 1891, *Man s.n.*, ex hb. Levier 743 (G); *ibid.*, 13 Jul 1891, *Man s.n.*, ex hb. Levier 775 (G); *ibid.*, 1893, *Man s.n.*, ex hb. Levier 742 (BM, G 5 packets, JE, S 2 packets); Nicobar Islands, Katchal, *Kurz* 3875 (G). **Thailand.** NAKHON SI THAMMARAT: Mt. Khao Luang, *Touw* 11642 (BKF), *Tagawa & Kitagawa* T5045, T5246 (G); Mt. Khao Nan Yai, *Sukkharak* 208, 348 (BCU); *ibid.*, San Yen, *Sukkharak* 769, 770, 787, 801, 803, 813 (BKF, GOET). **Malaysia.** JOHORE: Mt. Ophir, *Verdoorn* 123, 155, 188 (SING).—PAHANG: Frasers Hill, *Schäfer-Verwimp & Verwimp* 18593 (BR); at start of part to Pine Tree Hill, Fraser Hill, *Wood* 1343 (BM).—PENANG: Penang hill, *Ridley* 549, 553 (SING); Penara Bukit, *Ridley* 566 (SING).—SABAH: Mt. Kinabalu, camp on path to Paka cave, *Wood* 1526 (BM, JE); *ibid.*, Eastern Shoulder, ridge below Camp III, *Chew & al.* 2011, 2131, 2140 (BM, BM-K); *ibid.*, summit trail, *Sukkharak* 607, 616, 694 (BKF, GOET), *Wallace s.n.* (NSW); Tenompok, *Holttum* 25328 (SING).—SARAWAK: Mt. Dulit, Aug 1932, *Richards s.n.*, Hep. Sel. Crit. *Verdoorn* 400 (GOET, JE); *ibid.*, Oct 1932, *Richards s.n.*, Hep. Sel. Crit. *Verdoorn* 397 (BM, G, JE, SING, U, W), *Richards* 2012 (JE 2 packets), 2052 (BM-K, JE), 2357 (BM); plot 1, Mr. J. A. R. Anderson’s sample line at Kabang protected forest, *Wood* 1421 (BM, JE).—SELANGOR:

Semangko Pass, 1904, "*Nurdozc*" *s.n.* (SING). **Indonesia.** JAVA: Cibodas Botanical garden, *Gradstein* 10204, 10205, 12078 (GOET); *ibid.*, Apr 1894, *Schiffner s.n.*, Hep. Sel. Crit. Verdoorn 282 (BM-K 2 packets, BR, C, G 2 packets, GOET, JE, PC, S, SING, U, W); *ibid.*, Tjibeureum, Apr 1894, *Schiffner s.n.*, Hep. Sel., Crit. Verdoorn 283 (BM-K 2 packets, BR, C, G 2 packets, GOET, JE, PC, S, SING, U, W), *Massart* 1173, 1200 (BR), *Meijer* B3681 (G, PC, S, W), B3789 (BM-K, G, PC, S, W), *Renner* 127, 174, *s.n.* (JE); Yogyakarta, Gedongan, *Kurz s.n.* (G).—MALUKU ISLANDS: Ambon, *Zippelius s.n.* (L).—SUMATRA: Berastagi, garden of former BPM-hotel, *Sipman* 6897 (U).—SULAWESI: Central Sulawesi, Lake Kalimpaa, Lore Lindu National Park, *Gradstein* 10324 (GOET); *ibid.*, Mt. Rorekatimbu, *Gradstein* 12154, 12155, 12158 (GOET), 12156 (GOET, JE); *ibid.*, Bariri, *Gradstein* 12011 (GOET); Todjamboe, Jul 1929, *Kjellberg s.n.* (JE).—WESTERN NEW GUINEA: West Papua, Arfak Mts., *Beccari* 1875 (JE). **Philippines.** BENGUET: Baguio, *Burgeff* 8080 (JE).—NEGROS ORIENTAL: Laka Danao, Sibulan, *Edano* 13102 (L); Matangwa river, *Edano* 13027 (L).—ORIENTAL MINDORO: Mt. Halcon, *Salgado* 88.P.12131 (BR).—QUEZON: Polillo, *McGregor s.n.* (BM, L), *Robinson* 9299 (L); Tayabas, *Baler s.n.* (JE); Digisit beach, *Santos* 338 (JE); Dimasingay, *Santos* 360 (JE). **Papua New Guinea.** CENTRAL: Boridi, *Carr* 13531 (JE).—EASTERN HIGHLANDS: near Famin, Kainantu-Okapa road, *Streimann* 26392 (JE); track to Mt. Michael, *Streimann* 18803 (JE, LAE); Mt. Gahavisuki nature reserve, *Aptroot* 18780 (U).—GULF: Hepataewa, *Streimann* 33853 (JE).—MILNE BAY: Wapon, *Cruttwell* 511 (L).—MOROBE: Mt. Kaindi, *Streimann & Bellamy* 17690 (BR); *Gradstein* 3796 (U); Blue point, *Gradstein & Sipman* 7883 (G), *Gradstein* 3778 (U); Oomsis logging area, *Streimann* 25841, 25879, 25885, 25889 (JE); Herzog Mts., *Streimann & Umba* 10993 (JE, LAE); Gumi creek, *Streimann* 25052, 25137, 25141, 34943 (JE); Slate-Gumi creeks divide, *Streimann* 13829, 13918 (JE), 13834, 13856 (JE, LAE); upper Watut river, *Streimann* 33054 (JE); Ekuti divide, Bulolo-Aseki road, *Streimann* 26106 (JE); Aseki-Menyamya road, *Streimann & Tamba* 12156 (JE); Labu swamp, *Streimann* 25559, 25702 (JE); upper Nawatu Banda, *Streimann* 24883 (JE).—SOUTHERN HIGHLANDS: Lama sawmill, *Streimann* 26579, 26608, 26660 (JE); Kengaput, *Streimann* 26848 (JE); Piribu sawmill, *Streimann* 32515 (JE); Andawe river, *Streimann* 26530 (JE).—WEST NEW BRITAIN: Kapi T. R. P., Kapiura river, *Kolema* 107 (JE).—WEST SEPIK: Blackwater refugee camp, *Mundua* 300 (JE). **Solomon Islands.** GUADALCANAL: above Tasi-camp along track to Malakuna, *van Zanten* 68–2435/b (JE).—WESTERN: Kolombangara Island, *Braithwaite* 4429 (JE).

Thysananthus convolutus is closely related to *T. gottschei* but differs from the latter by toothed leave and underleaves (entire in *T. gottschei*) and triangular perianth teeth, 1–2 cells long (laciniate perianth teeth, 2–4 cells long in *T. gottschei*).

The original material in the Nees Herbarium (STR) contains 5 specimens. Four are *Thysananthus convolutus* and only one has the mention “ γ ”. Since var. “ γ ” was cited by Lindenberg in the protologue of *T. convolutus*, I have chosen the “ γ ” material as the lectotype also because it is good material with perianths. No type material of *T. convolutus* was found in the Lindenberg Herbarium (W). Although there is no collector cited, the material is from the same locality as *T. spathulistipus*, as mentioned in the protologue. I, therefore, assume that the material was collected by Blume.

Key to the varieties of *T. convolutus*

Keel of leaves without appendage. Underleaf apex plane or incurved. Perianth teeth triangular, 1–2 cells long..... 6a. *T. convolutus* var. *convolutus*

Keel of leaves on one side of stem with appendage (on the side where leaves and underleaves are free). Underleaf apex strongly recurved. Perianth teeth laciniate, 3–6 cells long..... 6b. *T. convolutus* var. *laceratus*

6a. *Thysananthus convolutus* var. *convolutus*

see under the species

6b. *Thysananthus convolutus* var. *laceratus* (Steph.) **comb. nov.** (Fig. 14)

Thysananthus laceratus Steph., Sp. Hepat. 4: 796. 1912.—Type: MALAYSIA. Sabah: “Brit. N Borneo, Ulu Moanat Labuh river”, *Alau Eltom s.n.* (holotype: G!); Icon. Steph. nr. 10190.

The distinguishing characters of this variety are (1) presence of appendage on the keel, on the side where leaves and underleaves are free and opposite to the adnate ones (appendages always curved towards the stems), (2) strongly recurved underleaf apex and (3) obovate, laciniate perianth teeth with 3–6 cells long.

Distribution and ecology. Malaysia (Sabah, Sarawak); without ecological information.

REPRESENTATIVE SPECIMENS. **Malaysia.** SABA: The type. SARAWAK: Mt. Dulit, *Richards 2357* (BM).

7. *Thysananthus discretus* Sukkharak & Gradst. (Fig. 15)

Cryptog. Bryol. 31: 113–119. 2010.—Type. INDONESIA. West Papua ["Netherlands New Guinea, distr. Hollandia"]: Cycloop Mountains, path Ifar-Ormoe, alt. 1220 m, 21 Aug 1961, *Royen & Sleumer 5896* (holotype: L!; isotypes: JE!, S!).

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, with vigorous shoots, yellowish brown in herbarium specimens, up to 6.5 cm long \times 2–3 mm wide. **Stems** strongly rigid; ventral merophyte 14–18 cell rows wide; in cross section orbicular-subelliptic in shape, 360–500 μm high \times 260–445 μm wide, composed of 76–80 epidermal cells surrounding 365–381 medullary cells in 16–22 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and strongly convolute, when moist clasping the stem; dorsal lobes asymmetrically ovate, 1.4–2.3 \times 1–1.8 mm, apex apiculate, dorsal base auriculate, auricle 100–150 \times 125–160 μm , dorsal margin entire or with 1–4 triangular teeth, the teeth consisting of 3–4 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, ventral margin upcurved over most of its length, becoming flat near the apex, entire or with 3–8 triangular teeth, the teeth consisting of 3–5 cells, 2–3 cells wide at base and ending in a row of 1–2 cells; cells elongate-hexagonal with acute ends, vitta cells absent, marginal lobe cells 10–12 \times 10–12 μm , median cells 32–45 \times 5–7 μm , basal cells 37–62 \times 17–25 μm , trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies 4–5 per cell, toward leaf base more numerous, up to 8 per cell (*Gradstein 3894*). **Lobules** rectangular, 0.6–0.7 \times 0.1–0.2 mm, 1/4–1/3 \times lobe length; appendage on surface of lobule base not developed; keels with appendages on one or both sides or not developed, orbicular-oblong, 215–375 \times 85–150 μm ; lobule apex oblique, longly continuing into the ventral lobe margin, apex with one triangular tooth, the tooth consisting of 5–12 cells, 2–4 cells wide at base and ending in a row of 1–2 cells. **Underleaves** imbricate, slightly squarrose, broadly oblong to rectangular, 1.2–1.9 \times 0.8–1.4 mm, 2–2.5 \times stem width, apex broadly rounded to truncate, plane, with 20–25 triangular teeth, the teeth consisting of 3–6 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, bases auriculate, the auricles 100–275 \times 200–400 μm , underleaf bases not adnate with leaves; cells 20–25 \times 5–7 μm . **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 6–10 pairs, bracts hypostatic, 0.7–0.8 \times 0.5–0.6 mm, apex acute, margins entire; antheridia 2 per bract. **Gynoecia** with 2 lejeuneoid innovations forming a dichasial pattern; lobe ovate, 2.4–2.7 \times 1.2–1.5 mm, apex

apiculate, margins in upper 1/3 with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; lobules broadly ovate, $2/3 \times$ lobe length, apex apiculate, margin with triangular teeth, the teeth consisting 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; bracteoles spatulate, $2.3\text{--}2.4 \times 1.1\text{--}1.3$ mm, apex emarginate, $1/2 \times$ bracteole length with triangular teeth, the teeth consisting of 3–7 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, margins slightly recurved. **Perianths** oblong, $2.5\text{--}2.6 \times 1.1\text{--}1.3$ mm, keels in upper 1/3 with numerous lacinate teeth, with 3–9 cells long at apex; beak $97\text{--}125$ μm with 4–7 cells long.

Chromosome number. Unknown.

Chemistry. Sesquiterpenoids, diterpenoids and sterols (Gradstein et al. 1985, under *Thysananthus convolutus* sample nr. 49).

Additional illustrations. Gradstein et al. (2002, p. 73, Fig. 45, as *Thysananthus convolutus*).

Distribution and ecology. Endemic to Western Melanesia: Papua (Indonesia), Papua New Guinea and the Solomon Islands; 760–2700 m; on trunks, branches and stems of treelets in rain forests (primary and secondary forests) and montane forests.

REPRESENTATIVE SPECIMENS. **Indonesia.** WESTERN NEW GUINEA: Papua, Cycloop Mts., *Royen & Sleumer 5907* (JE, L); Eipomek-Tal, *Hiepko & Schultze-Motel 2218, 2403* (JE). **Papua New Guinea.** CENTRAL: Boridi, *Carr 13531* (JE).—EASTERN HIGHLANDS: Daulo Pass, *Streimann 17990* (JE); Gahavisuka provincial park, *Streimann 18201* (JE).—MOROBE: Wau, Mt. Kaindi, *Gradstein 3778* (GOET), 3856, 3894, 3910 (U), *Schuster 67–5786, 67–5787, 67–5791/c, 67–5792, 67–6282* (JE); *Streimann 22497* (JE, LAE), *Streimann & Bellamy 17690* (JE, S, W); Araulu logging area, *Streimann 13622* (JE, LAE); Slate-Gumi creeks divide, *Streimann 13861* (JE); Spreader divide, *Streimann 26036* (JE), *Streimann 11846* (LAE), *Streimann & Tamba 11878* (JE, LAE); Aseki-Menyamya road, *Streimann & Tamba 12156* (LAE); Ekuti divide, Bulolo-Aseki road, *Streimann 20051, 20103, 26135* (JE); Sattelberg, *Clemens 265c* (JE, L).—WESTERN HIGHLANDS: Jimi-Waghi divide, *Streimann 20916* (JE, LAE), 20911 (LAE). **Solomon Islands.** GUADALCANAL: Mt. Papomanatsen, *Braithwaite 4773* (JE).

Thysananthus discretus is a polymorphic species with respect to the dentation of leaves, which varies from edentate to strongly dentate.

Collections of *Thysananthus discretus* were previously identified as “*T. appendiculatus*”, “*T. convolutus*”, “*T. gottschei*” and “*T. sp.*”. *Thysananthus discretus* is most

closely related to widespread Malesian *T. convolutus* and was illustrated as *T. convolutus* by Gradstein et al. (2002: Fig. 45). The illustration clearly shows the free underleaves characteristic of *T. discretus*, which are not connected with the leaves, and the presence of well-developed auricles at the underleaf bases. *Thysananthus discretus* shares with *T. convolutus* the asymmetric leaves but differs from the latter by (1) leaves when moist clasping the stem (squarrose in *T. convolutus*), (2) free underleaf bases, with well-developed auricles (underleaf bases adnate with leaves on one side and without auricles in *T. convolutus*) and (3) strongly rigid stems, with 14–18 cells wide ventral merophytes and medulla 16–22 cell layers high (less rigid stems, with 8–10 cells wide ventral merophytes and 14–17 layers high medulla in *T. convolutus*). *Thysananthus discretus* may also be confused with *T. appendiculatus*, a species endemic to New Guinea which may possess auricled underleaf bases like *T. discretus*. However, the leaf lobes in *T. appendiculatus* are symmetric and widely spreading when moist, while in *T. discretus* they are asymmetric and clasping the stem when moist. In addition, leaf and underleaf bases are connected in *T. appendiculatus* while in *T. discretus* they are never connected. In *T. discretus* the appendages are present on one or both sides of the stem and are sometimes lacking, while in *T. appendiculatus*, *T. convolutus* var. *laceratus* and *T. gottschei* var. *continuus* they are always found on one side of the stem only, on leaves that are free from underleaf bases and opposite to leaves that are connected with underleaf bases. Moreover, the appendages of *T. convolutus* var. *laceratus* and *T. gottschei* var. *continuus* are always curved towards the stem while in *T. discretus* and *T. appendiculatus* they are straight or curved.

8. *Thysananthus gottschei* (Jack & Steph.) Steph. (Figs. 16–17)

Sp. Hepat. 4: 787. 1912; Verdoorn (1933: 231). *Thysanolejeunea gottschei* Jack & Steph., Hedwigia 31: 20. 1892.—Type: PHILIPPINES. Luzon: Wallis s.n. (holotype: G!).

Thysananthus borneensis Steph., Sp. Hepat. 4: 786. 1912.—Type: MALAYSIA. Sarawak: Pearson s.n. (holotype: G!); Icon. Steph. nr. 10168.

Thysananthus reversus Steph., Sp. Hepat. 4: 789. 1912. *Thysanolejeunea reversa* Steph., Hedwigia 35: 139. 1896.—Type: PHILIPPINES. Zamboanga del Norte: Dapitan, Micholitz 44 (holotype: G!).

Thysananthus rigidus Steph., Sp. Hepat. 4: 790. 1912.—Type: PAPUA NEW GUINEA. New Ireland [“New Ireland, Nova Hibernia”]: Micholitz s.n. (holotype: G!); Icon. Steph. nr. 10207.

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, reddish brown in herbarium specimens, up to 3.5 cm long \times 2.5–3 mm wide. **Stems** rather rigid; ventral merogphyte 8–9 cell rows wide; in cross section round-orbicular in shape, 313–320 μm high \times 225–240 μm wide, composed of 45–49 epidermal cells surrounding 129–166 medullary cells in 12–16 layers high, epidermal cells not larger than medullary cells. **Leaves** strongly imbricate, when dry strongly convolute, when moist strongly concave, apical parts turn to ventral side, recurved; dorsal lobe asymmetrically ovate, 1.7–1.9 \times 1.5–1.7 mm, apex mucronate-apiculate, margin entire, dorsal base auriculate, auricle 130–165 \times 75–100 μm , ventral margin upcurved $2/3 \times$ leaf length; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 7–9 \times 4–7 μm , median cells 18–23 \times 5–7 μm , basal cells 25–29 \times 15–20 μm , trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies unknown. **Lobules** rectangular, 0.5–0.6 \times 0.1–0.2 mm, $1/3 \times$ lobe length; appendage on surface of lobule base not developed; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex with 1(–2) triangular teeth, the first tooth consisting of 3–6 cells, being 2–3 cells wide at base and ending in a row of 1–2(–3) cells, the second tooth of one cell only, often obsolete. **Underleaves** imbricate, slightly squarrose, broadly oblong-orbicular, 1.5–2.1 \times 0.9–1 mm, 3–4 \times stem width, apex truncate to rounded, plane to incurved, entire to with 17–20 triangular teeth, the teeth consisting of 3–5 cells, being 2 cells wide at base and ending in a row of 1–2 cells, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells 12–17 \times 7–10 μm . **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 3–4 pairs, bracts hypostatic, 0.9–1 \times 0.7–0.8 mm, apex acute, margins entire; antheridia 2 per bract. **Gynoeceia** with one lejeuneoid innovation forming a monochasial pattern; lobe widely ovate, 2.3–2.6 \times 1.7–1.8 mm, apex acute, margin entire; lobules broadly ovate, $2/3 \times$ lobe length, apex apiculate to obscurely bifid; margins with triangular teeth, the teeth consisting of 5–8 cells, being 2–3 cells at base and ending in a row of 1–2 cells; bracteoles spatulate, 2.2–2.4 \times 2–2.3 mm, apex slightly emarginate, $1/2 \times$ bracteole length with triangular teeth, the teeth consisting of 3–6 cells, being 2–3 cells wide at base, apex of one cell, margins recurved. **Perianths** oblong-cylindrical, 2.3–2.5 \times 0.8–1 mm long, keels in upper $1/3$ with numerous lacinate teeth, with 2–4 cells long at apex; beak 37–50 μm with 3–4 cells long or obsolete.

Chromosome number. Unknown.

Chemistry. High amounts of isolepidozene and (M^+)302, 190(100), 81(95) (Sukkharak et al., in press, under *Thysananthus convolutus* sample nr. 1–3).

Distribution and ecology. Indomalesia; 20–2100 m; on road-side trees, bark of living trees and fallen trees in rain forests (primary and secondary forests) and montane forests.

REPRESENTATIVE SPECIMENS. **India.** ANDAMAN AND NICOBAR ISLANDS: Andaman islands, Port Blair, Jul 1890, *Man s.n.*, ex hb. Levier 79 (G, PC). **Thailand.** NAKHON SI THAMMARAT: San Yen, *Sukkharak* 758, 810 (BKF, GOET). **Malaysia.** PAHANG: on Genting Highland road, *Sukkharak* 717, 718, 720 (BKF, GOET).—PENANG: Penang hill, 11 Feb 1949, *Allen s.n.* (BM-K).—SABAH: Kinabatangan, Bukit Garam, *Wood* 1432 (BM, BM-K, JE); Tawau, Bombay Burmeh Trading Co. Concession area, *Wood* 1389 (BM-K); Mt. Kinabalu, summit trail, *Sukkharak* 616 (BKF, GOET).—WESTERN NEW GUINEA: West Papua, Soron, *Beccari s.n.* (JE); Papua, Cycloop Mts., *Royen & Sleumer* 5907 (JE). **Indonesia.** JAVA: West Java, Tjibodas, *Nyman s.n.* (C 2 packets, G, S, W).—SULAWESI: Central Sulawesi, Lake Kalimpaa, Lore Lindu National Park, *Gradstein* 10324/2 (GOET).—SUMATRA: Bengkulu, Enggano Islands, “*Modigliani*” 139 (G 2 packets, PC). **Philippines.** NEGROS ORIENTAL: Cuernos Mts., May 1908, collector unknown. (BM, G 3 packets, JE, W).—QUEZON: Polillo, Bureau of science no. 10494, *McGregor* 2–39 (BM, BM-K). **Papua New Guinea.** CENTRAL: Kuriva logging area, *Streimann & Vinas* 14391 (LAE); near Dabamura on Ower’s Corner road, *Streimann & Naoni* 14900, 14904, 14961 (JE, LAE); Musgrave river road, Itikinu, *Streimann & Naoni* 16690 (JE, LAE); K. B. sawmill, Ehu creek, *Streimann & Naoni* 16567 (JE, LAE).—EASTERN HIGHLANDS: 25 miles S of Kainantu, *Kurokawa* 4370, 4371 (JE).—GULF: Bema-Kaintiba road, *Streimann* 33645 (JE, LAE).—MOROBE: logging area, 7° 18' S 146° 45' E, *Streimann & Bellamy* 13129 (JE, LAE); Manki Trig., Bulolo-Watut divide, *Streimann & Bellamy* 12997 (JE, LAE); Slate-Gumi creeks divide, *Streimann* 13832, 13861 (JE, LAE); Araulu logging area, *Streimann* 13639 (JE); upper Watut river, *Streimann* 23071, 23092, 23101 (LAE); Herzog Mts., *Streimann & Umba* 10983 (LAE); Ekuti divide, Bulolo-Aseki road, *Streimann* 22623 (JE, LAE); Oomsis logging area, *Streimann* 25836 (LAE, W); Gumi divide, head of Gumi creek, *Streimann* 25156 (JE, W); Sattelberg, *Nyman s.n.* (C).—WEST NEW BRITAIN: South Bunga T. R. P., *Bellamy* 1357 (JE, LAE, S); Evili river, *Streimann* 41598, 41608, 41609 (JE); Geleo-Lasilai logging area at Mt. Laliti, *Streimann* 41055, 41088, 41176, 41209, 41217, 41253/a (JE), 41237 (JE, LAE).—WEST SEPIK: Aitape subdistrict, *Darbyshire & Hoogland* 8000 (JE); Blackwater refugee camp, *Mundua* 314 (JE, LAE).

Thysananthus gottschei was reduced to a synonym of *T. convolutus* and has been called the edentate form of the latter (Grolle & Piippo, 1984). Phytochemical and molecular results showed that this species should be re-instated (Sukkharak et al., in press; Sukkharak et

al., submitted). The differences between *T. gottschei* and *T. convolutus* are discussed under the latter species.

Key to the varieties of *T. gottschei*

Keel of leaves without appendage. Lobule apex longly continuing into the ventral lobe margins. Underleaf apex plane or incurved.....8a. *T. gottschei* var. *gottschei*

Keel of leaves on one side of stem with appendage (on the side where leaves and underleaves are free). Lobule apex longly continuing into the ventral and dorsal lobe margins. Underleaf apex strongly recurved..... 8b. *T. gottschei* var. *continuus*

8a. *Thysananthus gottschei* var. *gottschei*

see under the species

8b. *Thysananthus gottschei* var. *continuus* var. nov. (Fig. 17)

Type: MALAYSIA. Sarawak: “Lunda”, Micholitz *s.n.* (holotype: G!). The name of the new variety refers to the free margin of lobules continuing into the lobe ventral margin over almost the entire length of the ventral margin, and sometimes into the dorsal margin of the lobes.

Carina appendiculata. Lobulus continuus in margine foliorum ventralibus. Amphigastria apice recurvata.

The distinguishing characters of this variety are (1) presence of appendage on the keel, on the side where leaves and underleaves are free and opposite to the adnate ones (always curved towards the stems), (2) free margin of lobules continuing into the lobe ventral margin over almost the entire length of the ventral margin, and sometimes into the dorsal margin of the lobes and (3) strongly recurved underleaf apex.

Distribution and ecology. Malaysia and Philippines; without ecological information.

REPRESENTATIVE SPECIMENS. **Malaysia.** SARAWAK: the type. **Philippines.** ILOILO: Panay, Robinson BS18185 (L).

9. *Thysananthus spathulistipus* (Reinw. et al.) Lindenb. (Figs. 18–19)

Syn. Hepat. 287. 1845; Stephani (1912: 799); Verdoorn (1934: 167); Mizutani (1969: 138; 1977: 135); Kitagawa (1973: 271); Thiers & Gradstein (1989: 71); Gradstein et al. (2002: 80); Wigginton (2004: 282). *Jungermannia spathulistipa* Reinw. et al., Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 212. 1824. *Jungermannia spathulistipa* var. α , β Nees, Enum. Pl. Crypt. Jav.: 38. 1830. *Lejeunea spathulistipa* (Reinw. et al.) Dum., Rec. d'Observ.: 12. 1835, Spruce (1884: 106, in subg. *Thysanolejeunea*). *Frullania spathulistipa* (Reinw. et al.) Nees, Naturgesch. Eur. Leberm. 3: 211. 1838. *Phragmicoma spathulistipa* (Reinw. et al.) Mont., Ann. Sci. Nat., Bot. (2) 16: 128. 1841.—Type: INDONESIA. Java [“Habitat in Javae montosis, v.c. in monte Leback Provinciae Bantam, frequens”]: *Blume s.n.* (holotype: STR!; isotypes: G 3 packets!, W!).

Thysananthus triquetrus (Mitt.) Steph., Sp. Hepat. 4: 783. 1912. *Lejeunea triquetra* Mitt., J. Proc. Linn. Soc., Bot. 7: 167. 1864.—Type: “Bagro river, W. Africa, 1861, *Mann s.n.*” (holotype: NY!; isotype: BM!), **syn. nov.**

Thysananthus monoicus Steph., Sp. Hepat. 4: 783. 1912.—Type: MADAGASCAR. Icon. Steph. nr. 10228.

Thysananthus sikkimensis Steph., Sp. Hepat. 4: 798. 1912.—Type: “Himalayas”, *Levier s.n.* (holotype: G!); Icon. Steph. nr. 10212.

Thysanolejeunea amboinensis Schiffn. ex Steph., Sp. Hepat. 4: 799. 1912, nom. inval.

Thysananthus hebridensis Steph., Sp. Hepat. 6: 565. 1924.—Type: VANUATU [“Novae Hebrides”]. *Gunn s.n.* (lectotype, here designated: G!; isoelectotypes: G 2 packets!); Icon. Steph. nr. 10184.

Mastigolejeunea tarkwana Pears., Ann. Crypt. Exot. 4: 63. 1931. (fide Wigginton & Grolle, 1996).

Thysananthus spathulistipus (Reinw. et al.) Lindenb. var. *borneensis* Herzog, Mitt. Inst. Allg. Bot. Hamburg: 199. 1931.—Type: INDONESIA. Kalimantan [West Borneo]: Bukit Mulu, 1000 m, 2 XII 1924, *H. Winkler 3333* (holotype: JE!), **syn. nov.**

Thysananthus minor Verd., Recueil Trav. Bot. Néerl. 30: 231. 1933; Gradstein et al. (2002: 74).—Type: INDONESIA. Sumatra: Mt. Brastagi, “Gouv. S. O. K., in silvis pr. cataractas torrentis Petani, infra Brastagi, ca 1350 m”, IX 1930, *Verdoorn s.n.* (holotype: FH!), **syn. nov.**

Thysananthus fuscobrunneus Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 252. 1934.—Type: TAIWAN. Taito: Mt. Chipon, Kiriya-Miyama, on bark, 31 XII 1932, *Y. Horikawa n. 10505a* (holotype: HIRO!), **syn. nov.**

Thysananthus grossidens Steph. ex Verd., Ann. Bryol., Suppl. 4: 168. 1934, nom. inval.

Plants autoicous, with projecting growth, turning upwards and becoming ascending to erect, green, brownish green to black in the older portion in the field, yellowish brown in herbarium specimens, up to 1.6 cm long \times 1.7–2.5 mm wide. **Stems** rather rigid; ventral merophyte 7–9 cell rows wide; in cross section round-orbicular in shape, 205–219 μm high \times 163–175 μm wide, composed of 32–46 epidermal cells surrounding 50–95 medullary cells in 14–18 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute, when moist weakly concave, apical parts plane, not recurved; dorsal lobe symmetrically ovate, 0.8–1.6 \times 0.5–1.1 mm, apex acute, dorsal base cordate, dorsal margin entire or with 1–4 triangular teeth, the teeth consisting of 3–6 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, ventral margin recurved to inrolled $1/2 \times$ leaf length, with 3–6 triangular teeth, the teeth consisting of 4–8 cells, being 2–3 cells wide at base, apex of one cell; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 5–10 \times 7–12 μm , median cells 17–27 \times 5–12 μm , basal cells 25–62 \times 15–25 μm , trigones cordate, often coalesced, intermediate thickenings 0–3 per cell wall; oil bodies 2–4 per cell (Mizutani, 1969: 4–6 oil bodies). **Lobules** oblong-rectangular, 0.3–0.5 \times 0.1–0.2 mm, $1/4$ – $1/3 \times$ lobe length; appendage on surface of lobule base not developed; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex with 1(–2) triangular teeth, the first tooth consisting of 3–4 cells, being 2 cells wide at base and ending in a row of 1–2 cells long, the second tooth of one cell only, often obsolete. **Underleaves** imbricate, slightly squarrose, broadly obovate-spathulate, 0.3–0.8 \times 0.4–0.7 mm, 3–4 \times stem width, apex truncate to slightly emarginate, plane, with 8–13 triangular teeth, the teeth consisting of 3–6 cells, being 2–3 cells wide at base and ending in a row of (1–)3–7 cells, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells 7–17 \times 5–12 μm . **Androecia** terminal-intercalary on branches, bracts and bracteoles in 2–8 pairs, bracts hypostatic, 0.6–0.8 \times 0.2–0.6 mm, apex acute, margins with 1–2 teeth; antheridia 2 per bract. **Gynoecia** with 1–2 lejeuneoid innovation forming monochasial pattern or dichasial pattern; lobe ovate, 1.3–1.9 \times 0.6–1.1 mm, apex apiculate, margins in upper $1/3$ with triangular teeth, the teeth consisting of 3–6 cells, being 2–3 cells at base and ending in a row of 1–2 cells; lobules broadly ovate, $1/3$ – $1/2 \times$ lobe length, apex apiculate, margins with triangular teeth, the teeth consisting of 5–11 cells, being 2–3 cells at base and ending in a row of 1–2 cells; bracteoles spatulate, 1.2–2.3 \times 0.5–1 mm, apex emarginate to shortly bifid, $1/2 \times$ bracteole length with triangular teeth, the

teeth consisting of 3–8 cells, being 2–3 cells wide at base and ending in a row of 1–3 cells, margins recurved. **Perianths** oblong-cylindrical, 1.6–2.4 × 0.6–1.1 mm, keels in upper 1/3–1/2 with triangular teeth, the teeth consisting 4–15 cells, being 2–4 cells wide at base and ending in a row of 1–2 cells; beak 50–55 µm with 3–4 cells long.

Chromosome number. A haploid number of $n = 9$ (Fritsch, 1991).

Chemistry. Isolepidozene (Sukkharak et al., in press), clerodane diterpenoids, 3β,4β:15,16-diepoxy-13(16),14-clerodadiene and thysaspathone (Harinantenaina et al., 2006).

Additional Illustrations. Horikawa (1934, p. 251, Fig. 49 as *Thysananthus fuscobrunneus*); Vanden Berghen (1950, p. 36, Fig. 1); Thiers & Gradstein (1989, p. 74, Fig. 28); Gradstein et al. (2002, p. 75, Fig. 47 as *T. minor*, p. 81, Fig. 51).

Distribution and ecology. Africa, Indochina, Malesia, Australia (Queensland) and the Pacific region; from sea level to 2800 m; on tree trunks, roots, rotten branches and logs along road sides, in the swamp forest, mangrove forest, rain forests (primary and secondary forests) and montane forests.

REPRESENTATIVE SPECIMENS. **Ivory Coast.** TAÏ: Taï National Park, *Assi 12739/B* (U). **Ghana.** WESTERN REGION: Ankasa river forest reservation, *Jones 1578b* (G); *ibid.*, 14 Feb 1971, *Jones s.n.* (JE). **Nigeria.** BENIN: Okomu forest reserve, *Jones 44, 174B* (BM). **Cameroon.** SOUTHWEST REGION: Bibundi, Sep 1891, *Dusén s.n.* (S 4 packets). **Gabon.** without location, 24 Jun 1927, *Testu s.n.* (PC, S). **Zaire.** KIVU: Irangi forest station (Bryotrop Expedition loc. 120), *Pócs 6601* (G, U), *6735* (G). **Seychelles.** BEAU VALLON: forest above Le Niol, *Norkett 16600* (BM).—PORT GLAUD: Morne Seychellois National Park, *Onraedt 74.S.258* (JE), *Norkett 16429, 16512, 16539, 16687* (JE), *Pócs 00105, 00105/B, 9335/B* (G); Congo Rouge Relict forest, *Norkett 17148* (BM, JE); La Misere road, *Norkett 16512, s.n.* (BM); summit of Morne Blanc, *Norkett 18603* (BM); Sans Souci road, *Norkett 16687* (BM); old Capucin Mission, Trois Frères road, *Norkett 16429* (BM, JE); Val Riche, *Pócs 9333/L* (G 4 packets, PC); NE escarpment of Trois Frères, *Pócs 9315/W* (GOET); Morne Seychellois national park, Copolia summit, *Pócs 9335/B* (G 2 packets); *ibid.*, in a depression of Mare aux Cochons valley, *Pócs s.n.* (G 2 packets).—SILHOUETTE ISLAND: near Pota Eau ridge, *Norkett 17741* (BM), without location, *Alexejev 13* (JE).—SOUTH EAST ISLAND: Ridge of Brulle, *Norkett 17933* (BM). **Madagascar.** ALAOTRA-MANGORO: forest in Analamazoata, *Camboué s.n.* (PC).—ANTSIRANANA: Diego-Suarez, Radama, *Aptroot & Hensen 13198B* (U); Tamatave, Andasibe, *Aptroot & Hensen 13433* (U).—ATSIMO-ANTSIRANANA: Renana stream, *Humbert 3451* (PC). **Réunion.** SAINT-BENOIT: between Grand Etang and road, “M” 17.855,

Onraedt 73.R.1387 (BR 2 packages). **Mauritius.** PLAINES WILHEMS: Le Patrin, “*Guého*” 48 (PC); without location, “*Bélauger*” *s.n.* (BM).

India. ANDAMAN AND NICOBAR ISLANDS: Andaman Islands, Port Blair, 14 Nov 1890, *Man s.n.*, ex hb. Levier 773 (G); *ibid.*, 1893, *Man s.n.*, ex hb. Levier 741 (G); *ibid.*, ex hb. Levier 774 (G 2 packets, JE, S 2 packets); *ibid.*, Oct 1898, *Man s.n.*, ex hb. Levier 1715 (BM, G 2 packets, PC); Port Monate, *Kurz s.n.* (BM 3 packets, PC); without location, *Kurz s.n.* (BM, G), 1622, 1631 (G). **Sri Lanka.** CENTRAL: Adam’s peak, *Onraedt 87.L.8801* (BR).—SOUTHERN: Beraliya forest reserve, *Onraedt 76.L.3284* (BR, JE); Hiniduma, *Onraedt 76.L.3508* (JE), 77.L.4304, 81.L.9291, 81.L.9292, 81.L.9370 (BR), 76.L.3454, 76.L.3508 (BR, JE), 76.L.3684 (PC); Kammeliya forest reserve, *Onraedt 77.L.4257* (BR). **China.** HAINAN: Kwangtung, *Chen Pang-Chieh & al.* 382, 435c, 633 (L). **Thailand.** CHANTHABURI: Khao Sa-Bab, *Sapanuchart s.n.* (BCU).—CHIANG MAI: Mt. Inthanon, *Touw 9613* (BKF).—LOEI: Mt. Phu Luang, *Thaithong 201* (BCU), *Touw 10530* (BKF); *ibid.*, north ridge, *Tagawa & Kitagawa T1366, T1377* (G); *ibid.*, eastern slope, *Tagawa & Kitagawa T1876* (G); *ibid.*, north-eastern ridge, *Tagawa & Kitagawa T1686, T1873* (G); Phu Kradung, *Touw 10959* (BKF), *Tagawa & Kitagawa T1019* (G); *ibid.*, Pen-Pop waterfall, *Thaithong 972* (BCU).—NAKHON RATCHASIMA: Khao Khiao, *Tixier 319* (PC).—NAKHON SI THAMMARAT: Mt. Khao Luang, *Smitinand 1027* (BCU, BKF), *Touw 10667, 11354, 11360, 11768, 11875, 11883, 12015, 12023* (BKF), 11686, 11738 (BKF, BR), *Tagawa & Kitagawa T5067, T5072, T5154* (G); Mt. Khao Nan Yai, *Sukkharak 50, 130, 170, 180, 183, 189* (BCU); *ibid.*, San Yen, *Sukkharak 739, 751, 752, 762, 766, 768, 784, 788, 793* (BKF, GOET).—PHANG NGA: on the way to Roe-Si-Sawan cave, *Boonkerd 14* (BCU); Sri Phang Nga National Park, *Chantanaorrapint 2089, 2096, 2099, 2100* (PSU).—PRACHINBURI: Khao Yai National Park, *Touw 12104, 12360* (BKF), 12103 (BKF, BR).—RANONG: La-Oon mangrove forest, *Thaithong 981* (BCU); hot spring, *Tixier 3895* (PC).—SATUN: Taritao Island, *Chantanaorrapint s.n.* (PSU).—TRAT: Chang Klau, Hui Range, *Smitinand 1453* (BCU, BKF); Koh Kood, *Sukkharak s.n.* (BKF, GOET); Koh Chang, 10 Feb 1900, *Schmidt s.n.* (C).—TRANG: Mt. Khao Chong, *Tagawa & Kitagawa T6877, T6965, T6970, T6974* (G). **Cambodia.** Tonle Sap, *Tixier 3864* (PC). **Cambodia.** KAMPOT: Mt. Bokor, *Tixier 2669, 3006, 3027, 3196, 3225, 3313, 3603, 3710* (PC); Tonle Sap, *Tixier 3835* (PC). **Vietnam.** LAM ĐỒNG: Da Lat, 21 Sep 1957, *Tixier s.n.* (PC). **Malaysia.** JOHORE: Mt. Ophir, *Verdoorn 58, 66, 100, 135, 170* (SING).—KADAH: Gg. Raya, *Haniff & Nur 7120* (SING); Kedah peak, *Tixier 6058* (PC), *Holtum 14889* (SING).—MALACCA: Gg. Tunduk, *Ridley 701* (SING).—NEGRI SEMBILAN: Bukit Putus, *Ridley 751* (SING).—PAHANG: Cameron Highland, trail to Gunung Jasar, *Gradstein 10400/1, 10400/2, 10404/1, 10404/2* (GOET); 2.5 miles on Genting Highland road,

Een s.n. (JE, S); Fraser's Hill, *Tixier* 4753 (PC); *ibid.*, 21 May 1997, *Schäfer-Verwimp & Verwimp s.n.* (G); the road to Genting Hightland, *Sukkharak* 716, 719, 722 (BKF, GOET).—PENANG: Penang hill, *Allen* 754 (L), *Ridley* 525 (SING).—PERAK: Taiping, *Ilkiu-Borges & al.* 2981 (GOET); Gunong Batu Putih, *Wray s.n.* (BM, G, SING, W); Buyong Malacca, *Ridley* 723 (SING).—SABAH: Mt. Kinabalu, Kamborangah, *Holttum s.n.* (SING); Silau-Silau trail, *Sukkharak* 562 (BCU), *Sukkharak* 549, 550, 593 (BKF, GOET).—SARAWAK: Mt. Dulit, Aug 1932, *Richards s.n.*, Hep. Sel. Crit. Verdoorn 400 (BR, C, GOET, PC, SING, U); *ibid.*, 1932, *Richards* 2276, Hep. Sel. Crit. Verdoorn 450 (BR, C, G, GOET, JE, PC, S, SING, U, W); *ibid.*, Oct 1932, *Richards s.n.*, Hep. Sel. Crit. Verdoorn 397 (C, GOET); *ibid.*, Nov 1932, *Richards s.n.*, Hep. Sel. Crit. Verdoorn 398 (C), *Richards* 1208, 2339 (SING), *Synge* 2083 (BM); *ibid.*, Dulit trail, *Richards* 1182 (JE); Sibul, Loba Kabang protected forest, *Wood* 1420 (BM-K, L); Banting, *Beccari* 1867 (U). **Singapore.** Chua Chu Kang, *Ridley* 441 (SING 2 packets); Gardens, *Ridley* 600 (SING). **Brunei.** TEMBURONG: 1.5 km NE of Kampong Semabat, *Seah* 534 (SING). **Indonesia.** JAVA: East Java, Tretes, on N-slope of Mt. Ardjuno, *Sipman* 6992 (U); Dorowatti, May 1929, *Clason s.n.* (L); West Java, Mt. Salak, *Fleischer* 76 (S); Mt. Gede, Artja, Apr 1894, *Schiffner s.n.*, Hep. Sel. Crit. Verdoorn 289 (BM, BR, C, G 2 packets, GOET, JE, PC, S, SING, W); *ibid.*, Perbawati, Jul 1930, *Verdoorn s.n.*, Hep. Sel. Crit. Verdoorn 290 (BM 2 packets, BR, C, G 2 packets, JE, PC, S, SING, U 2 packets, W); Cibodas, Apr 1894, *Schiffner s.n.*, Hep. Sel. Crit. Verdoorn 291 (BM 2 packets, BR, C, G 2 packets, GOET, JE, PC, S, SING, U, W); *ibid.*, Feb 1931, *Renner s.n.* (JE 2 packets), *Fleischer s.n.* (C); Tjiburum, Nov 1927, *Burgeff* 8103 (JE, S), “*Noeste*” 308 (JE); Mt. Pangerango, *Kurz s.n.* (BM 2 packets).—KALIMANTAN: East Kalimantan, peak of Balikpapan, *Meijer B1332c*, *B1416* (S); Nunukan, *Meijer B4921* (BM-K).—LESSER SUNDA ISLANDS: Bali, Bali Handara country club, *Schäfer-Verwimp & Verwimp* 20790 (GOET).—SULAWESI: Central Sulawesi, Lore Lindu National Park, Mt. Nokilalaki, *Gradstein & Ariyanti* 11000, 11041, 11052 (GOET), Central Sulawesi, Nov 1888, *Warburg s.n.* (JE).—SUMATRA: Bangka-Belitung, Balai, 1869–1870, *Teysmann s.n.*, Hep. Sel. Crit. Verdoorn 399 (BR, C, G, GOET, JE, PC, S, SING, U, W); Mt. Menoembing, *Teysmann* 30 (GOET), 30/A, 30/B (L); North Sumatra, Bandar Baroe, *Staal S-249* (L); West Sumatra, Singalang, Jul 1894, *Schiffner s.n.*, Hep. Sel. Crit. Verdoorn 288 (BR, C, PC, S, SING, U); Lubuk Sikaping, 1931, *Renner s.n.* (JE, S); Padang, *Schild* 107 (JE, W); Singalang, *Schiffner & Indicum* 2924, 4009 (U).—WESTERN NEW GUINEA: Papua, Cycloop Mts., *Royen & Sleumer* 6256 (BR, JE, U); Kadubaka, Swart valley, *Bergman H.50*, *H.51* (S); West Papua, Vogelkop Peninsula, *Royen & Sleumer* 7966 (BR, JE, U); Bian Katem, *van Zanten* 229 (U). **Philippines.** AGUSAN DEL NORTE: Butuan, *Weber* 1343 (BM-K); Mt. Urdaneta, Oct 1912, collector unknown. (BM, G,

PC, U, W).—BENGUET: Baguio, Feb 1928, *Burgeff s.n.* (S).—ORIENTAL MINDORO: Mt. Malasimbo, *Bartlett 13865* (JE); Mt. Banahao, *Alvarez 0-77512* (JE).—QUEZON: Botanical Garden of University of the Philippines Los Banõs, *Onraedt 85.P.11342* (BR).—SAMAR: Silanga, *Merrill 9005* (BM). **Papua New Guinea.** CENTRAL: Varirata National Park, *Sloover 42.564* (BR); Boridi, *Carr 13537* (JE), *13528* (BM, L 2 packets); near Dabamura on Owers Corner road, *Streimann & Naoni 14879, 14950* (JE, LAE); Kuriva logging area, *Streimann & Vinas 14421* (LAE), *14448* (JE, LAE); Bereina-Angabanga river road, *Streimann & Naoni 16303* (JE, LAE); K. B. sawmill, Ehu creek, *Streimann & Naoni 16499, 16633* (LAE), *16668* (JE, LAE); road to Musgrave river, *Streimann & Naoni 15239, 15953* (JE, LAE).—EAST SEPIK: Ambunti subdistrict, along Yapa, *Hoogland & Craven 10121, 10738* (JE).—MOROBE: Wau, Mt. Kaindi, Kunai Creek, *Gradstein 3964* (G 2 packets, U 3 packets), *3965* (U); Kaisenik logging area, *Shea 6404* (JE); Mt. Missim track, *Streimann 22911* (GOET), *22919* (JE, LAE); Molukkerne, *Nyman s.n.* (S); Yinimba, *Streimann 19032, 19095* (JE, W); Windowi village, *Streimann & Kumei 22648* (JE, LAE); logging area, 7° S 146° 45' E, *Streimann & Bellamy 13311* (JE, LAE); Slate-Gumi creeks divide, *Streimann 13831* (JE, LAE), *13973* (LAE); Gumi divide, *Streimann 22743* (LAE), *22733* (JE, LAE); Aiuwa-Bakia track, *Streimann & Tamba 12274* (LAE), *12399* (JE, LAE); Herzog Mts., *Streimann & Umba 10838, 10854, 10869, 10916, 10964, 11012* (JE, LAE); Araulu logging area, *Streimann 13565* (JE, LAE), *13553, 13571* (LAE); upper Watut river, *Streimann 23100* (BR, JE, LAE); Wau-Salamaua track, *Streimann 25392* (JE); upper Nawata Banda, *Streimann 19519, 24868, 24872, 33962* (JE); Bulolo-Watut divide, *Streimann 17480, 24968, 24995* (JE); *ibid.*, Manki Trig, *Streimann & Bellamy 13066* (LAE); Angabena ridge, Aseki-Bulolo road, *Streimann 25918* (JE); Gumi divide, head of Gumi creek, *Streimann 25136, 25066* (JE); Heads Hump, *Streimann 17374, 17402* (JE); Kaisenik logging area, *Shea 6404* (JE); Oomsis logging area, *Streimann 25839* (JE); Mt. Kaindi, Blue Point, *Gradstein 3793* (G, U 3 packets); Pouyu village, *Streimann & Tamba 12662* (LAE); Nauti logging area, *Streimann & Kairo 17299* (LAE).—NEW IRELAND: Mussau Island, Bismarck Archipelago, *Køie & Olsen 2070* (C, JE).—SOUTHERN HIGHLANDS: Tari-komo road, *Streimann 32712* (BR, JE, LAE, W); Piribu sawmill, *Streimann 32473* (JE); Lama sawmill, *Streimann 26605, 26611* (JE).—WEST NEW BRITAIN: slopes of Mt. Ulawun, *Streimann 41386* (JE); Nakanai Mts., *Streimann 40478* (JE); *ibid.*, Geleo-Lasilai logging area at Mt. Laliti, *Streimann 41086* (JE).—WEST PROVINCE: Star Mts, Sibil-valley, *van Zanten 559b* (L); *ibid.*, Antares Mts, *van Zanten 559/B* (L).—WESTERN HIGHLANDS: Baiyer river-Ruti road, Jimi valley, *Streimann 22061* (JE, LAE), *22242* (BR, JE, LAE).—WEST SEPIK: Antingin, Eliptamin, *Macrosimnok 4* (JE).

Australia. QUEENSLAND: Cardwell, Stoney creek, 21 May 1982, *Stone s.n.* (U); El Arish, 11 Jul 1982, *Stone s.n.* (U); Cook district, Bellenden Ker National Park, *Thiers & Halling* 2397 (U); Main coast range, Daintree river National Park, *Pócs & Streimann* 9987/L (GOET); Cape Tribulation area, Gap creek, *Pócs & Streimann* 99105/K (GOET); Boonjie state forest, *Streimann* 27553 (JE); Cooroo logging area, *Streimann* 29943, 29970 (JE); Dunn creek, Kirrima road, *Streimann* 31234, 31241, 31255, 31257 (JE); Cardwell range, *Streimann* 28591 (JE); Koombooloomba dam road, *Streimann* 28910, 28923 (JE); Culpha creek catchment, *Streimann* 28982 (JE); Mossman Gorge, 26 May 1975, *Stone s.n.* (JE); Main coast range, *Streimann & Gray* 27172 (JE); Walter Hill range, *Streimann* 30477 (JE); Mt. Lewis NW of Cairns, *Hicks* 11576 (U); *ibid.*, 29 Jun 1982, *Stone s.n.* (U); *ibid.*, 29 Jun 1984, *Stone s.n.* (U); The Boulders rain forest reserve along Babinda Creek, *Pócs & Streimann* 9983/L (G); North Kennedy, *Renner* 1679; *ibid.*, Babinda creek, *Renner* 1842c; *ibid.*, Little Birthday creek, 29 Jun 2005, *Brown* 2005/86 & *Renner s.n.* (NSW).

New Caledonia. NORTH: Diahot, l'Ignambi, *Hürlimann* 2858a (G, GOET, PC), 2858 (U); Mt. Panie, *Morat* 6909 (PC).—SOUTH: l'Est, *Hürlimann* 2215 (G, GOET, PC, U); Mé Amméri, *Guillaumin & Baumann* 9097 (GOET); south of Kouanémoa Mts., *Hürlimann* 2334 (G, GOET, PC, U); Rivière Bleue, *Guillaumin & Baumann* 10894 (GOET, PC, U); Mt. ouénarou, *Guillaumin & Baumann* 11875A (GOET); Mois de Mai, Yaté, *Baumann* 14028 (G, GOET, PC); Ni, *Hürlimann* 2709 (G, PC, U); Tao, Jan 1910, *Franc s.n.* (G, PC, S, W); Yaté, *Kee* 42654 (PC). **Fiji.** NAITASIRI: Mt. Tomanivi, *Hürlimann* T1096e (GOET). **Samoa.** UPOLU: montane forest west of Tiavi, *Schutze-Motel* 3601 (JE).

Reported from Philippines (Negros Oriental) by Mizutani (1977). Additional specimens reported from China, Hainan, Tianchi Forest Farm, *Lin* 3843 (IBSC); Yajia Forest Farm, 1974, *survey team* 3344 (IBSC) (J. Wang, pers. comm.).

Thysananthus spathulistipus is a rather polymorphic species with respect to the dentation of leaves, which varies from edentate to strongly dentate as seen in *T. comosus*, *T. discretus* and *T. mollis*. In montane forests of Sulawesi, Gradstein (pers. comm.) noted that phenotypes from below 2000 m were green in color and rather small whereas those from the upper montane cloud forest at 2300–2600 m were brown-green when fresh and more robust.

Thysananthus spathulistipus is closely related to *T. appendiculatus*. Differences are discussed under the latter species.

The original material of the species in the Nees herbarium in STR contains 10 specimens, mostly from "Bantam" but only one annotated as originating from "Leback". The latter specimen is considered the holotype.

***Thysananthus* series *Anguiformes* ser. nov.**

Cellulae epidermales dorsales dilatatae. Amphigastria adnata. Bracteeae et bracteolae femininae integra.

Type species: *Thysananthus anguiformis* (Hook. f. & Taylor) Steph.

Dorsal epidermis cells of stem larger than inner cells. Underleaf bases adnate with leaves on one side. Margins of female bracts and bracteoles entire.

Distribution: New Zealand and New Caledonia.

10. *Thysananthus anguiformis* (Hook. f. & Taylor) Steph. (Fig. 20)

Sp. Hepat. 4: 800. 1912. *Jungermannia anguiformis* Hook. f. & Taylor in Hooker, London J. Bot. 3: 567. 1844. *Mastigolejeunea anguiformis* (Hooker f. & Taylor) B. Thiers & Gradst., Mem. New York Bot. Gard. 52: 75. 1989.—Type. NEW ZEALAND. *Colenso s.n.* (lectotype, designated by B. Thiers & Gradstein, 1989: FH!; isolectotype: NY!; paralectotypes: BM-*Colenso* 226, 1222, 2121!).

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, yellowish to reddish brown in herbarium specimens, up to 3 cm long × 1–1.6 mm wide. **Stems** rather rigid; ventral merophyte 6–7(–9) cell rows wide; in cross section orbicular in shape, 123–211 µm high × 86–217 µm wide, composed of 15–27 epidermal cells surrounding 16–62 medullary cells in 6–11 layers high, dorsal epidermal cells larger and somewhat thinner-walled than medulla and ventral epidermal cells. **Leaves** imbricate, when dry suberect and slightly convolute, when moist concave, apical parts turn to ventral side, recurved; dorsal lobes asymmetric ovate, 0.7–1.2 × 0.5–1 mm, apex acute, margin entire, dorsal base cordate, ventral margin plane; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 7.5–10 × 7.5–12.5 µm, median cells 20–30 × 7.5–12.5 µm, basal cells 25–45 × 12.5–17.5 µm, trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies unknown. **Lobules** rectangular, 0.3–0.4 × 0.2–0.3 mm, ±1/2× lobe length, appendage on surface of lobule base not developed; keels sometimes with appendages on one side where leaves and underleaves are free and opposite to adnate ones; lobule apex truncate-rotundus, ending abruptly in a short point of ventral lobe margin, free margin slightly upcurved, apex with one triangular or elongate tooth, the tooth consisting of 5–9 cells, being 2–3 cells wide at base and ending in a row of 1–5 cells. **Underleaves** imbricate, slightly squarrose, broadly

obovate, $0.3\text{--}0.5 \times 0.5\text{--}0.7$ mm, $4\times$ stem width, apex broadly rounded to truncate, margins entire, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells $20\text{--}22.5 \times 7.5\text{--}10$ μm . **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 3–6 pairs, bracts epistatic, ovate, $0.7\text{--}0.8 \times 0.4\text{--}0.5$ mm, apex acute, margins entire; antheridia 2 per bract. **Gynoeceia** with 2 lejeuneoid innovation forming a dichasial pattern; lobe ovate, $0.9\text{--}1.3 \times 0.5\text{--}0.8$ mm, apex apiculate, margin entire; lobules broadly ovate, $1/2\times$ lobe length, apex apiculate, margin entire; bracteoles obovate, $0.7\text{--}0.9 \times 0.5\text{--}0.8$ mm, margins entire, slightly recurved. **Perianths** oblong, $1.2\text{--}1.3 \times 0.7\text{--}0.8$ mm, keel in upper $1/4$ with triangular teeth, the teeth consisting of 3–6 cells, being 2 cells wide at base and one long at apex; beak $82\text{--}200$ μm with 6–11 cells long.

Chromosome number. Unknown.

Chemistry. Unknown.

Distribution and ecology. Endemic to New Zealand; 50–150 m; on tree trunks, rotten logs, on branches in dense bush near sea shore, wet forest dominated by treeferns.

REPRESENTATIVE SPECIMENS. **New Zealand.** AUCKLAND: Waitakeke range near Auckland, 3 Aug 1983, *Braggins s.n.* (GOET, U); Great Barrier Island, *Kirk 218* (G); Coromandel state forest, *Schäfer-Verwimp & Verwimp 13731* (GOET).—BAY OF PLENTY: Mamaku forest, *Een NZ063, NZ064* (S); Rotorua, *Allison s.n.* (S); near Rotorua, 17 May 1929, “*Kwallison*” *s.n.* (JE); 3 miles west of Rotorua, 15 Apr 1966, *Wade s.n.* (JE).—NORTHLAND: Waipoua Kauri forest, *Hatcher 436, 475/b* (JE), *Schäfer-Verwimp & Verwimp 13662* (U); Bay of Islands, *Kirk 76* (G).—SOUTHLAND: Martin’s bay, *Hatcher 963/c* (JE); North of Mc Kerrow river, *Hatcher 808* (JE).—WELLINGTON: Akatarawa forest park, *Mues 80a, 80b* (U).—WEST COAST: Mt. Stormy trial, *Frahm 20–10* (GOET); Matheson lake, *Mues 80d* (U); Westland national park, *Schäfer-Verwimp & Verwimp 14058* (GOET 2 packets).

Thysananthus anguiformis was treated as *Mastigolejeunea anguiformis* by Thiers & Gradstein (1989). This species, together with *T. pancheri*, was long placed in *Mastigolejeunea* because of its entire female involucre and enlarged dorsal epidermis cells. Molecular work, however, has confirmed that *T. anguiformis* and *T. pancheri* are members of *Thysananthus* (Wilson et al., 2007a; Sukkharak et al, submitted). The robust sister-group relationship of ser. *Thysananthus* and ser. *Anguiformes* is supported by the presence of adnate underleaves (Sukkharak et al, submitted).

Thysananthus anguiformis characterized by truncate-rotundus apex lobules, ending abruptly in a short point of ventral lobe margin. This species varies in shape of lobule teeth, which are elongate, 2–5 cells long to triangular, 1–2 cells long.

11. *Thysananthus pancheri* (Steph.) Hürl. (Fig. 21)

Bauhinia 9: 167. 1989. *Mastigolejeunea pancheri* Steph., Sp. Hepat. 4: 771. 1912.—Type: NEW CALEDONIA. *Pancher 591* (isotypes: PC 3 packets!); Icon. Steph. n. 7448.

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, yellowish brown to reddish brown in herbarium specimens, up to 1.8 cm long \times 1.9–2.2 mm wide. **Stems** rather rigid; ventral merophyte 7–9 cell rows wide; in cross section orbicular-subelliptic in shape, 159–230 μ m high \times 159–176 μ m wide, composed of 25–33 epidermal cells surrounding 42–47 medullary cells in 9–10 layers high, dorsal epidermal cells larger and somewhat thinner-walled than medulla and ventral epidermal cells. **Leaves** imbricate, when dry suberect and convolute, when moist strongly concave, apical parts turn to ventral side, recurved; dorsal lobes asymmetric broadly ovate, 1.1–1.6 \times 0.9–1.2 mm, apex acute, margin entire, dorsal base auriculate, auricle 50–82 \times 125–75 μ m; cells elongate-hexagonal with acute ends, vitta cells absent, marginal cells 7.5–12.5 \times 10–15 μ m, median cells 22.5–27.5 \times 12.5–20 μ m, basal cells 25–45 \times 17.5–25 μ m, trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies unknown. **Lobules** rectangular, 0.6–0.7 \times 0.3–0.4 mm, $\pm 1/2 \times$ lobe length; appendage on surface of lobule base not developed; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex with one triangular tooth, the tooth consisting of 6–12 cells, being 2–4 cells wide at base and ending in a row of 1–3 cells. **Underleaves** imbricate, slightly squarrose, broadly obovate, 0.5–0.8 \times 0.6–1.2 mm, 2–2.5 \times stem width, apex broadly rounded to truncate, margins entire, bases cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells 22.5–17.5 \times 7.5–10 μ m. **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 3–8 pairs, bracts hypostatic and epistatic, 0.5–0.8 \times 0.4–0.6 mm, apex acute, margins entire; antheridia 2 per bract. **Gynoeceia** with one lejeuneoid innovation forming a monochasial perttern; lobe ovate, 1.1–1.4 \times 0.5–0.7 mm, apex apiculate, margin entire; lobules broadly ovate, $1/2 \times$ lobe length, apex apiculate, margin entire; bracteoles obovate, 1–1.2 \times 0.5–0.7 mm, apex truncate, margins entire, slightly recurved. **Perianths** oblong, 1.3–1.4 \times 0.5–0.8 mm, keels in upper $1/3$

with numerous lacinate teeth, with 2–6 cells long at apex; beak 57.5–112.5 μm with 6–8 cells long.

Chromosome number. Unknown.

Chemistry. Unknown.

Distribution and ecology. Endemic to New Caledonia; 40–1100 m; on bark in *Nothofagus balansae* (Baill.) Steenis, *Spermolepis* sp., *Leucopogon* sp., *Canariellum* sp. and *Exocarpos phyllanthoides* Endl. forests.

REPRESENTATIVE SPECIMENS. **New Caledonia.** NORTH: Oua Tilou, *Baumann-Bodenheim* 12421a (G, GOET); Voh, *Guillaumin & Baumann* 12165 (GOET); Mt. Ignambi, *Hürlimann* 2864 (GOET); Nehoue, *Kee* 36864 (PC).—SOUTH: Mt. Koghis, *Franc s.n.* (JE); Rivière Bleue, *Hürlimann* 2665a (G, GOET), 10864 (GOET); Rivière Blanche, *Baumann-Bodenheim* 13949 (G, GOET); Boulari valley, *Hürlimann* 2304a (G), 2303 (G, GOET, PC, U); ramp north-western of Mt. Quitchambo, *Hürlimann* 9343 (G, GOET); Mt. Sources, *Hürlimann* 2206 (G, PC, U), *Kee* 44013 (PC); Quinné valley of Mt. Dzumac, *Hürlimann* 2624 (G, GOET, PC, U), 2463 (GOET, PC, U); north-western of Mt. Natégou, *Hürlimann* 2279, 2292 (G), 2289a (GOET, PC, U); Kouébuni, *Hürlimann* 2249, 2255, 2256 (G), 2252 (G, U); Koéalagoguamba, *Hürlimann* 2584a (G); “southern woodland”, *Guillaumin & Baumann* 11703, 11704, 11713a (GOET); Rivière Pirogues, *Guillaumin & Baumann* 11703, 11704 (G); Rivière Voh, *Guillaumin & Baumann* 12165 (G, GOET); Yaté, *Kee* 42653 (PC).

Thysananthus pancheri varies in plant sizes, which are 48–57 mm to 70–75 mm. This species may be confused with *T. gottschei* but the latter species has epidermal cells not larger than medullary cells, spatulate underleaves and only one lejeuneoid innovation.

Incongruence between plastid and ITS data in one sample of *Thysananthus pancheri* led to the first report of a hybrid in Lejeuneaceae, and the first one in liverworts inferred from phylogenetic data (Sukkharak et al., submitted; Figs. 5–6). In the cpDNA phylogeny (Fig. 5) *T. pancheri* sample 2 is sister to *T. pancheri* sample 1, and both samples are placed in a well-supported clade with *T. anguiformis* in the cp DNA phylogeny. In contrast, in the nuclear ITS tree (Fig. 6) *T. pancheri* sample 2 is sister to the *T. appendiculatus*-*T. discretus* clade with significant support. The plastid phylogeny concurs with the current species circumscription, whereas the ITS phylogeny is probably the deviating one as *T. pancheri* is morphologically well separated from *T. appendiculatus* and *T. discretus*. Based on the single dated phylogeny of Lejeuneaceae (Wilson et al., 2007b) together with the larger plant size, these considerations provide first evidence that *T. pancheri* sample 2 is of hybrid origin. Given the maternal

inheritance of plastids in bryophytes, *T. pancheri* should be considered the maternal parent of *T. pancheri* sample 2, whereas either *T. appendiculatus* or *T. discretus* is probably the paternal parent of the hybrid. However, inference from a more detailed dated phylogeny of Ptychanthoideae may confirm the putative young age of the hybridization event. Further analyses including chromosome counts may determine a possible polyploidy of *T. pancheri* sample 2.

***Thysananthus* section *Dendrolejeunea* (Spruce) comb. nov.**

Lejeunea subg. *Dendrolejeunea* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 110. 1884. *Dendrolejeunea* (Spruce) Lacout., Rev. Bryol. 35: 104. 1908. *Thysananthus* sect. *Vittatae* Verd., Ann. Bryol. Suppl. 4: 182. 1934.—Type: *Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout. Taxon named for its dendroid habit.

Type species: *Thysananthus fruticosus* (Lindenb. & Gottsche) Schiffn.

Leaves with a vitta.

Distribution: Japan, Malesia, Australia, Pacific.

Thysananthus* series *Dendrolejeunea

Plants dendroid, with creeping stoloniform stems and ascending leafy stems. Branching of leafy stems regularly pinnate. Lobule bases without appendage.

Type species: *Thysananthus fruticosus* (Lindenb. & Gottsche) Schiffn.

Distribution: Malesia.

12. *Thysananthus fruticosus* (Lindenb. & Gottsche) Schiffn. (Figs. 22–23)

in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 130. 1893. *Bryopteris fruticosa* Lindenb. & Gottsche, Syn. Hepat. 737. 1847. *Dendrolejeunea fruticosa* (Lindenb. & Gottsche) Lacout., Rev. Bryol. 35: 104. 1908. *Caudalejeunea fruticosa* (Lindenb. & Gottsche) Steph., Sp. Hepat. 5: 14. 1912.—Type: INDONESIA. Java: Mt. Sajira, *Blume s.n.* (lectotype: STR!).

Bryopteris filicina (Sw.) Nees var. γ *fruticosa* Gottsche et al., Syn. Hepat. 285. 1845, nom. nud. syn. fide Verdoorn (1934): 182.

Thysananthus manillanus Gottsche, Ann. Sci. Nat., Bot (ser. 4) 8: 342. 1857.—Type: PHILIPPINES. “Manilla, *Gaudichaud 115*” (holotype: PC; isotype: PC-hb. Bescherelle!).

- Bryopteris vitata* Mitt., Fl. Vit: 411. 1873.—Type: AUSTRALIA. Norfolk Island: *Robinson s.n.* (holotype: G!).
- Thysanolejeunea lanceolata* Steph., Hedwigia 35: 139. 1896. *Thysananthus lanceolatus* (Steph.) Steph., Sp. Hepat. 4: 796. 1912.—Type: PAPUA NEW GUINEA. Morobe: “Sattelburg”, *Känbach 56* (holotype: G!).
- Thysananthus sinclairii* (Mitt.) Steph., Sp. Hepat. 4: 792. 1912. *Lejeunea sinclairii* Mitt., Bonplandia 10: 9. 1862.—Type: FIJI. “Insulae Vitienses” “inter nr. 843”, *Seemann s.n.*, “in Herb. Goullie et Mitten” *Sinclair s.n.* cf. Geissler & Bischler (1987), syn. fide Verdoorn (1934): 183.
- Thysananthus abietinus* Steph., Sp. Hepat. 4: 794. 1912.—Type: NEW CALEDONIA. “Insula Oneiteum, 1882, *Braitwaithe*” *s.n.* (holotype: G!); Icon. Steph. n. 10165.
- Thysananthus lauterbachii* Steph., Sp. Hepat. 4: 797. 1912.—Type: PAPUA NEW GUINEA. Madang: “Gogal”, *Lauterbach 1060* (holotype: G!); Icon. Steph. n. 10193.
- Thysananthus ovistipulus* Steph., Sp. Hepat. 4: 798. 1912.—Type: PAPUA NEW GUINEA. Without location, *Musgrave s.n.* (holotype: G!); Icon. Steph. n. 10202.
- Thysananthus bowienus* Steph., J. & Proc. Roy. Soc. New South Wales 48: 134. 1914.—Type: VANUATU [“Novae Hebrides”]. Sanma: Santo, *Watts 18* (holotype: G!); Icon. Steph. n. 10170.
- Thysananthus densus* Steph., Sp. Hepat. 6: 565. 1924.—Type: PAPUA NEW GUINEA. Milne Bay: *Conway s.n.* (holotype: G!); Icon. Steph. n. 10176.
- Thysananthus eminens* Gottsche ex Verd., Ann. Bryol. Suppl. 4: 183. 1934, nom. inval. [Art. 34.1 (c)], syn. fide Verdoorn (1934): 183.
- Thysananthus ovilobulus* Steph. ex Verd., Ann. Bryol. Suppl. 4: 183. 1934, nom. inval. [Art. 34.1 (c)], syn. fide Verdoorn (1934): 183.

Plants autoicous, with dendroid habit, having creeping stoloniform stems and upright, regularly pinnate branches, yellowish in herbarium specimens, up to 14.8 cm long × 1.8–2.1 mm wide. **Stems** rather rigid; ventral merophyte 6–11 cell rows wide; in cross section round-orbicular in shape, 170–340 µm high × 135–300 µm wide, composed of 30–62 epidermal cells, 25–50 subepidermal cells in 4–6 layers high surrounding 67–218 medullary cells in 9–20 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute, when moist weakly concave, apical parts plane, not recurved; dorsal lobe asymmetrically ovate-falcate, 1.1–2.7 × 0.5–1.3 mm, apex acute, dorsal base cordate, dorsal margin with 2–4 triangular teeth, the teeth consisting of 3–7 cells, being 3–4 cells wide

at base, apex of one cell, ventral margin plane, with 2–6 triangular teeth, the teeth consisting of 3–7 cells, being 3–4 cells wide at base, apex of one cell; cells elongate-hexagonal with acute ends, vitta present in midportion of lobe, extending to base, $\frac{2}{3} \times$ lobe length, 8–10 cell rows wide, 17–26 cells long, marginal cells $7.5\text{--}15 \times 7.5\text{--}12.5 \mu\text{m}$, median cells $17.5\text{--}25 \times 7.5\text{--}15 \mu\text{m}$, basal vitta cells $37.5\text{--}60 \times 12.5\text{--}22.5 \mu\text{m}$, trigones cordate, often coalesced, intermediate thickenings 0–1 per cell wall; oil bodies unknown. **Lobules** oblong, $0.1\text{--}0.5 \times 0.1\text{--}0.3 \text{ mm}$, $\pm \frac{1}{3} \times$ lobe length, appendage on surface of lobule base not developed; keel with appendages on both sides of stem; lobule apex transverse, not or shortly continuing into the ventral lobe margin, entire to with one triangular tooth, the tooth consisting of 3 cells, being 2 cells wide at base, apex of one cell. **Underleaves** imbricate, slightly squarrose, ovate, $0.5\text{--}1 \times 0.5\text{--}0.9 \text{ mm}$, $3\text{--}4 \times$ stem width, apex truncate to emarginate, with 8–12 triangular teeth, the teeth consisting of 7–9 cells, being 2–3 cells wide at base and ending in a row of 6–7 cells, bases cuneate-slightly auriculate, underleaf bases not adnate with leaves; cells $22.5\text{--}42.5 \times 7.5\text{--}10 \mu\text{m}$. **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 5–21(–38) pairs, bracts hypostatic, $0.6\text{--}1.3 \times 0.3\text{--}0.6 \text{ mm}$, apex acute, margin entire; antheridia 2 per bract. **Gynoecia** with 1–2 lejeuneoid innovation forming monochasial or dichasial pattern; lobe lanceolate, $1.4\text{--}2 \times 0.3\text{--}0.6 \text{ mm}$, apex apiculate, margins in upper $\frac{1}{3}$ with triangular teeth, the teeth consisting of 3–10 cells, being 2–4 cells wide at base and ending in a row of 1–2 cells; lobule broadly ovate, $\frac{1}{2} \times$ lobe length, apex apiculate, margins with triangular teeth, the teeth consisting 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; bracteole spatulate, $1.3\text{--}2 \times 0.6\text{--}0.8 \text{ mm}$, apex truncate, $\frac{1}{2} \times$ bracteole length with triangular teeth, the teeth consisting of 3–7 cells, being 2–3 cells wide at base, apex of one cell, margins recurved. **Perianths** oblong-cylindrical, $1.3\text{--}2.3 \times 0.7\text{--}0.9 \text{ mm}$, keels in upper $\frac{1}{3}$ with lacinate teeth, with 2–5 cells long at apex; beak $32.5\text{--}75 \mu\text{m}$ with 3–5 cells long.

Chromosome number. Unknown.

Chemistry. Sesquiterpene alcohol guaia-6,9-dien-4 β -ol and the unidentified diterpenoid (M^+)304, 271(100), 105(90) as most characteristic components (Sukkharak et al., in press, under *Dendrolejeunea fruticosa*).

Additional illustrations. Thiers & Gradstein (1989, p. 72, Fig. 27); Gradstein et al. (2002, p. 21, Fig. 11).

Distribution and ecology. Malesia, Australia (Queensland) and the Pacific region; 25–2000 m; on tree trunks, twigs and rotten logs in rain forests (primary and secondary forests) and montane forests.

REPRESENTATIVE SPECIMENS. **Thailand.** PHANG NGA: Sri Phang Nga national park, *Chantanaorrapint* 2112 (PSU). **Malaysia.** JOHORE: Gg. Sumalayang, *Chin* 744 (SING).—PAHANG: Ulu Cheneras, *Burkill* 15669(*b*) (SING); Kuala Tembeling, *Holttum* 20541 (SING).—SABAH: Danum valley conservation area, *Ellis* 38 (BM); 2 miles north of Kinabatangan river at Bukit Garam, *Wood* 1437 (BM-K); Sandakan, Sapagaya F. R., *Kadir & Enggoh* 10564 (BM-K); Timbun Mata Island, Mapat river, *Keith* 7358 (BM-K); Tawau, “*Kadir*” A2023 (BM-K).—SARAWAK: Baram district, *Evereth s.n.* (G 2 packets); Mt. Dulit, *Richards* 2277 (BM-K, JE, SING).—SELANGOR: Hulu Langat, Congkat river, *Ilkiu-Borges & Yong* 3026 (GOET). **Singapore.** Chan Chu Kan, *Ridley s.n.* (G). **Indonesia.** KALIMANTAN: peak of Balikpapan, *Meijer B1339e* (BM-K 2 packets, G, PC, SING), *B1391a* (SING).—SUMATRA: Engano Islands, “*Modigliani*” *s.n.*, ex hb. Levier 152 (BM-K, G 3 packets, PC).—SULAWESI: without location, “*Kiese*” *s.n.* (S 2 packets).—WESTERN NEW GUINEA: Bird’s Head peninsula, *van Royen & Sleumer* 7268 (BR, U); Mt. Arfak, *Beccari s.n.* (JE); Andai, *Beccari s.n.* (JE, U); “Bogaljim”, *Missionare s.n.* (S 3 packets); Padang, *Blum s.n.* (JE); Mt. Jaya, *Edwards* 4103A (BM). **Philippines.** BENGUET: Baguio and vicinity, *Robinson* 2–107, Bureau of science no. 14101 (BM-K).—LAGUNA: Siniloan national botanical garden, *Alvarez & al* 0–771073 (JE).—NUEVA ECIJA: without location, *Santos* 212 (JE).—QUEZON: Botanical garden of University of the Philippines Los Banõs, *Onraedt* 85.P.11304 (BR); Polillo, *McGregor* 2–39, 10499 (BM-K, G); *ibid.*, Bureau of science no. 10495 (G); Tayabas, *Robinson* 89604 (G); Dimasingay, Baler, *Santos* 235 (JE).—SAMAR: Mt. Purog, *Edãno s.n.* (U).—SURIGAO DEL SUR: Muni river, “*Pahl*” 85.P.11973 (BR).—TAYABAS: without location, *Robinson* 89604 (BM-K). **Papua New Guinea.** CENTRAL: Moroka, Jul-Aug 1893, *Loria s.n.*, ex hb. Levier 109 (BM-K 2 packets, G 4 packets, PC); Koitaki plantation, *Carr* 12078, Hep. Sep. Crit. Verdoorn 449 (BM-K 3 packets, BR, C, G, GOET, JE, PC, SING 2 packets, U 2 packets); 30 miles north of Port Moresby, *Robbins* 4132 (JE); Angabanga river, *Streimann & Naoni* 16213 (JE, LAE); Kuriva logging area, *Streimann & Vinas* 14399, 14408, 14426, (JE, LAE), 14434 (BR, JE, LAE); road to Muscrave river, *Streimann & Naoni* 15206 (JE), 15191, 15214, 15250 (JE, LAE).—EASTERN HIGHLANDS: Kassam pass, *Streimann & Umba* 11431 (JE, LAE).—EAST SEPIK: Hawain river range, *Robbins* 2081 (JE); Wewak-Angoram, *Robbins* 2345 (JE); Hunstein river, *Hoogland & Craven* 10.752 (JE 2 packets); Kassam pass, *Streimann & Umba* 11451 (JE, LAE); Prince Alexander Mts., *Robbins* 2016 (JE).—MILNE BAY: Goodenough Island, *Brass* 22982 (JE); north slope of Mt. Dayman, *Brass* 22185 (JE).—MADANG: Lower Ramu-Atitau, *Robbins* 1433, 1691 (JE).—MOROBE: Busu river logging area, *Weber s.n.* (JE, U); Herzog Mts., *Streimann & Umba* 11038, 11055 (LAE), 11054 (JE, LAE), 11053 (BR, JE, LAE); Gurakor creek, Lae-Bulolo road, *Bellamy*

1248 (JE, LAE); logging area, 15 km East of Bulolo, *Streimann & Bellamy 13184* (BR), 13152, 13184 (JE, LAE), 13762 (LAE); Gumi divide, head of gumi creek, *Streimann 25733* (JE, LAE); Slate creek and Gumi creek divide, *Streimann 13954* (BR); heads Hump, *Streimann 17437, 17440* (JE); near Nauti village, *Streimann & Elix 26229* (JE); Nauti logging area, upper Watut river, *Streimann & Kairo 17245, 17263, Streimann 17321, 17327* (JE), 17309 (GOET, JE, LAE); Sattelberg, *Clemens 264/e* (JE); *ibid.*, Jun 1988, *Nyman s.n.* (BM-K, C 2 packets), *Pösch s.n.*, Museo Hist. Natur. Vindobonensi 4035 (G, S 2 packets, U).—NEW IRELAND: Mussau Island, Bismarck Archipelago, *Køie & Olsen 2051, 2061* (C).—ORO: Managalase area, *Pullen 5685* (JE).—SOUTHERN HIGHTLANDS: Batteri, Kagua-Erave road, *Streimann 23433* (JE, LAE).—WEST NEW BRITAIN: Willaumez Peninsula, *Kolema 28* (JE); Mosa N.T.A., Lakemata reforest creek, *Kolema 101* (JE); Honde-Laulimi T. R. P., *Kolema 121* (JE).—WESTERN SEPIK: headwaters of Kong Kong creek, *Mundua 283* (JE). **Solomon Islands.** CENTRAL: Russel Islands, Dec 1935, *Lever s.n.* (BM-K). GUADALCANAL: without location, *van Zanten 68–2360, 68–2370* (JE).

Cook Islands. Rarotonga, *Gardner 72/e* (JE). **Vanuatu.** New Hebrides, 1909, *Bowie s.n.* (BM). **Fiji.** REWA: Suva, *Armstroy s.n.* (G). **Samoa.** Upolu Island, *graeffe 628, s.n.* (G), *Reinecke s.n.* (G). **American Samoa.** Tuluaita Island, *Graeffe 664* (G).

Reported from Australia, Queensland, *Brown s.n. & s.d.* (NY) and Norfolk Island, *Robinson s.n. & s.d.* (BM) by Thiers & Gradstein (1989).

Thysananthus fruticosus was originally described as a species of *Bryopteris* and was placed in a separate subgenus *Dendrolejeunea* (of *Lejeunea* s.l.) by Spruce (1884). Lacouture (1908) raised *Dendrolejeunea* to generic range but this has not been followed by later authors who accepted Schiffner's attribution (1893) of *T. fruticosus* to *Thysananthus*. The genus *Dendrolejeunea* was reinstated for *T. fruticosus* again by Gradstein (1992a). *Thysananthus fruticosus* differs from other members of *Thysananthus* by its dendroid habit, having creeping stoloniform stems and upright, regularly pinnate branches. The species shares the presence of a vitta with *T. mollis*, *T. montanus* and *T. retusus* and was for this reason placed by Verdoorn (1934) in *Thysananthus* sect. *Vittatae*, which is equivalent to *T.* sect. *Dendrolejeunea*. However, the molecular results showed that *D. fruticosa* is a member of *Thysananthus* (Sukkharak et al., submitted).

Thysananthus series *Sandeanthus* (B. Thiers & Gradst.) **comb. nov.**

Thysananthus subg. *Sandeanthus* B. Thiers & Gradst., Mem. New York Bot. Gard. 52: 66. 1989.

Type species: *Thysananthus retusus* (Reinw. et al.) B. Thiers & Gradst.

Plants with projecting growth and irregularly pinnate branching. Lobule bases with appendages.

Distribution: Japan, Malesia, Australia, Pacific.

13. *Thysananthus mollis* Steph. (Figs. 24–25)

Sp. Hepat. 4: 798. 1912; Gradstein et al. (2002: 76).—Type: PAPUA NEW GUINEA. Owen Stanley Range, Summit, 1889, *McGregor s.n.*, (holotype: G!); Icon. Steph. nr. 10198.

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, pale yellow in herbarium specimens, up to 5.7 cm long \times 3–5 mm wide. **Stems** rather rigid; ventral merophyte 10–13 cell rows wide; in cross section round-orbicular in shape, 370–293 μm high \times 270–298 μm wide, composed of 38–57 epidermal cells surrounding 123–225 medullary cells in 18–20 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute or laterally appressed to the stem, when moist weakly concave, apical parts plane, not recurved; dorsal lobe symmetrically lanceolate, 2.2–2.8 \times 0.8–1.2 mm, apex apiculate, dorsal base auriculate, auricle 27–150 \times 62–150 μm , dorsal margin entire to with 3–10 teeth, the teeth consisting of 3–7 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, ventral margin plane or upcurved $1/2 \times$ leaf length, with 3–12 teeth, the teeth consisting of 3–7 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; cells elongate-hexagonal with acute ends, vitta cells present in midportion of lobe, extending to base, $2/3 \times$ lobe length, 18–21 cell rows wide, 27–30 cells long, marginal cells 7–10 \times 7–10 μm , median vitta cells 27–60 \times 7–10 μm , basal vitta cells 40–65 \times 10–17 μm , trigones cordate, often coalesced, intermediate thickenings 0–2 per cell wall; oil bodies unknown. **Lobules** oblong, 0.2–0.4 \times 0.1–0.2 mm, $1/10$ – $1/8 \times$ lobe length; appendages on surface of lobule base on both sides of stem; keel without appendage, lobule apex oblique, longly continuing into the ventral lobe margin, apex entire to with one elongate tooth, the tooth consisting of 5–6 cells, being 2–3 cells wide at base and ending in a row of 3–8 cells. **Underleaves** imbricate, slightly squarrose, broadly obovate to spatulate, (0.8–)1.3–2 \times 0.6–1.2 mm, 3–5 \times stem width, apex emarginate-lunulate, plane or plicate, entire or with 12–13 triangular teeth, the teeth consisting of 3–10 cells, being 2–4 cells wide at base and ending in

a row of 1–2 cells, bases cuneate, underleaf bases not adnate with leaves; cells $25\text{--}37 \times 5\text{--}7$ μm . **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 4–10(–23) pairs, bracts hypostatic, $0.6\text{--}2.3 \times 0.3\text{--}0.8$ mm, apex acute, margins entire; antheridia 2 per bract. **Gynoecia** with 1–2 lejeuneoid innovation forming monochasial or diochasial pattern; lobe lanceolate, $3.1\text{--}3.4 \times 0.8\text{--}1.2$ mm, apex apiculate, margins in upper 2/3 with laciniate teeth with 2–4 cells long at apex; lobules broadly ovate, $1/2 \times$ lobe length, apex bifid, margin with laciniate teeth with 1–4 cells long at apex; bracteoles spatulate, $2.2\text{--}2.5 \times 1\text{--}1.6$ mm, apex emarginate, $1/2 \times$ bracteole length with laciniate teeth with 1–4 cells long at apex, margins plane. **Perianths** oblong-cylindrical, $2.5\text{--}3.2 \times 0.8\text{--}1.3$ mm, keels in upper 1/3 with triangular teeth, the teeth consisting of 3–14 cells, being 2–5 cells at base and ending in a row of 1–2 cells; beak 50–65 μm with 4–5 cells long.

Chromosome number. Unknown.

Chemistry. Poor in sesquiterpenoids (mainly caryophyllene and alloaromadendrene), rich in diterpenoid content, sterols (Gradstein et al., 1985).

Additional illustrations. Gradstein et al. (2002, p. 76, Fig. 48).

Distribution and ecology. Endemic to Western Melanesia; 1200–3100 m; on roots, bark of trees, twigs, fallen branches and logs in the understory of montane forests.

REPRESENTATIVE SPECIMENS. **Papua New Guinea**. CENTRAL: The type.—CHIMB: trail from Keglsugl to Pindaunde lakes, *Gradstein 4145* (U); trail from Keglsugl to Pindaunde lakes, *Gradstein & Sipman 8304* (G).—EASTERN HIGHLANDS: Lipizauga Botanical Sanctuary, *Thiers 3699* (U); Daulo Pass, *Streimann 18003* (JE, W).—ENGA: Mape creek, Mt. Hagen-Wapenamanda, *Streimann 21646* (JE, LAE).—MOROBE: Ogeramnang, *Clemens 5527/H-d*; *ibid.*, 17 Feb 1937, *Clemens s.n.* (JE); near Kaindi village, 23 Nov 1975, *Inoue s.n.* (U); Mt. Kaindi, *Gradstein 3779, 3794, 3884, 3980* (U), *3798* (G, U), *3795* (G, U 2 packets), *3792* (G, GOET, U 3 packets), *Gradstein & Sipman 7865, 7899* (G), *Schuster 67–6319, 67–6361, 67–6364* (JE); Slate-Gumi creeks divide, *Streimann 13954, 33938* (JE), *13817* (LAE), *13921, 13924, 13927* (JE, LAE); Wagau-Malolo track, *Streimann 19565* (JE); Gumi divide, head of Gumi creek, *Streimann 25132, 25305* (JE), *Streimann 22786* (LAE); Spreader divide, *Streimann 25974, 25993, 26004, 26014* (JE), *26021* (JE, LAE), *Streimann & Tamba 11883, 11905, 11914* (JE, LAE), *11957, 11970, 11980, 11992* (LAE); Bulolo-Watut divide, *Streimann 25032, 25220* (JE), *Streimann & Bellamy 13049* (JE), Manki Trig, *Streimann & Bellamy 12971* (LAE); Wau-Salamaua track, *Streimann 25675* (JE, LAE, S, W); Mt. Kaindi road, *Streimann 33397* (JE); Araulu logging area, *Streimann 13560* (JE).—SOUTHERN HIGHLANDS: Tambul-Mendi road, *Streimann 26800* (JE); Iaro river, *Streimann 23855, 23888*

(JE, LAE); Lama sawmill, *Streimann* 26631 (JE).—WESTERN HIGHLANDS: Baiyer river-Ruti road, Jimi valley, *Streimann* 22075 (JE), 22239 (LAE), 22008 (JE, LAE).—WESTERN SEPIK: Amisumbil, Eliptamin, *Macrosimnok* 27 (JE, LAE).

Reported from the Solomon Islands by Gradstein et al. (2002).

Thysananthus mollis varies in leaves and underleaves, which are sharply toothed to entire. *Thysananthus mollis* may be confused with *T. fruticosus* but the latter species is dendroid, has regularly pinnate branching, keels of all leaves with appendages, laciniate perianth teeth, 2–5 cells long and is autoicous. *Thysananthus mollis* is closely related to *T. montanus*; differences are discussed under the latter species.

14. *Thysananthus montanus* Gradst. et al. (Fig. 26)

Acta Bot. Fenn. 174: 77. 2002.—Type: PAPUA NEW GUINEA. Morobe: Lake Wamba, 5 km S of Teptep airstrip, Teptep-Wantuat trail 10 km S of Teptep, open montane forest on ridge sloping NE, alt. 2550–2700 m, 6°2.5'S 146°33'E, *Koponen* 33958b (holotype: H!).

Plants dioicous, with projecting growth, turning upwards and becoming ascending to erect, pale brown in herbarium specimens, up to 3.5 cm long × 1.5–2.6 mm wide. **Stems** rather rigid; ventral merophyte 8–10 cell rows wide; in cross section round-orbicular in shape, 215–240 µm high × 303–329 µm wide, composed of 43–48 epidermal cells surrounding 141–150 medullary cells in 14–17 layers high, epidermal cells not larger than medullary cells. **Leaves** imbricate, when dry suberect and convolute, when moist weakly concave, apical parts plane, not recurved; dorsal lobe symmetrically oblong, 1.6–1.8 × 0.6–0.8 mm, apex acute-apiculate, margin entire, dorsal base auriculate, auricle 57–96 × 57–76 µm, ventral margin upcurved 1/2× leaf length; cells elongate-hexagonal with acute ends, vitta cells present in midportion of lobe, extending to base, 2/3× lobe length, 8–17 cell rows wide, 13–20 cells long, marginal cells 10–12 × 5–7 µm, median vitta cells 25–45 × 5–7 µm, basal vitta cells 50–67 × 10–15 µm, trigones cordate, often coalesced, intermediate thickenings 0–2 per cell wall; oil bodies unknown. **Lobules** rectangular, 0.8–1 × 0.3–0.4 mm, 1/4–1/3× lobe length; appendages on surface of lobule base on both sides of stem; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex with one elongate tooth, the tooth consisting of 7–9 cells, being 2–3 cells wide at base and ending in a row of 6–7 cells. **Underleaves** imbricate, slightly squarrose, spatulate, 1.2–1.3 × 0.6–0.7 mm, apex

round, plane, margins entire, bases cuneate, underleaf bases not adnate with leaves; cells $27-37 \times 2-5 \mu\text{m}$. **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 6–13(–20) pairs, bracts hypostatic, $0.7-0.9 \times 0.2-0.5 \text{ mm}$, apex acute, margins entire; antheridia 2 per bract. **Gynoecia** with 2 lejeuneoid innovations forming a dichasial pattern; lobe lanceolate, $2.7-2.8 \times 0.8-0.9 \text{ mm}$, apex acute, margins entire or in upper 2/3 with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; lobules broadly ovate, $1/2 \times$ lobe length, apex bifid, margin with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells; bracteoles spatulate, $2.4-2.5 \times 0.7 \text{ mm}$, apex emarginate to shortly bifid, entire or $1/2 \times$ bracteole length with teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base and ending in a row of 1–2 cells, margins plane. **Perianths** oblong-cylindrical, $2.6-2.7 \times 0.7-0.8 \text{ mm}$, keels entire; beak $62-65 \mu\text{m}$ with 4–5 cells long.

Chromosome number. Unknown.

Chemistry. Unknown.

Additional illustrations. Gradstein et al. (2002, p. 78, Fig. 49).

Distribution and ecology. Endemic to Papua New Guinea; 1900–2300 m; on tree trunks, lianas and branches in open montane forests.

REPRESENTATIVE SPECIMENS. **Papua New Guinea.** EASTERN HIGHLANDS: Gahavisuka National Park, *Thiers 3656* (G).—MOROBE: Gumi divide, *Streimann 22707* (JE, LAE); Mt. Kaindi, *Streimann 22511* (LAE); Araulu logging area, *Streimann 13639* (LAE); Nauti logging area, upper Watut river, *Streimann 17150* (LAE).

Thysananthus montanus varies in the female bracts and bracteoles, which are entire to dentate. The type specimen was previously identified as *Thysananthus planus* (= *T. retusus*). By its oblong, entire leaves *T. montanus* approaches *T. retusus* but differs from the latter by (1) leaves when dry convolute (widely spreading, loosely reflexed or plane in *T. retusus*), (2) dorsal base auriculate (cordate in *T. retusus*), (3) leaf cells elongate-hexagonal, vitta cells 8–17 cell rows wide (subisodiametric, 4–6 in *T. retusus*), (4) being dioicous (autoicous in *T. retusus*), and (5) entire perianths (toothed perianths in *T. retusus*). *Thysananthus montanus* is closely related to *T. mollis*. The latter species differs essentially by its leaf, which is lanceolate in outline, emarginate-lunulate underleaf apex and toothed perianths.

15. *Thysananthus retusus* (Reinw. et al.) B. Thiers & Gradst. (Figs. 27–28A, C–E)

- Mem. New York Bot. Gard. 52: 67. 1989; Gradstein et al. (2002: 78). *Jungermannia retusa* Reinw. et al., Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 214. 1824; Nees (1830: 214; var. *α*). *Ptychanthus retusus* (Reinw. et al.) Nees, Syn. Hepat. 292. 1845.—Type: INDONESIA. Java [“inter muscos Javae insulae, rarior”]: *Blume s.n.* (holotype: STR; isotypes: S!, W 3 packets!).
- Thysananthus planus* Sande Lac., Ned. Kruidk. Arch. 3(4): 419. “1855”; Lacoste (1856: 55); Mizutani (1969: 139), syn. fide Thiers & Gradstein (1989): 67.—Type: INDONESIA. Java: *Junghuhn s.n.* (holotype: L!).
- Mastigolejeunea wattiana* Steph., Sp. Hepat. 4: 780. 1912.—Type: AUSTRALIA. New South Wales: Richmond River, Fernleigh, tree, 2 Aug 1900. *W.W. Watts s.n.* (holotype: G!); Icon. Steph. nr. 7467, **syn. nov.**
- Thysananthus subplanus* Steph., Sp. Hepat. 4: 790. 1912.—Type: PHILIPPINES. Bataan: Mt. Mariveles, *E. D. Merrill 3984* (holotype: G!); Icon. Steph. nr. 10217.
- Brachiolejeunea grossivitta* Steph., J. & Proc. Roy. Soc. New South Wales 48: 10. 1914.—Type: VANUATU [New Hebrides]. “Aneityum”, *Gunn s.n.* (isotype: JE!).
- Thysananthus furcatus* Herzog, Ann Bryol. 4: 87. 1931.—Type: PHILIPPINES. Benguet: “Baguio, 20.V.15, *C. J. Baker (n. 7004) n. 7053*” (syntype: JE!).
- Thysananthus flavescens* (S. Hatt.) Gradst., Trop. Bryol. 4: 13. 1991. *Archilejeunea flavescens* S. Hatt., Bull. Tokyo Sci. Mus. 11: 95. 1944. *Leucolejeunea flavescens* (S. Hatt.) S. Hatt., J. Hattori Bot. Lab. 8: 33. 1952. *Mastigolejeunea flavescens* (S. Hatt.) Mizut., J. Hattori Bot. Lab. 24: 159. 1961.—Type: JAPAN. Osumi: Sata-mura, Hetka, on bark, April 18, 1939. *S. Hattori 2399* (isotype: NICH!), **syn. nov.**
- Thysananthus australis* (Steph.) B. Thiers & Gradst., Mem. New York Bot. Gard. 52: 66. 1989. *Archilejeunea australis* Steph., Sp. Hepat. 4: 734. 1911.—Type: AUSTRALIA. New South Wales: Back of Wickham’s farm near Ballina, on tree, 3 Jun 1902, *W. W. Watts 415* (holotype: G!), **syn. nov.**

Plants autoicous, with projecting growth, turning upwards and becoming ascending to erect, dull green in the field, yellowish to reddish brown in herbarium specimens, up to 1.6 cm long × 1–2.5 mm wide. **Stems** rather fragile, ventral merophyte 7–9 cell rows wide; in cross section round-orbicular in shape, 119–125 µm high × 92–98 µm wide, composed of 18–21 epidermal cells surrounding 27–34 medullary cells in 8–10 layers high, epidermal cells not larger than medullary cells. **Leaves** contiguous to slightly imbricate; when dry wide spreading and flat, dorsal lobe symmetrically ovate to ligulate, 1.3–1.5 × 0.4–0.6 mm, apex acute-shortly apiculate, margins entire, dorsal base cordate, ventral margin plane; non-vitta cells

subisodiametric to isodiametric, vitta cells present in midportion of lobe, extending to base, $2/3 \times$ lobe length, 4–6 cell rows wide, 12–18 cells long, marginal cells $5-7 \times 5-7 \mu\text{m}$, median cells $12-15 \times 10-12 \mu\text{m}$, basal vitta cells $35-52 \times 12-15 \mu\text{m}$, vitta cell trigones coalesced, intermediate thickening 1–2(–3) per cell walls, non-vitta cells trigones and intermediate thickening faint; oil bodies 3–5 per non-vitta cell and 4–8 per vitta cell. **Lobules** oblong, $0.2-0.3 \times 0.1-0.2 \text{ mm}$, $1/4-1/3 \times$ lobe length; appendages on surface of lobule base on both sides of stem; keel without appendage; lobule apex oblique, longly continuing into the ventral lobe margin, apex with one elongate tooth, the tooth consisting of 4–5 cells, being 2–3 cells wide at base and ending in a row of 1–6 cells. **Underleaves** slightly imbricate, slightly squarrose, obovate, $0.3-0.6 \times 0.3-0.5 \text{ mm}$, $3-4 \times$ stem width, apex truncate to emarginate, recurved, margins entire, bases cuneate, underleaf bases free or adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches; cells $12-15 \times 5-7 \mu\text{m}$. **Androecia** terminal-intercalary on lateral branches, bracts and bracteoles in 3–10 pairs, bracts hypostatic, $0.9-1 \times 0.3-0.4 \text{ mm}$, apex acute to apiculate, margins entire, antheridia 2 per bract. **Gynoecia** with 1–2 lejeuneoid innovations forming monochasial or dichasial pattern or both; lobe ligulate, $1.6-1.7 \times 0.6-0.7 \text{ mm}$, apex apiculate, margins entire or in upper $1/3$ with triangular teeth, the teeth consisting of 3–5 cells, being 2–3 cells wide at base, apex of one cell; lobules broadly ovate, $1/3-1/2 \times$ lobe length, apex apiculate to obscurely bifid, with triangular teeth, the teeth consisting of 3–5 cells, 2–3 cells wide at base and ending in a row of 1–2 cells; bracteoles ligulate, $0.9-1.4 \times 0.3-0.6 \text{ mm}$, apex bifid, entire or toothed along margins, the teeth consisting of 3–7 cells, being 2–3 cells wide at base, apex of one cell, slightly recurved at base, margins plane. **Perianths** obovate, $0.8-1 \times 0.4-0.6 \text{ mm}$, keels in upper $1/3$ with triangular teeth, the teeth consisting of 3–5 cells, being 2 cells wide at base, apex of one cell; beak $30-45 \mu\text{m}$ with 3–5 cells long.

Chromosome number. Unknown.

Chemistry. Pinguisane sesquiterpenoids, unidentified diterpenoid (M^+)318, 81(100), 206(98) (Sukkharak et al., in press) and sterols (Gradstein et al., 1985, under *Thysananthus fruticosus*).

Additional illustrations. Hattori (1944, p. 95, Fig. 60; p. 96, Fig. 61 as *Archilejeunea flavescens*); Mizutani (1961, p. 160, Fig. VIII. as *Mastigolejeunea flavescens*); Thiers & Gradstein (1989, p. 70, Fig. 26; p. 68, Fig. 25 as *Thysananthus australis*); Gradstein et al. (2002, p. 79, Fig. 50).

Distribution and ecology. India (Uttarakhand), Southern Japan, Malesia, Australia (Queensland and New South Wales), and the Pacific region; there is a doubtful records from Mascarene Islands by Miller et al. (1983) (fide Thiers & Gradstein, 1989), which may have

been mislabeled or misidentified; 125–1700 m; on shaded stems of treelets and tree trunks in the *Eucalyptus* sp. dominated grasslands, and in the understory of rain forests and montane forests.

REPRESENTATIVE SPECIMENS. **India.** UTTARAKHAND: Mussoorie, Sep 1930, *Chopra s.n.*, Hep. Sel. Crit. Verdoorn 260 (JE). **Japan.** KAGOSHIMA: type of *Thysananthus flavescens*; a pass between Hanaze and Hekka, *Mizutani 41481* (U), *s.n.*, Hep. Jap. Exs. Mizutani 628 (BM-K). **Thailand.** NAKHON SI THAMMARAT: Mt. Khao Luang, *Tagawa & Kitagawa T4728, T4754, T5169, T5179, T5216, T5219* (G); Mt. Khao Nan Yai, *Sukkharak 44, 291, 423* (BCU); San Yen, 19 Feb 2009, *Chantanaorrapint s.n.* (PSU), *Sukkharak 733, 741, 743* (BKF, GOET). **Indonesia.** JAVA: Pantjar, Dec 1893, *Schiffner s.n.*, Hep. Sel. Crit. Verdoorn 284 (BM-K 2 packets, BR, C, G 2 packets, GOET, JE, PC, SING, U); Bogor, 1843, collector unknown (S); without location, *Lehman s.n.* (S); Mt. Gede-Pangrango National Park, *Haerida 1H811* (BZ). **Philippines.** BATAAN: Mt. Mariveles, *Merrill 3984* (BM-K).—BENGUET: Baguio and vicinity, 19 May 1191, *Robinson s.n.* (BM).—DAVAO ORIENTAL: Aliwagwag falls, “*Georges-Pahl*” 86.P.12004 (BR). **Papua New Guinea.** CENTRAL: Angabanga river, *Streimann & Naoni 16136* (JE, LAE).—MOROBE: Kunai Creek, *Gradstein 3963* (G 2 packets, U 2 packets), 3980 (U); Mt. Missim, *Gradstein & Sipman 7929* (G), *Gradstein 3833a* (U); Situm logging area, *Streimann 41733* (JE); Herzog Mts., *Streimann & Umba 10923* (JE, LAE), 10834, 10994 (LAE); Busu-Butibum ridge, *Streimann 22679* (JE, LAE).—EAST NEW BRITAIN: Nakanai Mts., *H. Streimann 40492, 40547* (JE). **Solomon Islands.** GUADALCANAL: Mt. Gallego, 16 Sep 1966, *Dennis 20025b* (JE), *s.n.* (S); Mt. Popemanaseu, *van Zanten 68–2545/b2* (JE).

Australia. NEW SOUTH WALES: type of *Thysananthus australis*; Baliina, *Watts 17* (NSW); Protestors falls, Nightcap rang national park, *Renner 1492* (NSW); Minyon Falls, Nightcap Range National park, 20 Oct 2009, *Brown s.n.* (NSW); 6.6 km south-southwest of Alstonville, Victoria Park Nature Reserve, 21 Oct 2009, *Brown s.n.* (NSW); Cambden Haven state forest, *Streimann 38462* (JE).—QUEENSLAND: Big Tableland, *Streimann 30895* (JE); near Mt. Walker, *Streimann 30989* (JE); main coast range, Mary L.A., *Streimann & Gray 27135* (JE); Mossman Gorge national park, *Thiers & Halling 2560* (U); Bellenden Ker National park, *Thiers 2395* (U); McDowell range north of the Daintree river, *Hicks 11495* (U); Birthday creek (Townsville university experimental plot), *Pócs & Streimann 9972/AQ* (GOET); Daintree National Park, *Pócs & Streimann 9991/A* (G); Tully Gorge, *Renner 1808* (NSW); Second stream ford, Cardwell state forest, *Renner 1653* (NSW); Finch Hatton Gorge, Eungella National park, *Renner 1514, 1516, 1519* (NSW).

Vanuatu. Type of *Brachiolejeunea grossivitta*. **Fiji.** CAKAUDROVE: Mt. Uluigalau, *Degelius P-223* (JE, S), *P-234/d* (S).—RA: Navai, *Hürlimann T1019e, T1021b* (G); *ibid.*, Mt. Victoria, *Hürlimann T1082a* (G). **Samoa.** Upolu, *Schultze-Motel 3078* (JE), *Rechinger 3272* (BM); Tutuila, *Stevenson 14946, 14982* (JE). **American Samoa.** Tutuila, *Stevenson 14946, 14982* (JE).

Thysananthus retusus varies in the length of the lobule tooth, which may be 1–6 cells long. This species is a small and rather fragile plant which differs from other species of the genus, including (1) leaves widely spreading, loosely reflexed or plane when dry, (2) leaf cells subisodiametric with confluent trigones, and (3) vitta cells 4–6 cell rows wide.

Key to the varieties of *T. retusus*

Lobule 2× longer than wide..... 15a. *T. retusus* subsp. *retusus*

Lobule 5× longer than wide..... 15b. *T. retusus* subsp. *sellingii*

15a. *Thysananthus retusus* subsp. *retusus*

see under the species

15b. *Thysananthus retusus* subsp. *sellingii* (Herzog) **comb. nov.** (Fig. 29: B, G)

Thysananthus sellingii (Herzog) Hürl., *Bauhinia* 9: 168. 1989. *Mastigolejeunea sellingii* Herzog, *Ark. Bot.* 3: 60. 1953.—Type: NEW CALEDONIA. South: slope above N. branch of Yaté River, humid forest with *Dacrydium*, *O. Selling* 44 (holotype: JE!; isotypes: S 2 packets!).

Thysananthus retusus subsp. *sellingii* differs from subsp. *retusus* in the much greater length of lobule, which is 5× longer than wide. *Thysananthus sellingii* is treated here as a subspecies of *T. retusus* because it differs from the latter by only one diagnostic morphological character and by its different geographical range (see chapter Classification).

Distribution and ecology. Endemic to New Caledonia; 400–700 m; on tree trunks in rain forests.

REPRESENTATIVE SPECIMENS. **New Caledonia.** SOUTH: Mé Amméri, *Guillaumin & Baumann* 8902, 9136 (G, GOET); Rivière Blanche, *Guillaumin & Baumann* 11900 (G,

GOET); Rivière Bleue, *Guillaumin & Baumann 10893* (GOET); Koghis Mts., Bouo summit, *Hürlimann 2111* (G, GOET, U); Pourina, *Hürlimann 2647c* (GOET).

***Thysananthus* subgenus *Mastigolejeunea* (Spruce) comb. nov.**

Mastigolejeunea (Spruce) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 129. 1893. *Lejeunea* subg. *Mastigolejeunea* sect. *Trigonolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburg 15: 100. 1884.

Type species: *Thysananthus auriculatus* (Wils.) comb. nov. (= *Mastigolejeunea auriculata* (Wils.) Schiffn.)

Characters as in *Thysananthus* except for the perianths which are always entire and the elaters which are presumably 72 per capsule (Gradstein, 1994), vs. 66 in subg. *Thysananthus*.

Distribution: tropical America, Africa, Indochina, Malesia, Australia, Pacific.

The species currently accepted in *Mastigolejeunea* are briefly listed here and transferred to *Thysananthus*. A full treatment of the subg. *Mastigolejeunea* should be the subject of future work.

16. *Thysananthus auriculatus* (Wils.) comb. nov.

Mastigolejeunea auriculata (Wils.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 129. 1893; Schuster (1980: 729); Gradstein (1994: 76). *Jungermannia auriculata* Wils., in Drummond, Musci Amer. Exsicc. (Southern States) nr. 170. 1841. *Lejeunea auriculata* (Wils.) Sullivant, in Gray, Manual Bot. 2: 699. 1856. *Ptychocoleus auriculatus* (Wils.) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. 3, 4: 405. 1877. *Marchesinia auriculata* (Wils.) Kuntze, Revis. Gen Pl. 2: 837. 1891. *Phragmicoma versicolor* Lehm. & Lindenb., Syn. Hepat. 297. 1845, nom. superfl. fide Gradstein 1994.—Type: U.S.A. Louisiana: New Orleans, *Drummond s.n.*, Musci Americani (Southern States) 170 (holotype: BM!; isotypes: MANCH, PC).

Description. Fl. Neotrop. Monogr. 62: 76–81 (1994).

Illustrations. Gradstein (1994, p. 78, Fig. 21).

Distribution. Tropical America, Africa.

17. *Thysananthus calcaratus* (Steph.) comb. nov.

Mastigolejeunea calcarata (Steph.) Verd., Blumea 1: 218–230. 1934; Thiers & Gradstein (1989: 44). *Archilejeunea calcarata* Steph., Sp. Hepat. 4: 724. 1911. *Phragmicoma calcarata* Mitt., in Seemann, Fl. Vit. 413. 1873, hom. illeg., *non* Mont., 1843.—Type: FIJI. Ovalau: *Seemann s.n.* (holotype: NY).

Description. Mem. New York Bot. Gard. 52: 44, 46 (1989).

Illustrations. Thiers & Gradstein (1989, p. 45, Fig. 16);

Distribution. Australia (Queensland) and Fiji.

18. *Thysananthus floreus* (Mitt.) **comb. nov.**

Mastigolejeunea florea (Mitt.) Paris, Rev. Bryol. 33: 42. 1906; Wigginton (2004: 273). *Phragmicoma florea* Mitt., J. Linn. Soc., Bot. 22: 323. 1886 “1887”.—Type: “Niger”. cf. Geissler & Bischler (1985).

Description. E. W. Jones’s Liverwort and Hornwort Flora of West Africa: 273 (2004).

Illustrations. Vanden Berghen (1949).

Distribution. West Africa.

19. *Thysananthus humilis* (Gottsche) **comb. nov.**

Mastigolejeunea humilis (Gottsche) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 129. 1893; Mizutani (196: 156); Mizutani (1986: 281). *Phragmicoma humilis* Gottsche, in Gottsche et al., Syn. Hepat. 299. 1845. *Ptychocoleus humilis* (Gottsche) Trevisan, Mem. Reale Ist. Lomb. Mat. Nat. 3, 4: 405. 1877. *Lejeunea humilis* (Gottsche) Spruce, Trans. & Proc. Bot. Soc. Edinburg 15: 101. 1884.—Type: INDONESIA. Java: *Junghuhn s.n.* (isotypes: G, W).

Description. J. Hattori Bot. Lab. 61: 281–283 (1986).

Illustrations. Mizutani (1961, p. 157, Fig. VII); Mizutani (1986, p. 282, Fig. 1); Gradstein et al. (2002, p. 42, Fig. 24 as *Mastigolejeunea auriculata*).

Distribution. India, Japan, Indochina, Malesia, Pacific

20. *Thysananthus integrifolius* Steph.

Sp. Hepat. 4: 788. 1912. *Mastigolejeunea integrifolia* (Steph.) Verd., Blumea 1: 239. 1934.—Type: AUSTRALIA. Torres Straits: Possession Island, Aug 1897, *Micholitz s.n.* (holotype: G!; isotype: FH); Icon. Steph. nr. 10188.

Mastigolejeunea indica Steph., Sp. Hepat. 4: 776. 1912; Mizutani (1986: 295); Thiers & Gradstein (1989: 46); Gradstein et al. (2002: 43).—Type: INDIA. Nicobar Island: *Man s.n.*, ex hb. Levier 40 (holotype: G).

Description. Mem. New York Bot. Gard. 52: 46, 48 (1989).

Illustrations. Mizutani (1986, p. 296, Fig. 8 as *Mastigolejeunea indica*); Thiers & Gradstein (1989, p. 47, Fig. 17 as *M. indica*); Gradstein et al. (2002, p. 43, Fig. 25 as *M. indica*).

Distribution. India (Nicobar Island), China (Yunnan), Malesia, Australia.

Thysananthus integrifolius was treated as a synonym of *Mastigolejeunea indica* by Thiers & Gradstein (1989). However, since the two species were described on the same date (5 March 1912) I have chosen the name *Thysananthus integrifolius* Steph. as the correct name for this species, to avoid the introduction of a new name.

21. *Thysananthus innovans* (Spruce) **comb. nov.**

Mastigolejeunea innovans (Spruce) Steph., Sp. Hepat. 4: 765. 1912; Gradstein (1994: 81). *Lejeunea innovans* Spruce, Trans & Proc. Bot. Soc. Edinburgh 15: 103. 1884.—Type: BRAZIL. Amazonas: Rio Uaupés, Panuré, “ad arborum truncos”, *Spruce L42* (holotype: MANCH; isotype: BM); Icon. Steph. n. 7403.

Description. Fl. Neotrop. Monogr. 62: 81–82 (1994).

Distribution. Brazil (Amazonas), French Guiana.

22. *Thysananthus ligulatus* (Lehm. & Lindenb.) **comb. nov.**

Mastigolejeunea ligulata (Lehm. & Lindenb.) Schiffn., in Engler & Prantl., Nat. Pflanzenfam. 1, 3: 129. 1895; Mizutani (1986: 285); Thiers & Gradstein (1989: 48); Gradstein et al. (2002: 44). *Jungermannia ligulata* Lehm. & Lindenb., Nov. Stirp. Pug. 6: 39. 1834. *Ptychanthus ligulatus* (Lehm. & Lindenb.) Nees, Nat. eur. Leberm. 3: 212. 1838. *Phragmicoma ligulata* (Lehm. & Lindenb.) Gottsche et al., Syn. Hepat. 301. 1845. *Lejeunea ligulata* (Lehm. & Lindenb.) Mitt., J. Proc. Linn. Soc. Bot. 5: 110. 1861.—Type: MALAYSIA. “Pulo Penang”, collector unknown, “Herb. Hook. 1832” (holotype: S; isotypes: G, L, NY, S, W-hb. Lindenberg 6022).

Description. Mem. New York Bot. Gard. 52: 48–50 (1989).

Illustrations. Mizutani (1986, p. 286, Fig. 3); Thiers & Gradstein (1989, p. 49, Fig. 18); Gradstein et al. (2002, p. 45, Fig. 26).

Distribution. Malesia, Australia, Pacific.

23. *Thysananthus plicatiflorus* (Spruce) **comb. nov.**

Mastigolejeunea plicatiflora (Spruce) Steph., Sp. Hepat. 4: 766. 1912; Gradstein (1994: 82). *Lejeunea plicatiflora* Spruce, Trans & Proc. Bot. Soc. Edinburgh 15: 104. 1884.—Type: VENEZUELA. Amazonas: San Carlos del Ro Negro, “ad arbores”, Spruce, *Hapaticae Amazonicae et Andinae 1543* (lectotype, designated by Gradstein, 1994: MANCH 15909; isolectotypes: BM, G, W); Icon. Steph. n. 7405.

Description. Fl. Neotrop. Monogr. 62: 82–83 (1994).

Distribution. Northern South America (Amazonia, Guianas, etc.)

24. *Thysananthus reconditus* (Steph.) **comb. nov.**

Mastigolejeunea recondita (Steph.) Mizut., J. Hattori Bot. Lab. 32: 134. 1969; Gradstein et al. (2002: 46). *Ptycholejeunea recondita* Steph., Hedwigia 35: 122. 1896. *Brachiolejeunea recondita* (Steph.) Steph., Sp. Hepat. 5: 134. 1912.—Type: PHILIPPINES. cf. Mizutani (1969).

Description. Acta Bot. Fenn 174: 46 (2002).

Illustrations. Mizutani (1969, p. 135, Fig. IV); Gradstein et al. (2002, p. 47, Fig. 27).

Distribution. Eastern Malesia.

25. *Thysananthus recurvifolius* (Mizut.) **comb. nov.**

Mastigolejeunea recurvifolia Mizut., J. Hattori Bot. Lab. 61: 294. 1986.—Type: MALAYSIA. Sabah: Batu Puteh, on limestones, *G. Shea* 3278 (holotype: NICH).

Description. J. Hattori Bot. Lab. 61: 294–295 (1986).

Illustrations. Mizutani (1986, p. 295, Fig. 7).

Distribution. Malaysia (Sabah).

26. *Thysananthus repletus* (Taylor) **comb. nov.**

Mastigolejeunea repleta (Taylor) A. Evans, Mem. Torrey Bot. Club 8: 131. 1902; Mizutani (1986: 283); Gradstein et al. (2002: 46). *Lejeunea repleta* Taylor, London J. Bot. 5: 392. 1846.—Type: INDIA. Madras, *Wight s.n.* (isotypes: G, W)

Description. J. Hattori Bot. Lab. 61: 283–285 (1986).

Illustrations. Mizutani (1986, p. 284, Fig. 2); Gradstein et al. (2002, p. 48, Fig. 28).

Distribution. Indochina, Malesia.

27. *Thysananthus truncatus* (Mizut.) comb. nov.

Mastigolejeunea truncata Mizut., J. Hattori Bot. Lab. 61: 292. 1986; Gradstein et al. (2002: 48).—Type: MALAYSIA. Sabah: Madai cave, SW of Lahad Datu, East Coast, alt. 30–70, upper surface of rock, 1963, *Iwatsuki* 5426 (holotype: NICH).

Description. J. Hattori Bot. Lab. 61: 292–294 (1986).

Illustrations. Mizutani (1986, p. 293, Fig. 6); Gradstein et al. (2002, p. 49, Fig. 29).

Distribution. Malesia.

28. *Thysananthus undulatus* (Gradst. & Grolle) comb. nov.

Mastigolejeunea undulata Gradst. & Grolle, in Hiepko & Schultze-Motel, Mensch, Kultur und Umwelt im zentralen Bergland von West-Neuguinea 7: 13. 1981; Mizutani (1986: 290); Thiers & Gradstein (1989: 50); Gradstein et al. (2002: 50).—Type: INDONESIA. West Irian, Jayawijaya Prov.: Eipomek-Tal, *Hiepko & Schultze-Motel* 2266 (holotype: B; isotypes: JE, U).

Description. Mem. New York Bot. Gard. 52: 50–51, 53 (1989).

Illustrations. Mizutani (1986, p. 291, Fig. 5); Thiers & Gradstein (1989, p. 52, Fig. 19); Gradstein et al. (2002, p. 50, Fig. 30).

Distribution. Eastern Malesia (Philippines, Moluccas, New Guinea).

29. *Thysananthus virens* Ångstr.

Mastigolejeunea virens (Ångstr.) Steph., Sp. Hepat. 4: 776. 1912; Mizutani (1986: 287); Thiers & Gradstein (1989: 53); Gradstein et al. (2002: 52). *Thysananthus virens* Ångstr., Öfvers. Förh. Kongl. Svenska. Vetensk.-Akad. 5: 131. 1873. *Lejeunea virens* (Ångstr.) Steph., in Bescherelle, J. Bot (Monot) 12: 141. 1898.—Type: SOCIETY ISLANDS. Moorea, *Andersson s.n.* (holotype: G; isotype: FH).

Description. Mem. New York Bot. Gard. 52: 53, 55 (1989).

Illustrations. Mizutani (1986, p. 288, Fig. 4); Thiers & Gradstein (1989, p. 54, Fig. 20); Gradstein et al. (2002, p. 53, Fig. 32).

Distribution. Sri Lanka, Malesia, Australia Pacific.

EXCLUDED TAXA

Thysananthus africanus Steph., in Engler, Bot. Jahrb. 8: 93. 1887.—Type: EQUATORIAL GUINEA. Bioko [“Fernando Po Island”]: “*Mönkemeyer 545*” (holotype: G!) = *Caudalejeunea africana* (Steph.) Steph., Hedwigia 34: 233. 1895.

Thysananthus brasiliensis S. Arnell, in Schiffner & S. Arnell, Österr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. 111: 118. 1964.—Type: BRAZIL. “São Paulo: prope Salto Grande do Rio Paranapanema, ca. 500 m, ..Hb. W”, *Schiffner 2199* (holotype: W) = *Caudalejeunea lehmanniana* (Gottsche) A. Evans, Bull. Torrey Bot. Club 34: 554. 1907, syn. fide Gradstein (1994): 121.

Thysananthus crispatus Steph., Sp. Hepat. 6: 567. 1924.—Type: NEW GUINEA. “*Ledermann s.n.*” (holotype: G); Icon. Steph. nr. 10175 = *Spruceanthus polymorphus* (Sande Lac.) Verd., Ann. Bryol., Suppl. 4: 155. 1934, syn. fide Verdoorn (1934): 155.

Thysananthus elongatus (Austin) A. Evans, Trans. Connecticut Acad. Arts 10: 423. 1900. *Phragmicoma elongata* Austin, Proc. Acad. Nat. Sci. Philadelphia 21: 225. “1869” 1870.—Type: HAWAII. “*Andersson s.n.*” (holotype: G!) = *Spruceanthus polymorphus* (Sande Lac.) Verd., Ann. Bryol., Suppl. 4: 155. 1934, syn. fide Verdoorn (1934): 155.

Thysananthus evansii Fulford, Bull. Torrey Bot. Club 68: 34. 1941.—Type: BELIZE. Punta Gorda: collector unknown (holotype: CINC) = *Fulfordianthus evansii* (Fulford) Gradst., Bryologist 95: 46. 1992.

Thysananthus fragillimus Herzog, in Handel-Mazzetti, Symb. Sin. 5: 45. 1930.—Type: CHINA. Setchwan: “... auf dem Lungdschu-schan, bei Huili, 3000 m,...”, 24 Mar 1914, *Handel-Mazzettii 971* (not seen) = *Spruceanthus semirepandus* (Nees) Verd., Ann Bryol., Suppl. 4: 153. 1934, syn. fide Verdoorn (1934): 153.

Thysananthus lehmannianus (Nees) Steph., Sp. Hepat. 4: 785. 1912. *Phragmicoma lehmanniana* Nees in Gottsche et al., Syn. Hepat. 302. 1845.—Type: JAMAICA. “Hb. Lehmann” (not seen) = *Spruceanthus semirepandus* (Nees) Verd., Ann Bryol., Suppl. 4: 153, 1934, syn. fide Geissler & Gradstein (1994): 202.

Thysananthus mexicanus Taylor, London J. Bot. 7: 199. 1848.—Type: ECUADOR. “on Pichincha, Feb 1847, W. Jameson s.n.” (not seen) = *Brachiolejeunea laxifolia* (Taylor) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 128. 1893, syn. fide Gradstein (1994): 172.

Thysananthus moenkemeyeri Steph., Hedwigia 34: 234. 1895, nom. nud. = *Caudalejeunea africana* (Steph.) Steph., Hedwigia 34: 233. 1895, syn. fide Vanden Berghen (1948): 96.

Thysananthus mutabilis Sande Lac. ex Verd., Ann. Bryol., Suppl. 4: 156. 1934, nom. inval. [Art. 34.1 (c)]. Material: ? = *Spruceanthus polymorphus* (Sande Lac.) Verd., Ann. Bryol., Suppl. 4: 155. 1934, syn. fide Verdoorn (1934): 155.

Thysananthus oblongifolius Chen & Wu, Acta Phytotax. Sin. 9: 227. 1964.—Type: CHINA. Yunnan: Jing-hong, 1100 m, 29 Aug 1936, Wang 9445 (not seen) = *Caudalejeunea recurvistipula* (Gottsche) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 129. 1893, syn. fide Zhu & So (2001): 97.

Thysananthus obovatus B. Y. Yang, Taiwania 9: 24. 1963.—Type: TAIWAN. “Hualien Hsien, Mt. Tsing-shui, Dec 1961”, T. Shimizu & M. T. Kao 317 (not seen) = *Spruceanthus semirepandus* (Nees) Verd., Ann. Bryol., Suppl. 4: 153. 1934, syn. fide Kitagawa (1981): 71.

Thysananthus obtusifolius Steph., Sp. Hepat. 4: 792. 1912.—Type: NEW CALEDONIA. (Holotype: G); Icon. Steph. nr. 10199, **syn. nov.** = *Spruceanthus polymorphus* (Sande Lac.) Verd., Ann. Bryol., Suppl. 4: 155. 1934. Verdoorn (1934) considered *T. obtusifolius* as a synonym of *Spruceanthus*. Judging from the original description and the drawing of *T. obtusifolius* of Stephani’s “Icones Hepaticarum Ineditae”, this is *S. polymorphus*.

Thysananthus olivaceus Steph. ex S. Arnell, Svensk Bot. Tidskr. 56: 349. 1962, nom. inval. [Art. 32.1(d)]. Material: ECUADOR. “Prov. Guayas: Rio Daule, below Pichincha, Hacienda Santa Barbarita (4737)” (not seen); Icon. Steph. nr. 10225: Brazil, Rio Branco, Ule 655, **syn. nov.** = *Bryopteris filicina* (Sw.) Nees, in Gottsche, Lindenberg & Nees, Syn. Hepat. 284. 1845. Judging from the drawing of *T. obtusifolius* of

Stephani's "Icones Hepaticarum Ineditae", which shows one leaf and one underleaf, this is *B. filicina*.

Thysananthus ophiocephalus Taylor, London J. Bot. 5: 384. 1846.—Type: NEW ZEALAND. "Bay of Islands", *Sinclair s.n.* (holotype: FH!; isotype: S!), **syn. nov.** = *Archilejeunea olivacea* (Hooker f. & Taylor) Steph., Sp. Hepat 4: 734. 1912. Stephani (1912) considered *T. ophiocephalus* a synonym of *Mastigolejeunea anguiformis* (Hooker f. & Taylor) B. Thiers & Gradst. Judging from the type specimens, this is *A. olivacea*.

Thysananthus paucidens Steph., Sp. Hepat. 4: 793. 1912.—Type: HAWAII. (not seen); Icon. Steph. nr. 10203 = *Spruceanthus polymorphus* (Sande Lac.) Verd., Ann. Bryol., Suppl. 4: 155. 1934, syn. fide Verdoorn (1934): 155.

Thysananthus polymorphus (Sande Lac.) Schiffn., Consp. Hep. Archip. Ind.: 305. 1898. *Phragmicoma polymorpha* Sande Lac., Nat. Tijdschr. N. I. X.: 396. 1856.—Type: INDONESIA. Java: *F. Junghuhn s.n.* (not seen) = *Spruceanthus polymorphus* (Sande Lac.) Verd., Ann. Bryol., Suppl. 4: 155. 1934.

Thysananthus pterobryoides (Spruce) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 130. 1893. *Lejeunea pterobryoides* Spruce. Trans. & Proc. Bot. Soc. Edinburgh 15: 109. 1884.—Type: ECUADOR. "ad fluvium Pastasa, 400 m,...", *Spruce s.n.* (not seen) = *Fulfordianthus pterobryoides* (Spruce) Gradst., Bryologist 95: 44. 1992.

Thysananthus renilobus (Gottsche) Schiffn., Consp. Hep. Archip. Ind.: 306. 1898. *Phragmicoma reniloba* Gottsche in Gottsche, Lindenberg & Nees, Syn. Hepat. 301. 1845.—Type: INDONESIA. Java: "Hb. Nees" (not seen) = *Caudalejeunea reniloba* (Gottsche) Steph., in Gottsche et al., Syn. Hepat.: 326. 1845. Zhu & So (2001) erroneously proposed the younger name *C. recurvistipula* (Gottsche) Steph. as the correct name for this species (S. R. Gradstein, pers. comm.).

Thysananthus rotundistipulus Steph., Sp. Hepat. 6: 566. 1924.—Type: INDIA. Nilgiri: *Lüthi s.n.* (holotype: G); Icon. Steph. nr. 10209 = *Spruceanthus semirepandus* (Nees) Verd., Ann. Bryol., Suppl. 4: 153. 1934, syn. fide Verdoorn (1934): 153.

Thysananthus schiffneri S. Arnell, in Schiffner & S. Arnell, Österr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. 111: 119. 1964.—Type: BRAZIL. “Paraná: ... ad cataractas Salto Grande, ...ca. 500 m”, *Schiffner 2097* (not seen) = *Acanthocoleus aberrans* (Lindenb. & Gottsche) Kruijt var. *laevis* Gradst., Fl. Neotrop. 62: 193. 1994, syn. fide Gradstein (1994): 193.

Thysananthus scutellatus Taylor, London J. Bot. 5: 383. 1846.—Type: NEW ZEALAND. “Mr. H. Watson’s Herb.”, *A. Cunningham s.n.* (not seen) = *Archilejeunea olivacea* (Hook. & Taylor) Steph., Bot. Jahrb. Syst. 23: 314. 1886, syn. fide Gradstein & Buskes (1985): 101.

Thysananthus semirepandus (Nees) Schiffn., Österr. Bot. Z. 49: 205. 1899. *Jungermannia semirepanda* Nees, Enum. Pl. Crypt. Jav. 39. 1830.—Type: INDONESIA. Java: (not seen) = *Spruceanthus semirepandus* (Nees) Verd., Ann. Bryol. 4, Suppl.: 153, 1934.

FURTHER NAMES IN *THYSANANTHUS*

Thysananthus africanus (Sim) S. Arnell, Bot. Not.: 282. 1953, nom. illeg. [Art. 53.1] *Thysanolejeunea africana* Sim, Trans. Roy. Soc. South Africa 15: 50. 1926.—Type: South Africa. “Perie forest, Kaffraria”, *Sim 346* (not seen). Wigginton & Grolle (1996) mentioned: “To be clarified. Collected only once?”.

Thysananthus erosus Steph., Sp. Hepat. 6: 568. 1924.—Type: NEW GUINEA. “*Ledermann s.n.*” (not seen); Icon. Steph. nr. 10180 = *Conoscyphus* Mitt.? Verdoorn (1934) considered *T. erosus* as a member of Jungermannieae. Judging from the original description and the drawing of *T. erosus* of Stephani’s “Icones Hepaticarum Ineditae”, which shows one leaf and one underleaf, this might be *Conoscyphus*.

Thysananthus frauenfeldii Reichardt, Verh. K. K. Zool.-Bot. Ges. Wien 16: 958. 1866. *Mastigolejeunea frauenfeldii* (Reichardt) Verd., Blumea 1: 230. 1934.—Type: TAHITI. Novara Exped., “...um Papiete, *Jelineck s.n.*” (not seen).

Thysananthus fruticosus fo. *pendula* Herzog, Trans. Brit. Bryol. Soc. 1: 319. 1950, nom. inval. [Art 32.1(d)]. Material: MALAYSIA. Sarawak: “Dulit, ... n. 2277”, 1932, *P. W. Richards* s.n. (not seen).

Thysananthus hebridensis Steph., in Stephani & Watts, J. & Proc. Roy. Soc. New South Wales 48: 134. 1914, nom. inval. [Art 32.1(d)]. Material: VANUATU [“New Hebrides”]. Tafea: Aneityum, *Gunn* s.n. (not seen).

Thysananthus integerrimus Steph., Sp. Hepat. 6: 567. 1924.—Type: NEW GUINEA. “*Ledermann* s.n.” (not seen); Icon. Steph. nr. 10187. Verdoorn (1934) considered *T. integerrimus* as a member of *Jungermannieae*.

Thysananthus lacerostipulus Steph., Sp. Hepat. 6: 567. 1924.—Type: NEW GUINEA. *Ledermann* s.n. (not seen); Icon. Steph. nr. 10223 = *Conoscyphus* Mitt. ? Verdoorn (1934) considered *T. lacerostipulus* as a member of *Jungermannieae*. Judging from the original description and the drawing of *T. lacerostipulus* of Stephani’s “Icones Hepaticarum Ineditae”, which shows one leaf and one underleaf, this might be *Conoscyphus*.

Thysananthus polymorphus var. *β planifolia* (Sande Lac.) Schiffn., Consp. Hep. Archip. Ind.: 305. 1898. *Phragmicoma polymorphua* fo. *β planifolia* Sande Lac., Syn. Hepat. Jav.: 58. 1856.—Type: INDONESIA. Java: “ad montem Salak, Zollinger, coll. *sub* 3560 (pl. femina); Herb. v. d. Bosch (pl. mascula)” (not seen).

Thysananthus sikkimensis Steph ex Schiffn., Österr. Bot. Z. 49: 205. 1899, nom. inval. [Art 32.1(d)]. Material: BHUTAN. “between Maria Basti & Labar, 5000–6000 ft.”, 12 Apr 1898, *R. L. Durel* 159 (not seen).

Thysananthus ungulatus (Mitt.) Steph., Sp. Hepat. 6: 567. 1924. *Lejeunea ungulata* Mitt., J. Proc. Linn. Soc., Bot. 5: 110. 1861.—Type: BURMA. “in Pegu, ad Rangoon,...”, *McClelland* s.n. (not seen) = *Spruceanthus* Verd.? Verdoorn (1934) doubtfully referred *T. ungulatus* to *Spruceanthus* (“cf. *sub Spruceanthus*”). Judging from the original description, this might indeed be *Spruceanthus*.

Thysananthus wardianus (Mitt.) Verd. (“Steph.”), Ann Bryol., Suppl. 4: 166. 1934 as in Index Hepaticarum (Geissler & Bischler, 1990). *Lejeunea wardiana* Mitt., J. Proc. Linn. Soc., Bot. 5: 109. 1861.—Type: INDIA. “in Assam superiore”, *Griffith s.n.* (not seen) = ***Thysananthus* subg. *Mastigolejeunea*** (Spruce) comb. nov., syn. fide Verdoorn (1934): 166.

Thysananthus yokogurensis (Steph.) S. Hatt., J. Hattori Bot. Lab. 8: 32, 1952, nom. inval. [Art 32.1(d)]. *Thysanolejeunea yokogurensis* Steph. ex Yoshinaga, Bot. Mag. (Tokyo) 15: 93. 1901, nom. inval. [Art 32.1(d)]. Material: JAPAN. (not seen).

ACKNOWLEDGEMENTS

The research was supported by a Royal Thai government scholarship in cooperation with the German Academic Exchange Service (DAAD). This research also received support from the SYNTHESYS Project (<http://www.synthesys.info/>) financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Program. I am deeply grateful to Prof. S. R. Gradstein for his contribution to the manuscript text and useful comments and suggestions on the manuscript. I would like to thank J. Wang for providing useful information. I express my gratitude to the curators of the following herbaria for making the specimens available and the loan of specimens: BCU, BKF, BM, BM-K, BR, BZ, C, FH, G, GOET, H, HIRO, JE, L, LAE, NICH, NSW, NY, PC, PSU, S, SING, STR, U and W. Thanks are also due to C. Gehrig-Downie and S. Chantanaorrapint for additional fresh materials, and to B. Raufeisen for the base map of the world.

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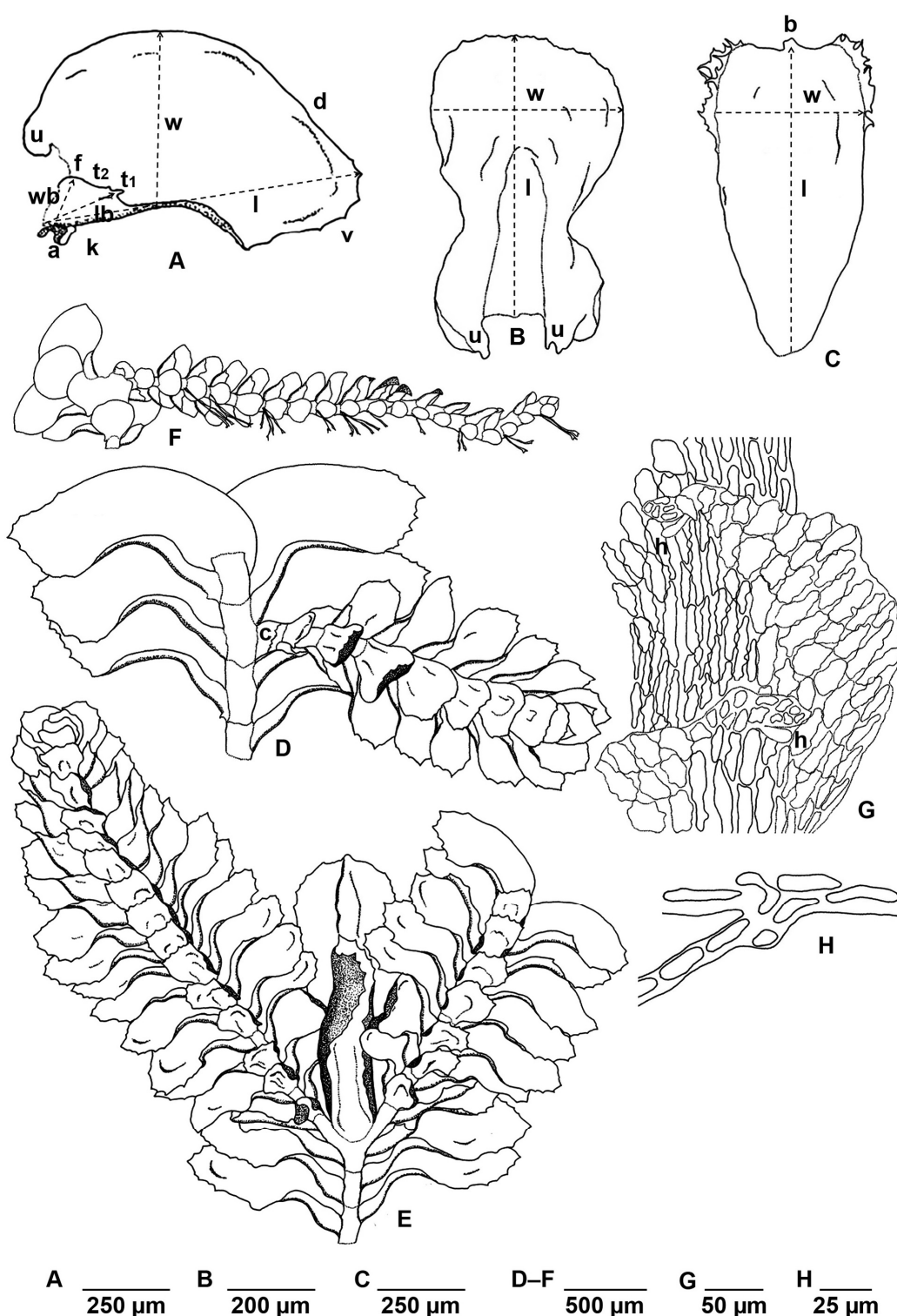


FIG. 1. Method of measurement in subg. *Thysananthus*. A. Leaf, ventral view: a = appendage, d = dorsal leaf margin, f = lobule free margin, k = keel, l = leaf length, lb = lobule length, $t_{1,2}$ = lobule teeth, u = auricle, v = ventral leaf margin, w = leaf width, wb = lobule width. B. Underleaf, ventral view: u = auricle, l = underleaf length, w = underleaf width. C. Perianth, ventral view: b = beak, l = perianth length, w = perianth width. D. Portion of shoot with *Lejeunea*-type branching, ventral view: c = collar. E. Portion of shoot with androecia, gynoeceium and lejeuneoid innovation (dichasial pattern), ventral view. F. Flagella at stem base, ventral view. G. Lateral merophyte cells arranged in straight longitudinal line: h = hyaline appillae. H. Underleaf base in longitudinal section. (A from lectotype of *T. appendiculatus*; B–C from holotype of *T. discretus*; D from *T. spathulistipus*, Sukkharak 766 (BKF, GOET); E from *T. spathulistipus*, Sukkharak 746 (BKF, GOET); F from isolectotype of *T. comosus*; G from *T. spathulistipus*, Sukkharak 761 (BKF, GOET); H from holotype of *T. discretus*).

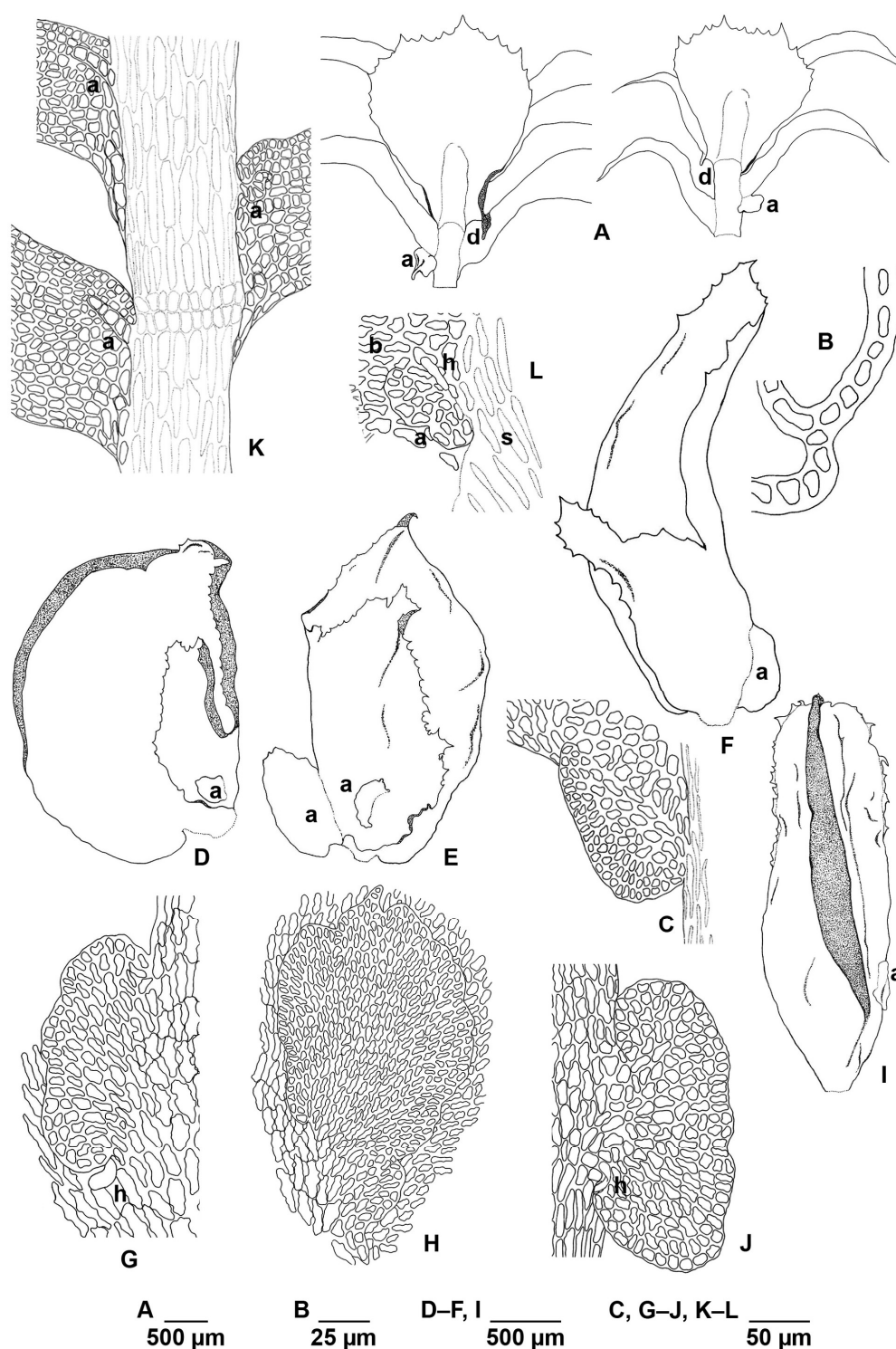


FIG. 2. Leaves and underleaves adnation and appendages in subg. *Thysananthus*. A. Portions of plant, ventral view: d = adnation, a = appendage. B. Adnation in longitudinal section. C. Appendages at bases of leaf keels. D–F. Female bracts, ventral view: a = appendage. G. Appendage and hyaline papilla at base of bract keels: h = hyaline papilla. H. Appendage at mid-basal portion of bract lobule. I. Perianth, ventral view: a = appendage. J. Appendage and hyaline papilla of perianth: h = hyaline papilla. K. Portions of plant showing appendage at lobule base, ventral view: a = appendage. L. Appendage: b = lobule, a = appendage, h = hyaline papilla, s = stem. (A from isoelectotype of *T. comosus*; B from *T. spathulistipus*, Sukkharak 766 (BKF, GOET); C, E, H from holotype of *T. discretus*; D from holotype of *T. gottschei* var. *continuus*; F from *T. appendiculatus*, Gradstein 3875 (U); G from *T. appendiculatus*, Streimann & Tamba 12358 (JE); I–J from *T. mollis*, Gradstein 3795 (U); K from *T. retusus* subsp. *retusus*, Sukkharak 733 (BKF, GOET); L from *T. montanus*, Streimann 13639 (LAE)).

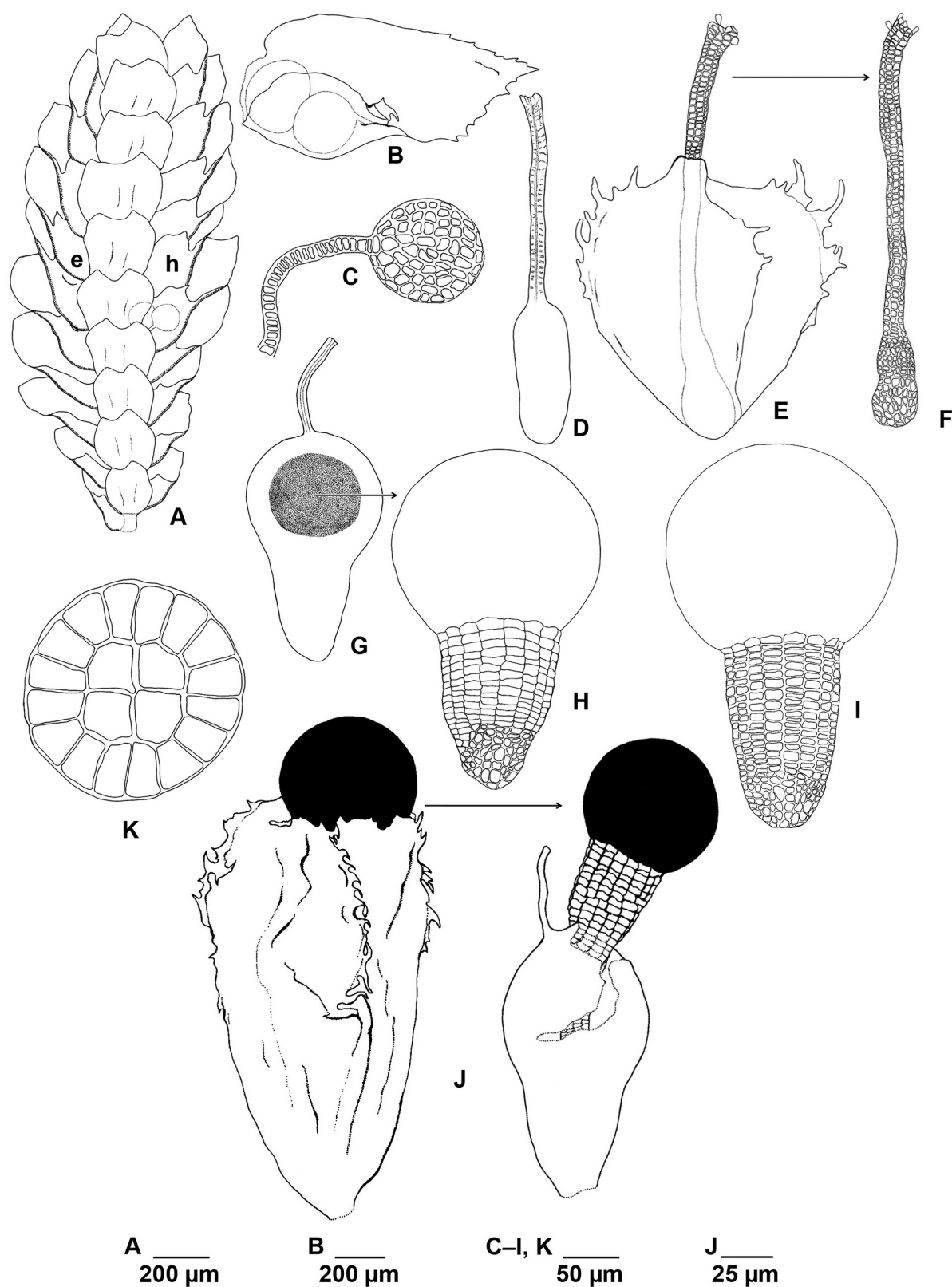


FIG. 3. Androecia, Gynoecia and young sporophyte in subg. *Thysananthus*. A. Portion of androecial spike showing epistatic and hypostatic lobules, ventral view: e = epistatic, h = hypostatic. B. Male bract with 2 antheridia. C. Antheridia. D. Juvenile perianth. E. perianth and protruding archegonial neck. F. Archegonium and archgonial neck. G. Later stage of development. H. Sporophyte prior to elongation of seta. I. Sporophyte after partial elongation of seta. J. Mature perianth, just dehiscence. K. Transverse section of seta. (A from *T. amazonicus*, Cornelissen & Steeger C682 (U); B from *T. spathulistipus*, Gradstein 3964 (U); C from *T. spathulistipus*, Gradstein 3965 (U); D–G from *T. spathulistipus*, Sukkharak 766 (BKF, GOET); H–I, K from *T. retusus* subsp. *retusus*, Streimann 40547 (JE); J from *T. spathulistipus*, Sipman 6992 (U)).

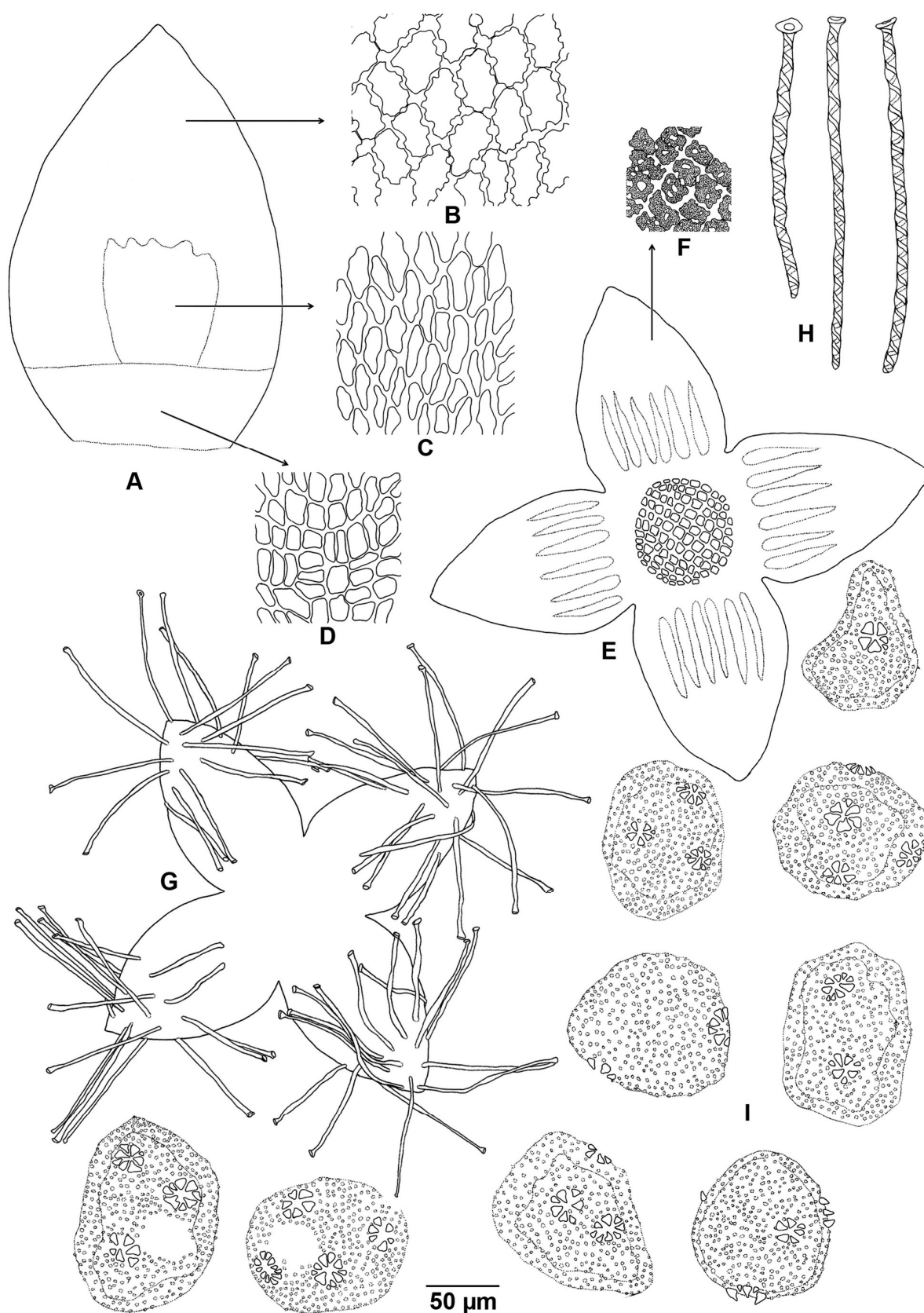


FIG. 4. Sporophyte in subg. *Thysananthus*. A. Outer surface of capsule valve, showing rectangular-shaped hinge. B–D. Cells of the outer layer of the capsule valve, surface view. E. Inner surface of dehiscent capsule, showing base of capsule and longitudinal ridges. F. Cells of the inner layer of the capsule valve, surface view. G. Inner surface of dehiscent capsule, showing elaters patterns of either 1+3+5+6 or 2+4+6+6 per valve. H. Elaters. I. Spores. (A–G from *T. spathulistipus*, Yong & Ponniah 2981 (GOET); H from *T. spathulistipus*, Thiers & Roy 2397 (U); I from *T. spathulistipus*, Sipman 6992 (U)).

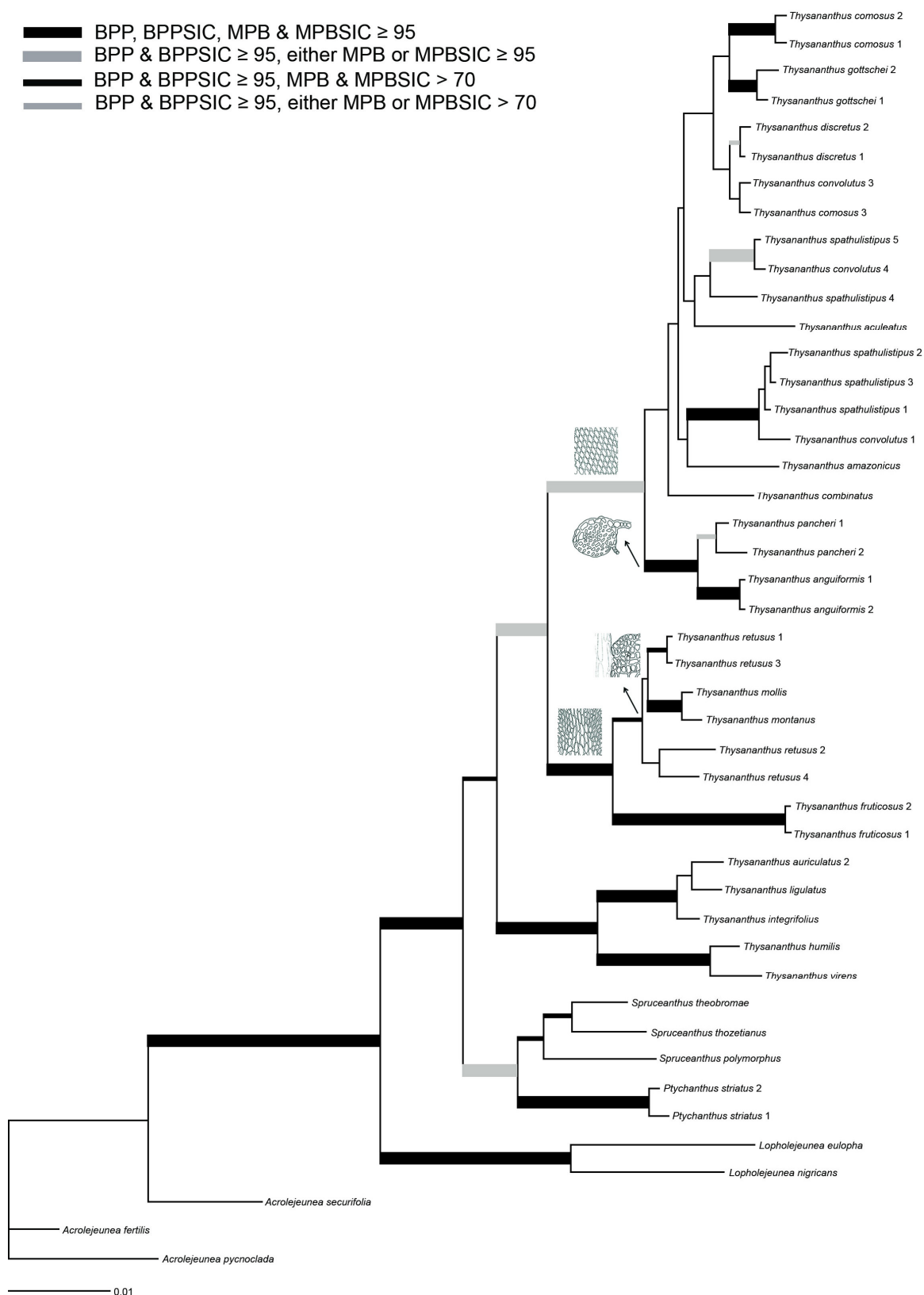


FIG. 5. Majority rule Bayesian phylogram inferred from the combined chloroplast dataset including differences in sequence lengths (indels). Branch thickness and color indicate bootstrap support and posterior probability values. BPP = posterior probability values from Bayesian analysis, in which gaps treated as missing data; BPPSIC = posterior probability values from Bayesian analysis, in which gaps treated as informative by a simple indel coding strategy; MPB = bootstrap support values from the maximum parsimony optimality criterion, in which gaps treated as missing data; MPBSIC = bootstrap support values from the maximum parsimony optimality criterion, in which gaps treated as informative by a simple indel coding strategy. Modified after Sukkharak et al. (Submitted).

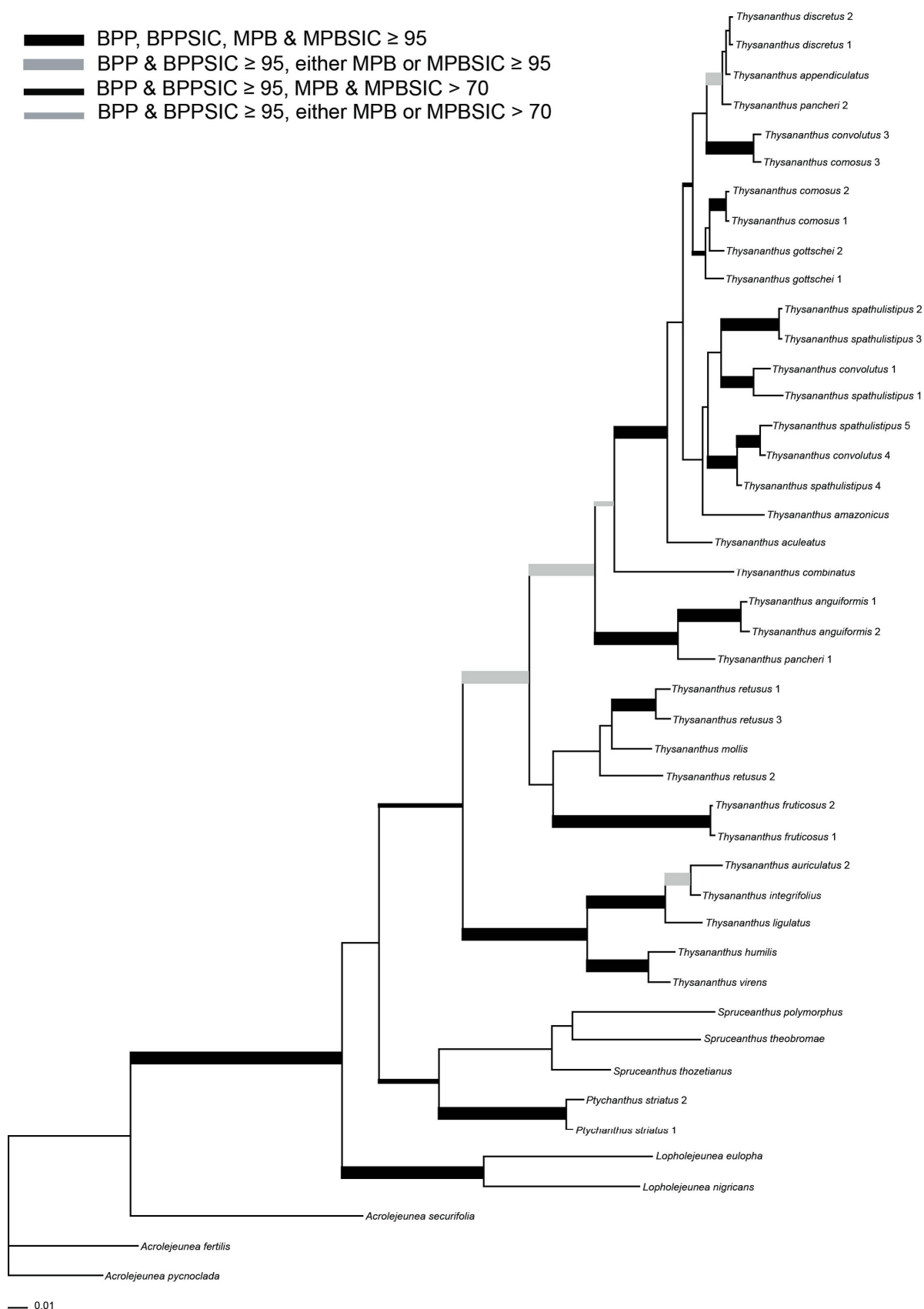


FIG. 6. Majority rule Bayesian phylogram inferred from the ITS dataset. For further explanation see Fig. 5. Modified after Sukkharak et al. (Submitted).

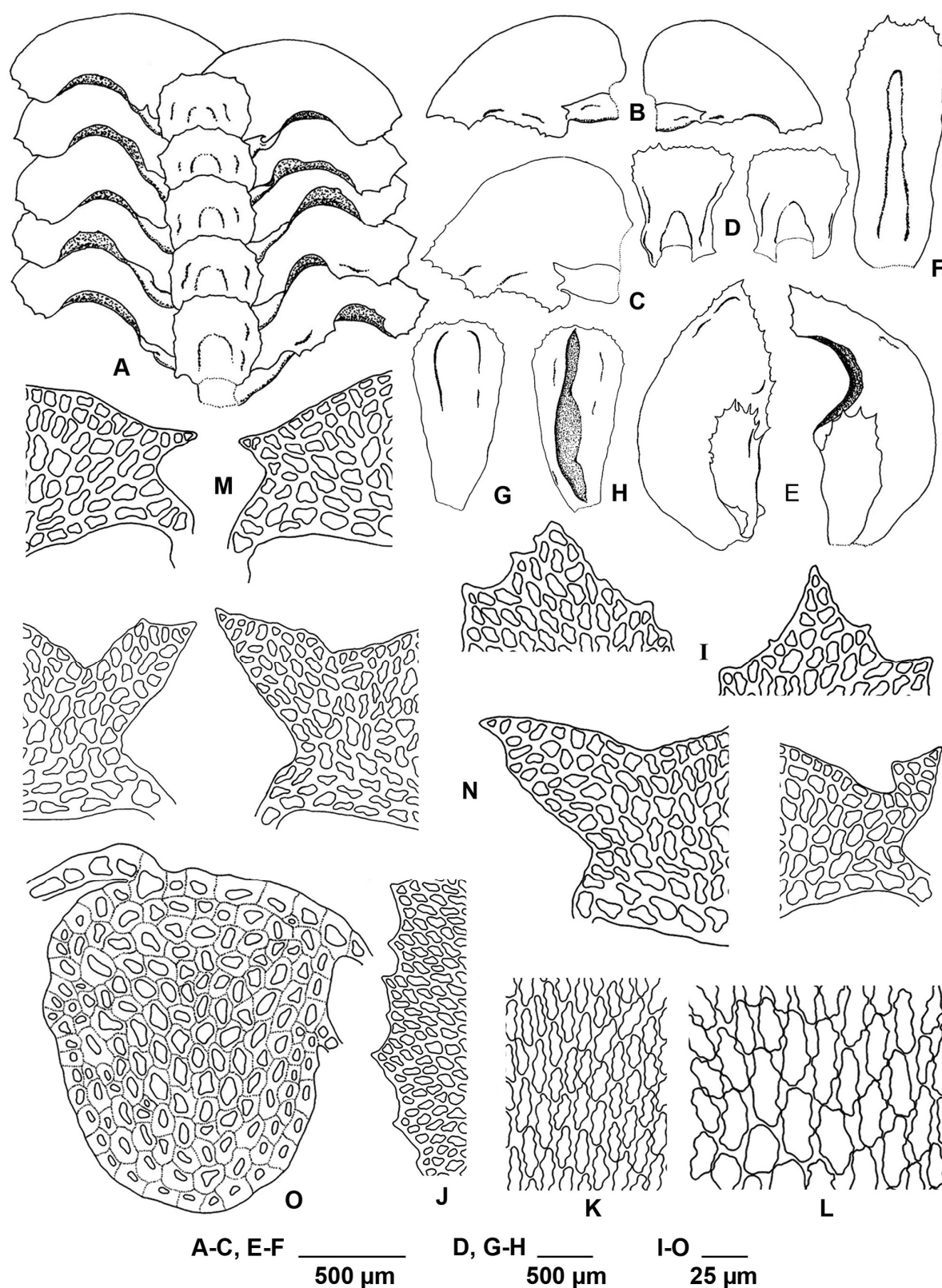


FIG. 7. *Thysananthus aculeatus* Herzog. A. Portion of shoot, ventral view. B–C. Leaves, ventral view. D. Underleaves, ventral view. E. Female bracts, ventral view. F. Female bracteole, ventral view. G. Perianth, dorsal view. H. Perianth, ventral view. I. Leaf apices. J. Margin cells of leaf lobe. K. Median cells of leaf lobe. L. Basal cells of leaf lobe. M–N. Leaf lobule apices. O. Cross section of stem. (A–B, D–M, O from the lectotype; C, N from paralectotype).

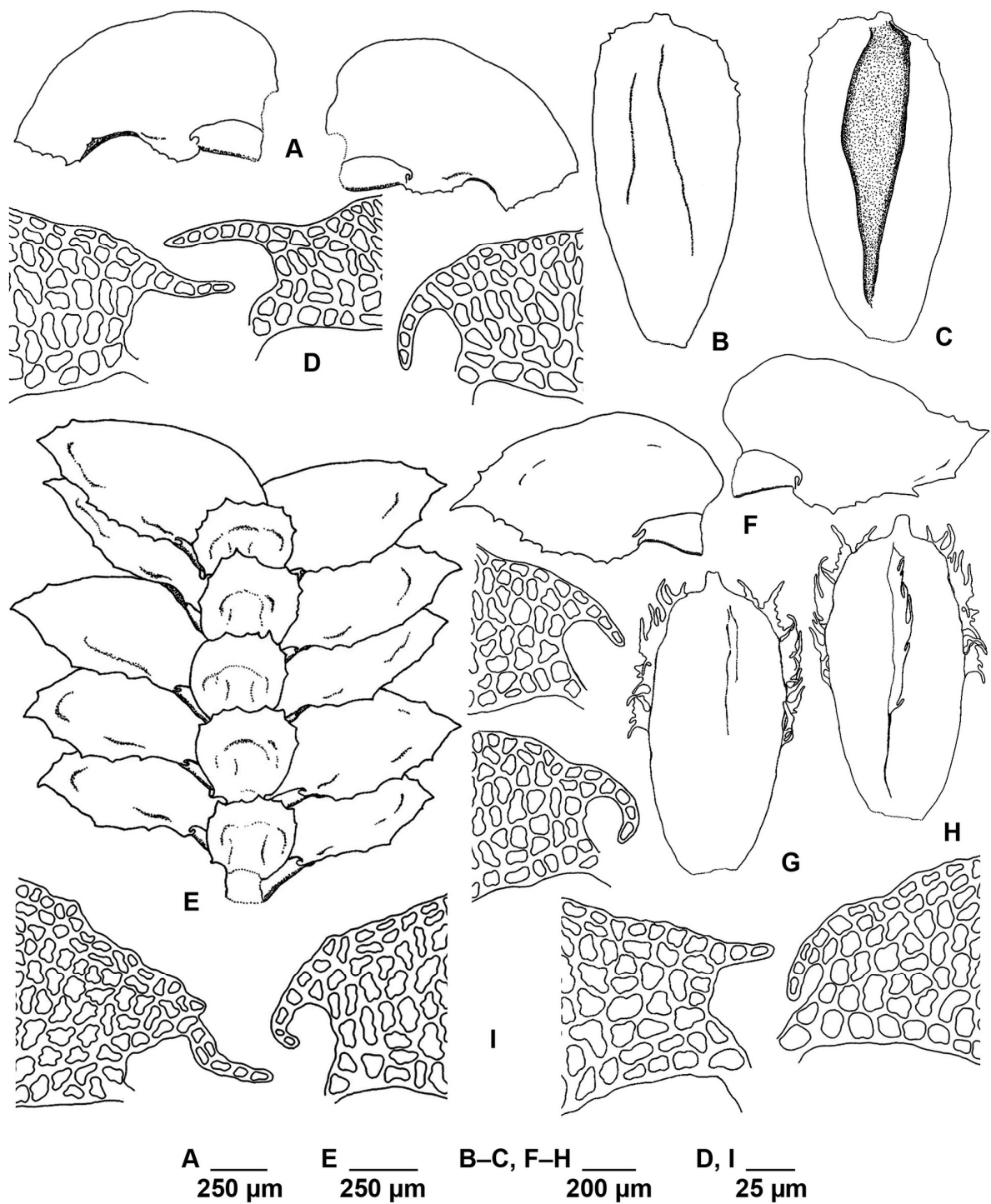


FIG. 8. *Thysananthus aculeatus* Herzog. A. Leaves, ventral view. B. Perianth, dorsal view. C. Perianth, ventral view. D. Leaf lobule apices. E. Portion of shoot, ventral view. F. Leaves, ventral view. G. Perianth, dorsal view. H. Perianth, ventral view. I. Leaf lobule apices. (A–D from holotype of *T. formosanus*; E–I from the holotype of *T. richardsianus*).

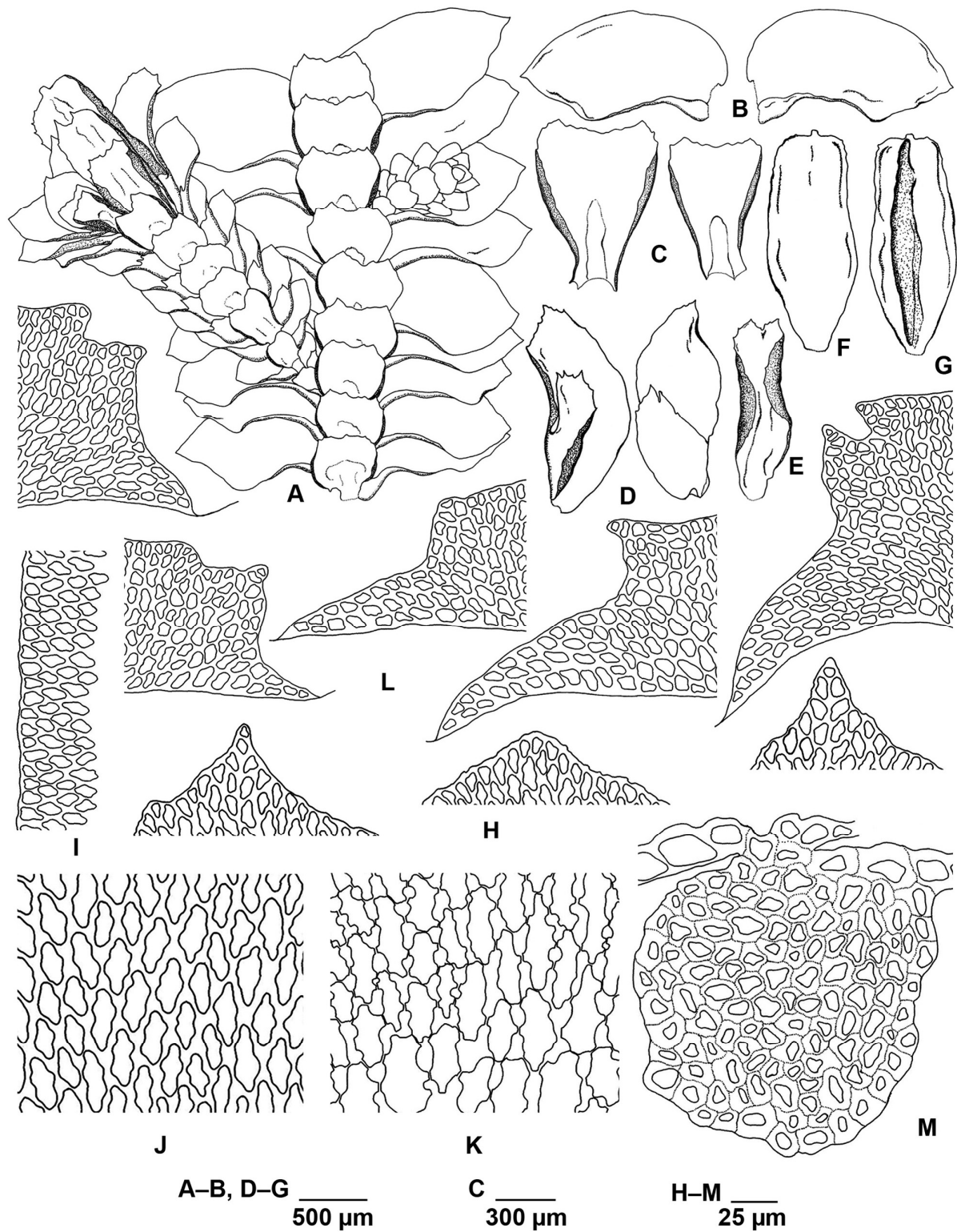


FIG. 9. *Thysananthus amazonicus* (Spruce) Schiffn. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apices. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices. M. Cross section of stem. (All from *Gradstein s.n.* (GOET)).

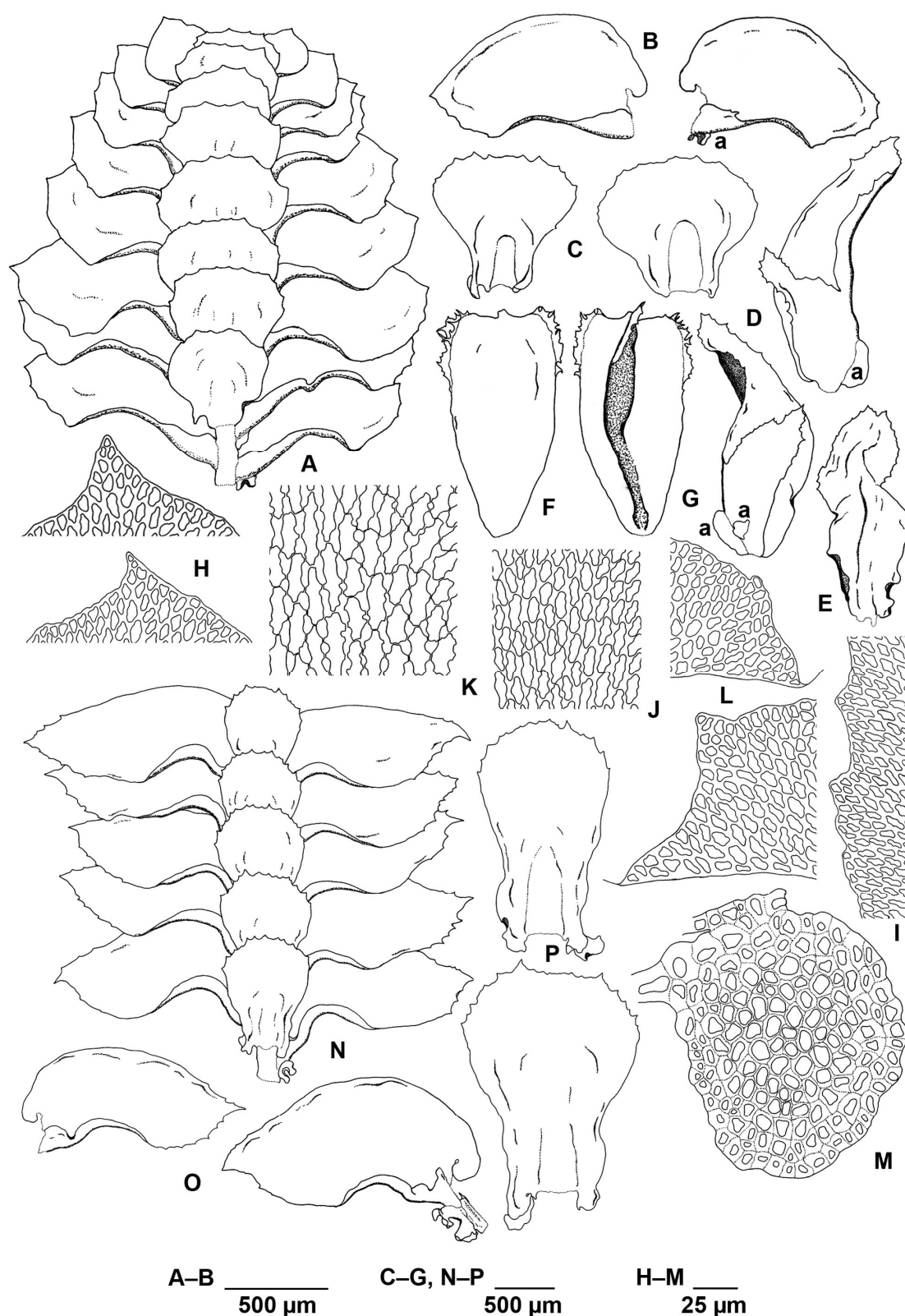


FIG. 10. *Thysananthus appendiculatus* Steph. A. Portion of shoot, ventral view. B. Leaves, ventral view: a = appendage. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apices. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices. M. Cross section of stem. N. Portion of shoot, ventral view. O. Leaves, ventral view. P. Underleaves, ventral view. (A–C, H–M from the lectotype; D–G from *Streimann 13859* (JE); N–P from *Gradstein 3875* (GEOT)).

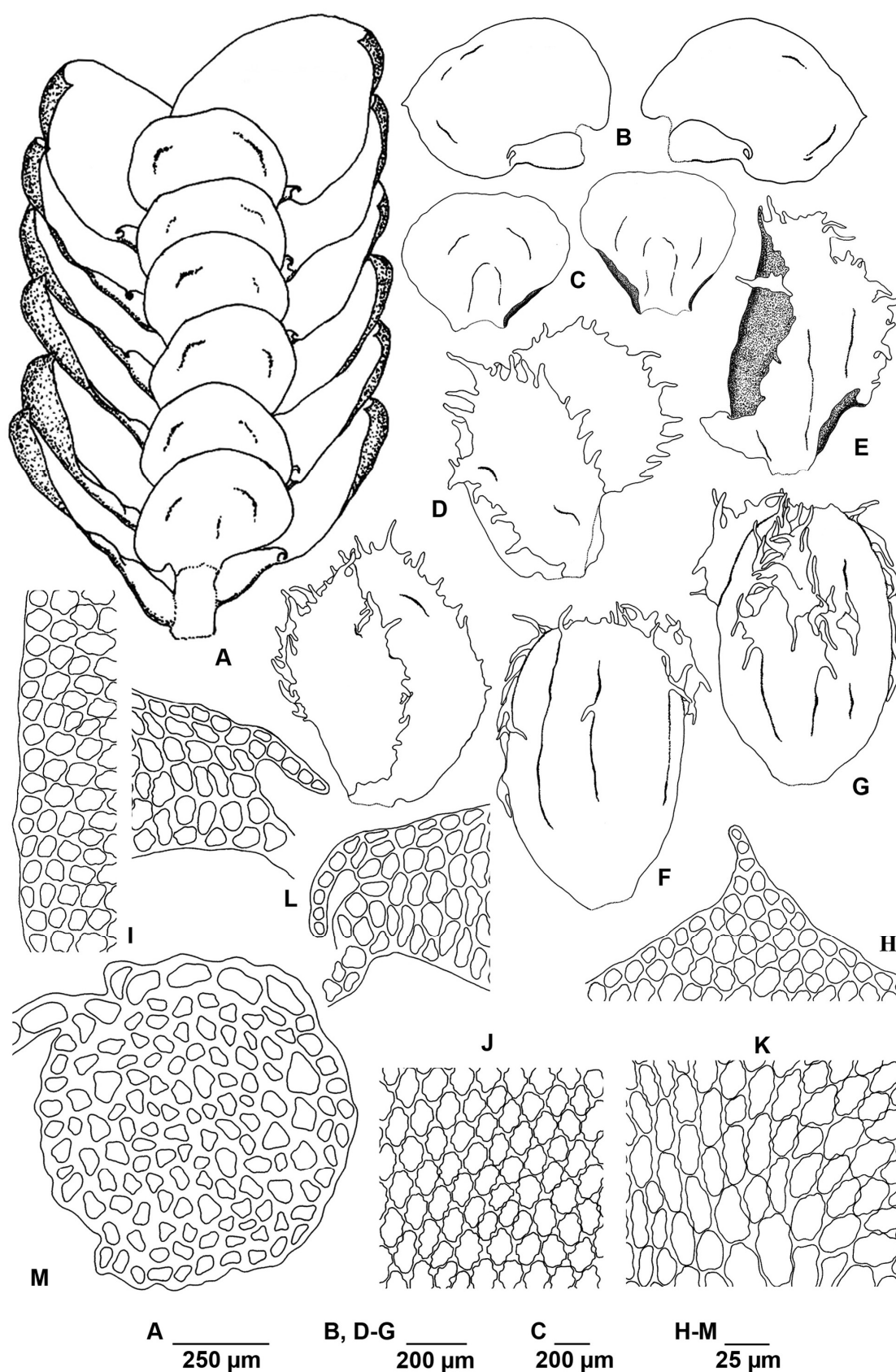


FIG. 11. *Thysananthus combinatus* sp. nov. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apex. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices. M. Cross section of stem. (All from the holotype).

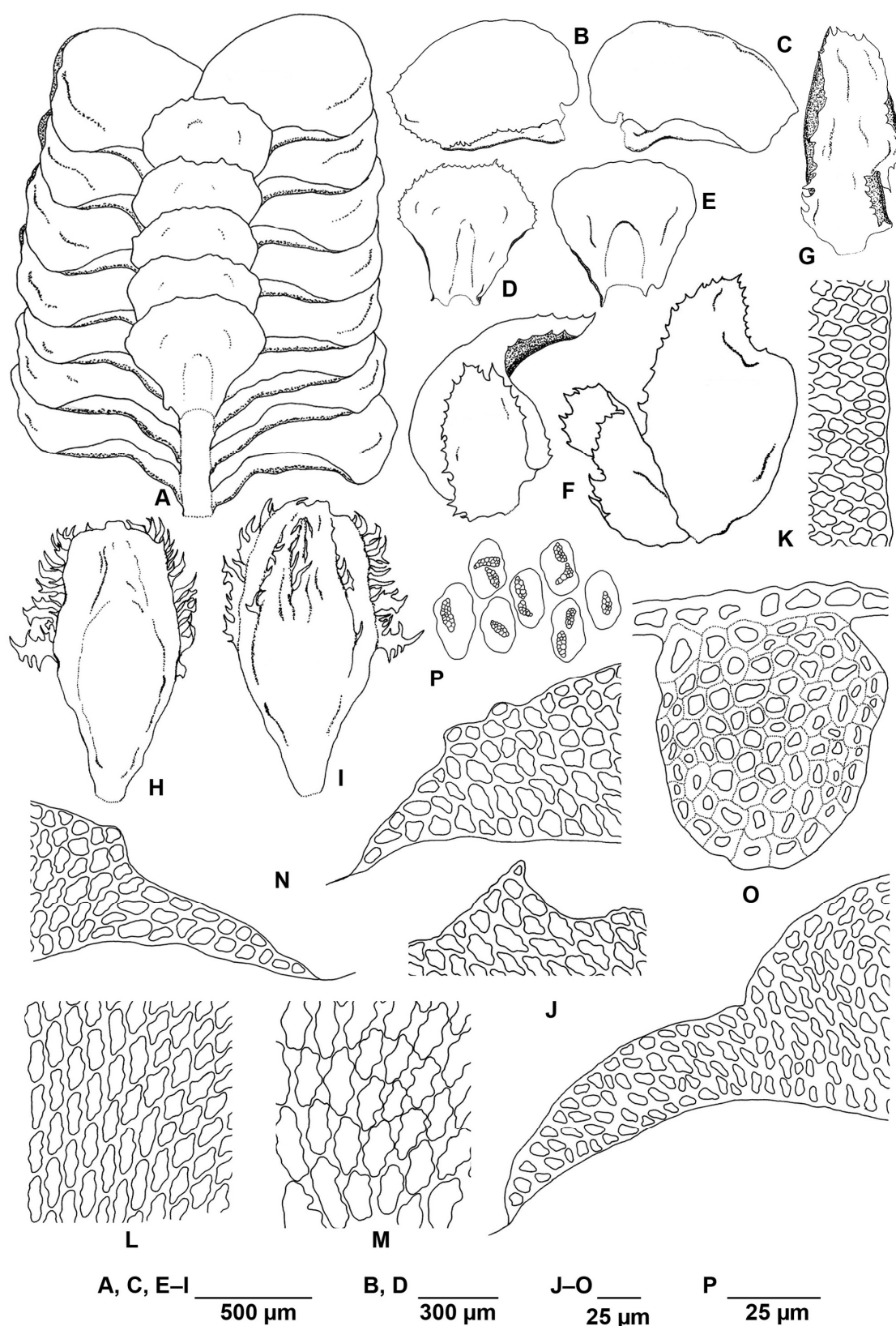


FIG. 12. *Thysananthus comosus* Lindenb. A. Portion of shoot, ventral view. B–C. Leaves, ventral view. D–E. Underleaves, ventral view. F. Female bracts, ventral view. G. Female bracteole, ventral view. H. Perianth, dorsal view. I. Perianth, ventral view. J. Leaf apex. K. Margin cells of leaf lobe. L. Median cells of leaf lobe. M. Basal cells of leaf lobe. N. Leaf lobule apices. O. Cross section of stem. P. Oil bodies (A, C, E–O from the lectotype, B, D from *Schiffner s.n.* (GOET), P from *Sukkharak 730* (BKF, GOET)).

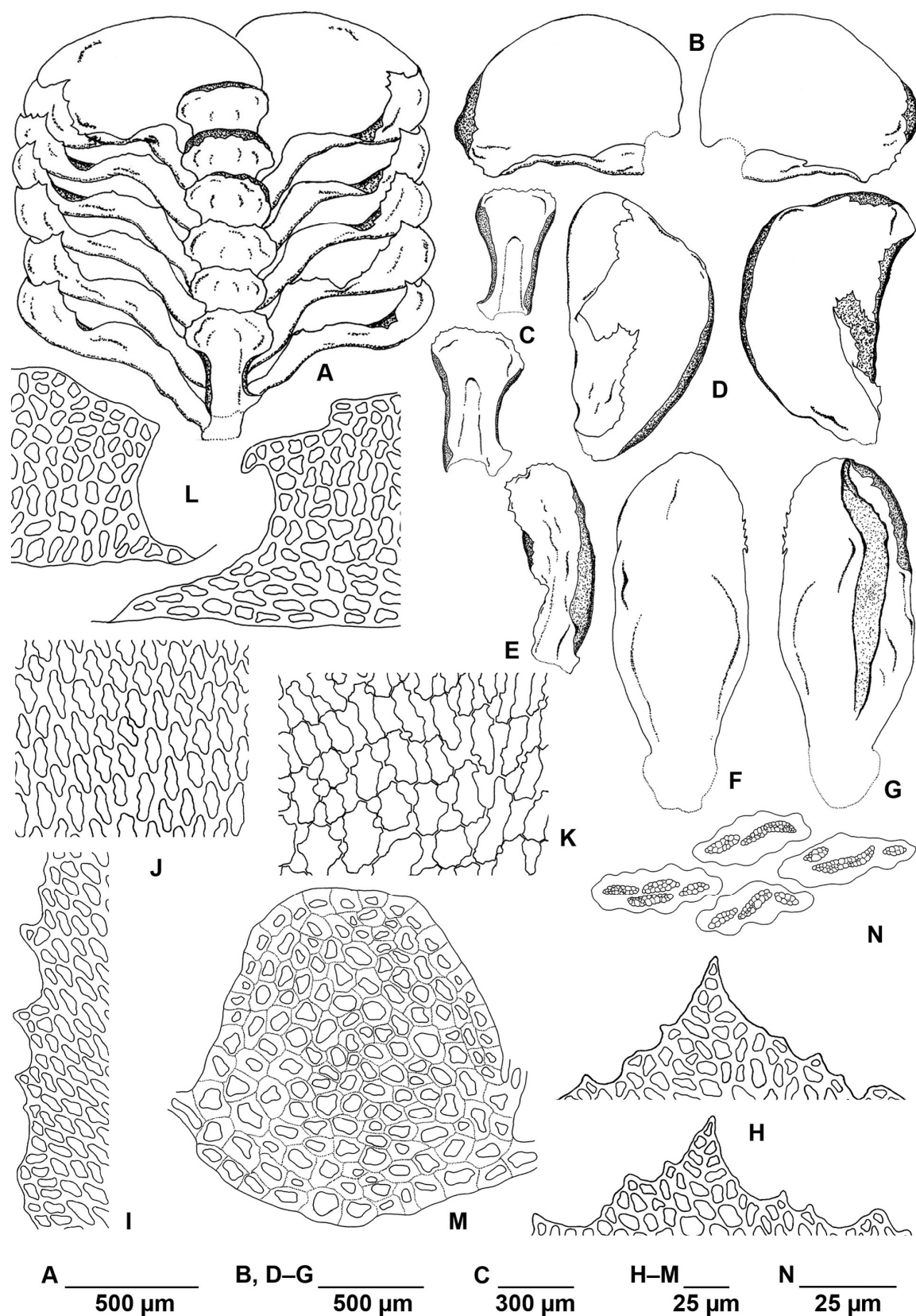


FIG. 13. *Thysananthus convolutus* Lindenb. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apices. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices. M. Cross section of stem. N. Oil bodies. (A–M from the lectotype; N from *Sukkharak 717* (BKF, GOET)).

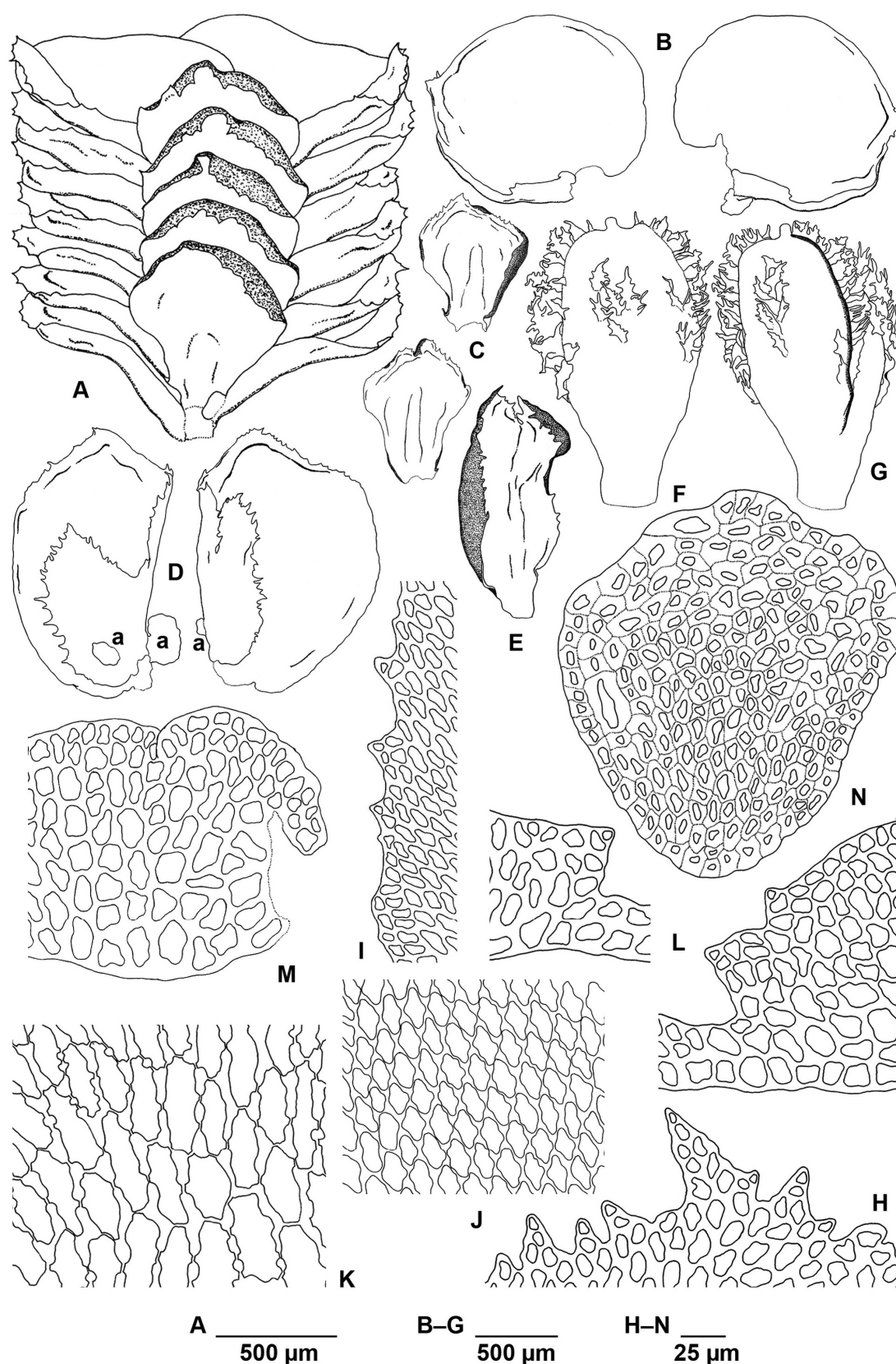


FIG. 14. *Thysananthus convolutus* var. *laceratus* (Steph.) comb. nov. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apex. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices. M. Leaf lobule base. N. Cross section of stem. (All from the lectotype).

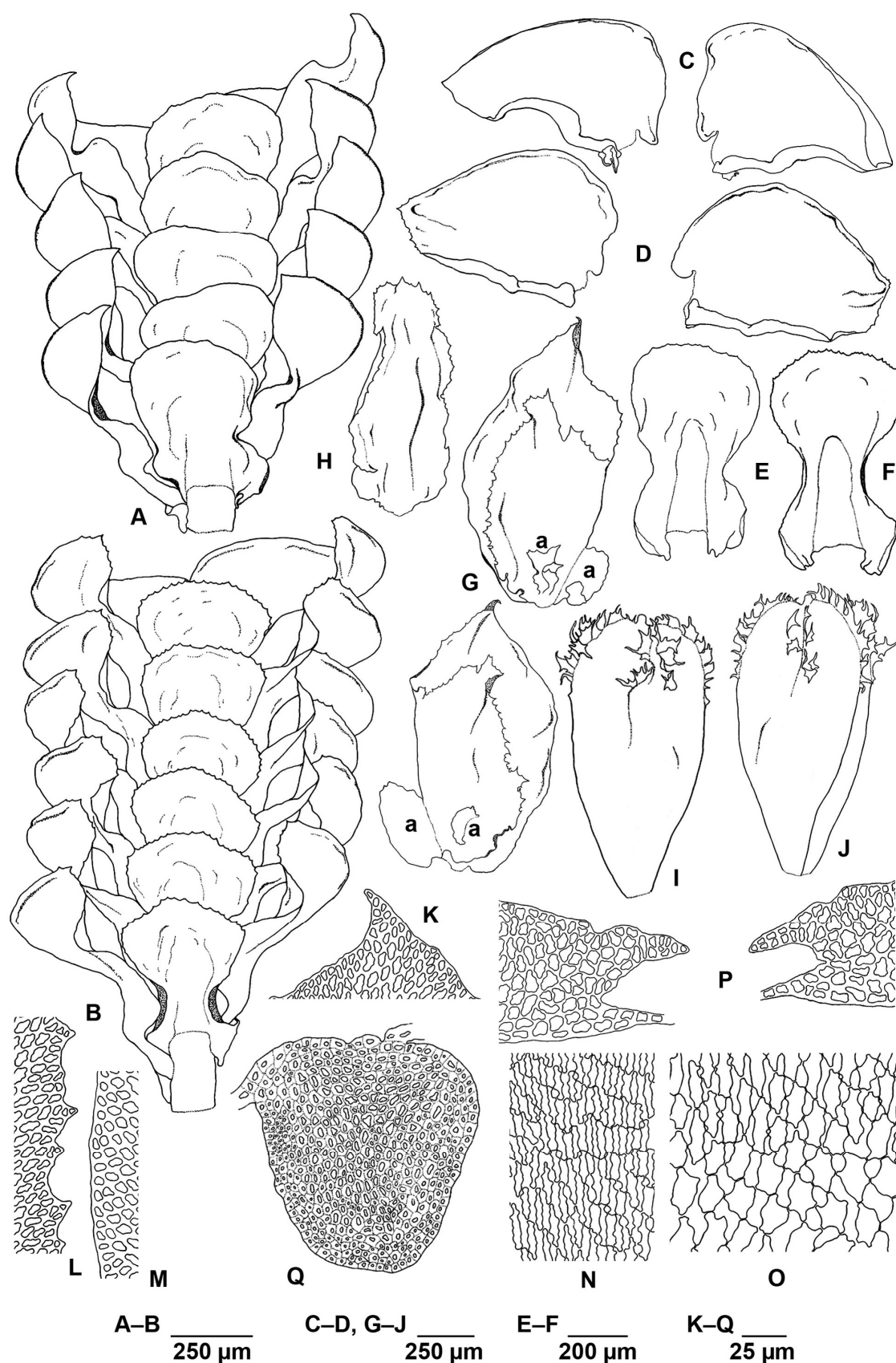


FIG. 15. *Thysananthus discretus* Sukkharak & Gradst. A–B. Portion of shoot, ventral view. C–D. Leaves, ventral view. E–F. Underleaves, ventral view. G. Female bracts, ventral view: a appendage. H. Female bracteole, ventral view. I. Perianth, dorsal view. J. Perianth, ventral view. K. Leaf apex. L–M. Margin cells of leaf lobe. N. Median cells of leaf lobe. O. Basal cells of leaf lobe. P. Leaf lobule apices. Q. Cross section of stem. (A, C, E, G–K, M–Q from the holotype; B, D, F, L from *Streimann 13622* (JE)).

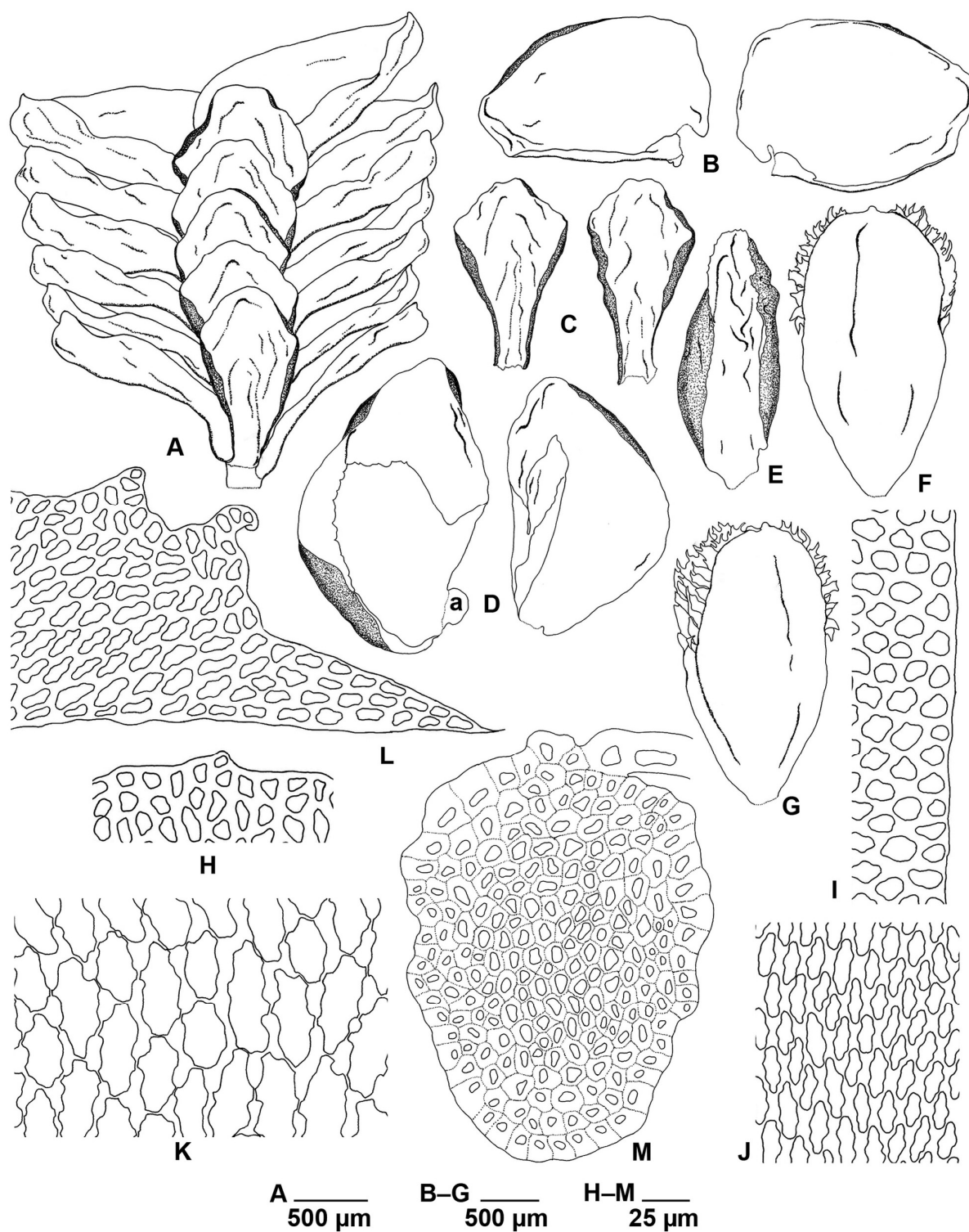


FIG. 16. *Thysananthus gottschei* (Jack & Steph.) Steph. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apex. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apex. M. Cross section of stem. (A–C, H–M from the lectotype; D–G from *Gradstein 10324* (GOET)).

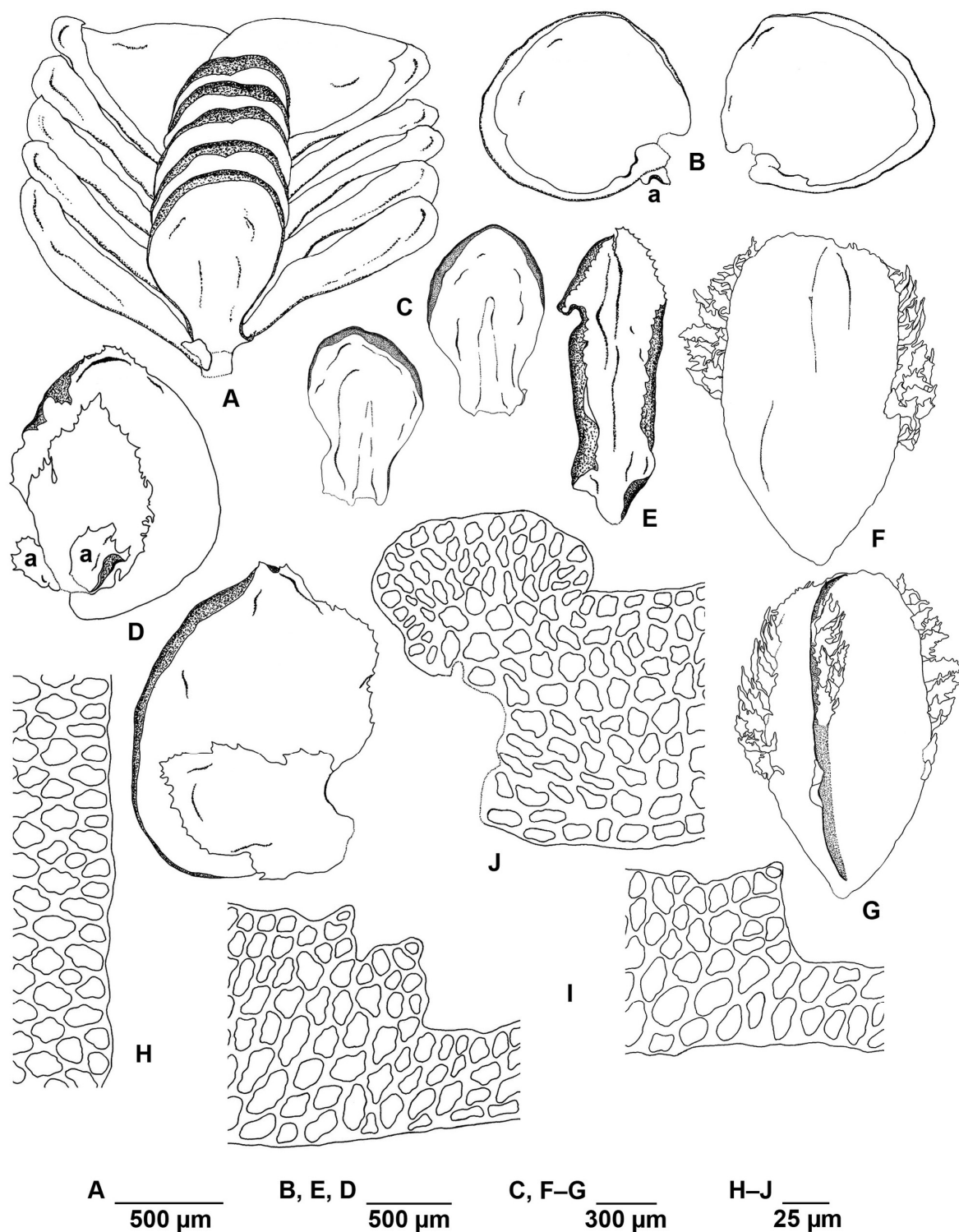


FIG. 17. *Thysananthus gottschei* var. *continuus* var. nov. A. Portion of shoot, ventral view. B. Leaves, ventral view: a = appendage. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Margin cells of leaf lobe. I. Leaf lobule apices. J. Leaf lobule base. (All from the lectotype).

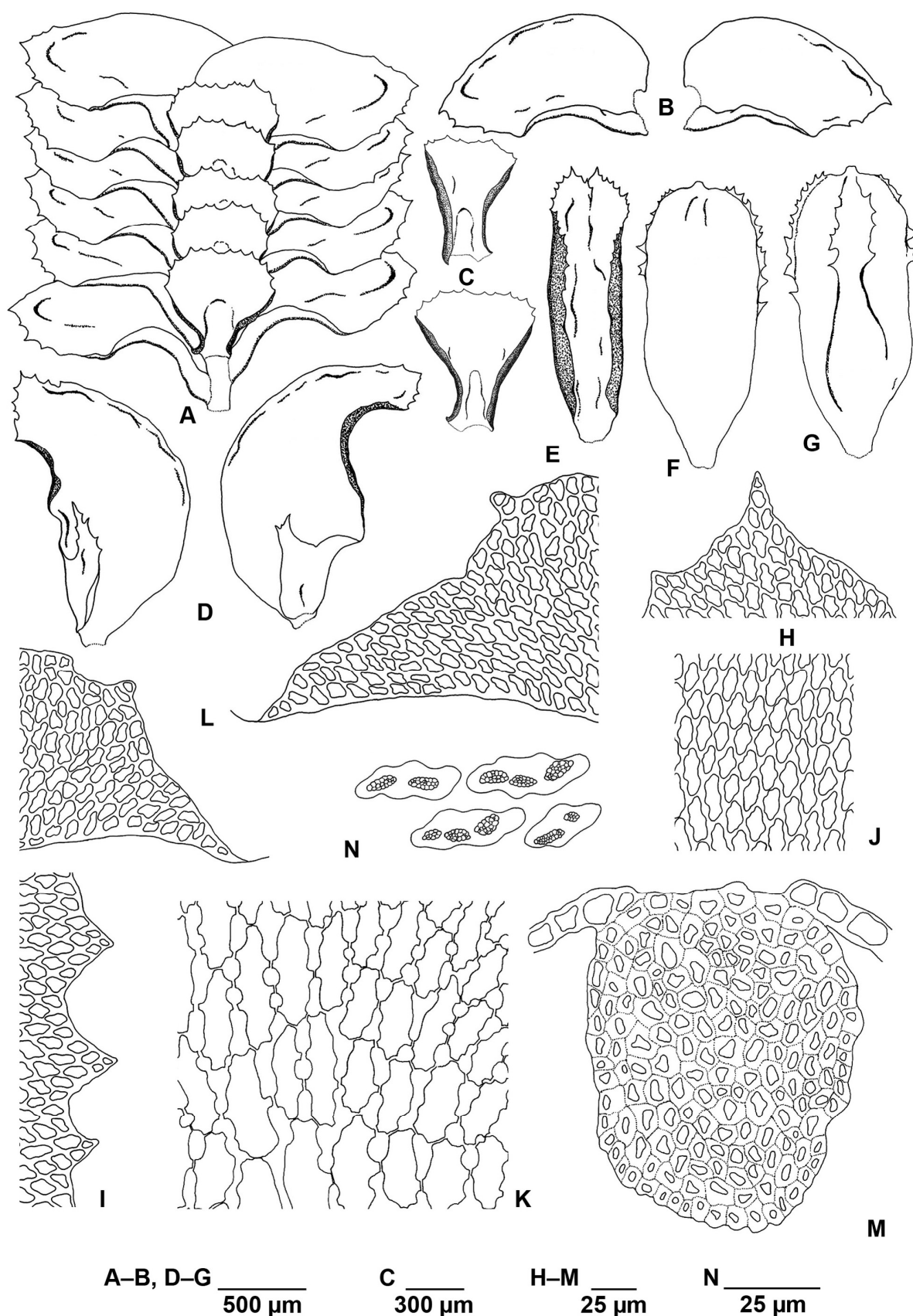


FIG. 18. *Thysananthus spathulistipus* (Reinw. et al.) Lindenb. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apex. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices. M. Cross section of stem. N. Oil bodies. (A–M from the holotype; N from *Sukkharak 716* (BKF, GOET)).

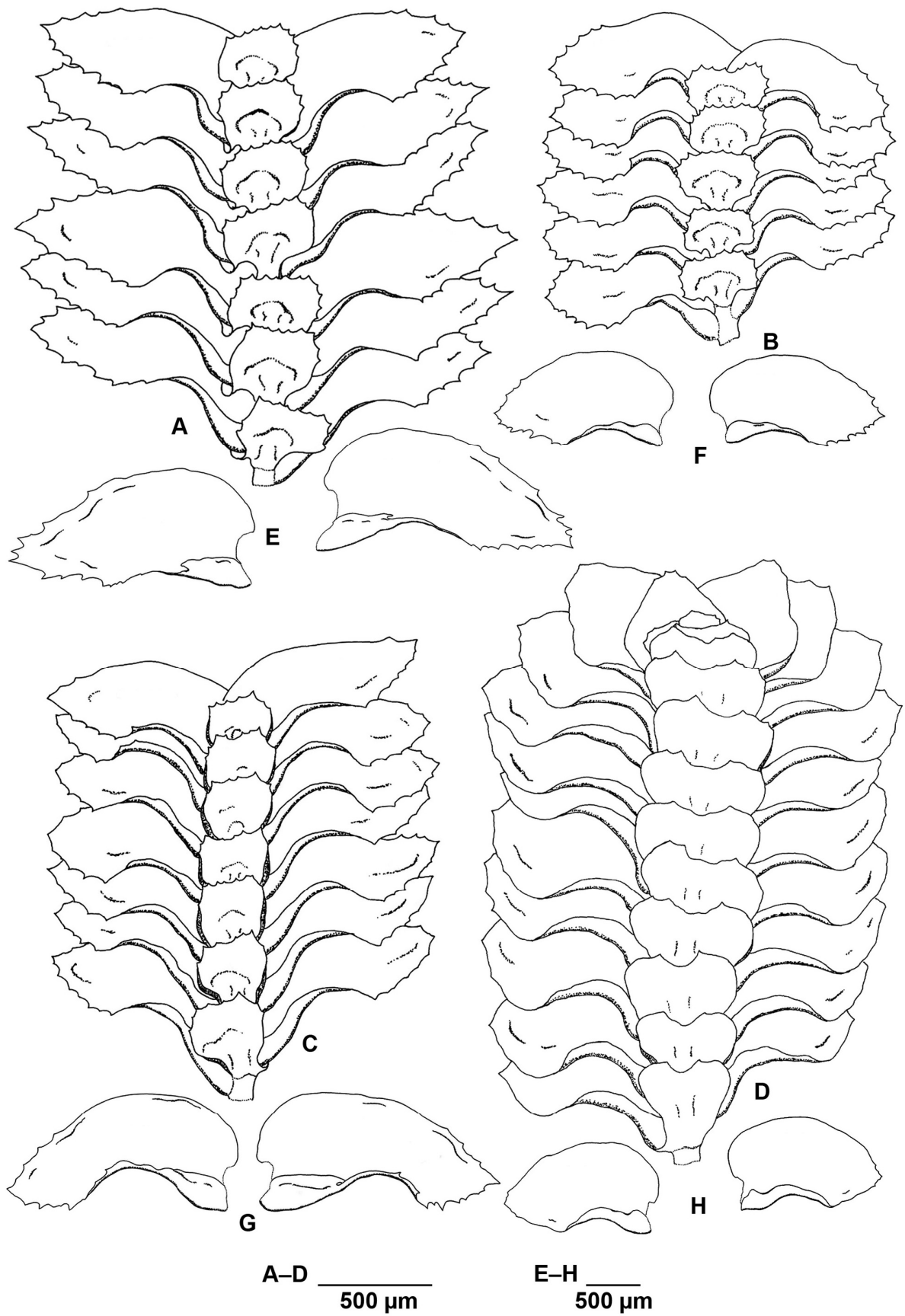


FIG. 19. *Thysananthus spathulistipus* (Reinw. et al.) Lindenb. A–D. Portion of shoot, ventral view. E–H. Leaves, ventral view. (A, E from the holotype of *T. spathulistipus* var. *borneensis*; B, F from holotype of *T. minor*; C, G from holotype of *T. fuscobrunneus*; D, H from holotype of *T. triquetrus*).

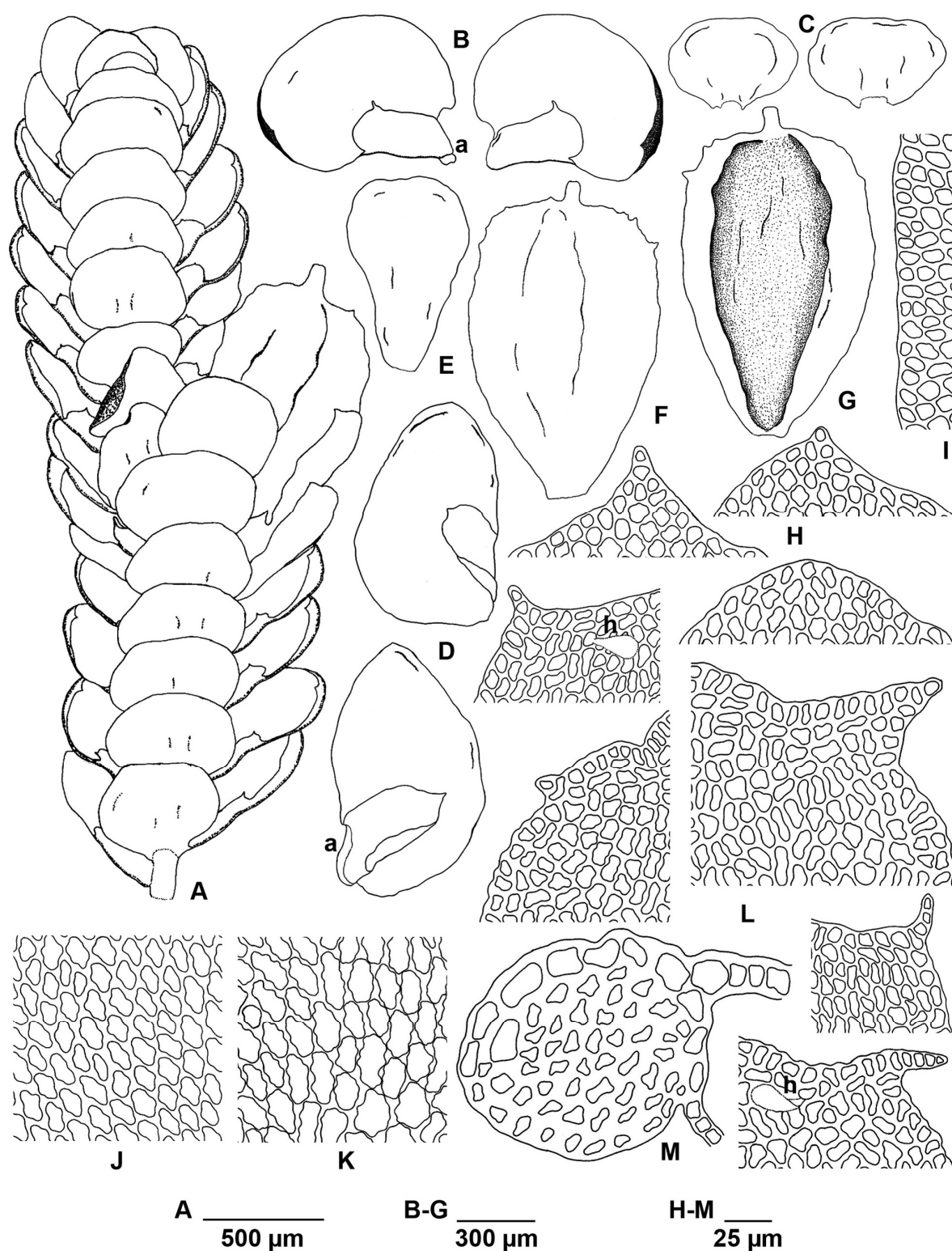


FIG. 20. *Thysananthus anguiformis* (Hook. f. & Taylor) Steph. A. Portion of shoot, ventral view. B. Leaves, ventral view: a = appendage. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apices. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices: h = hyaline papilla. M. Cross section of stem. (All from the lectotype).

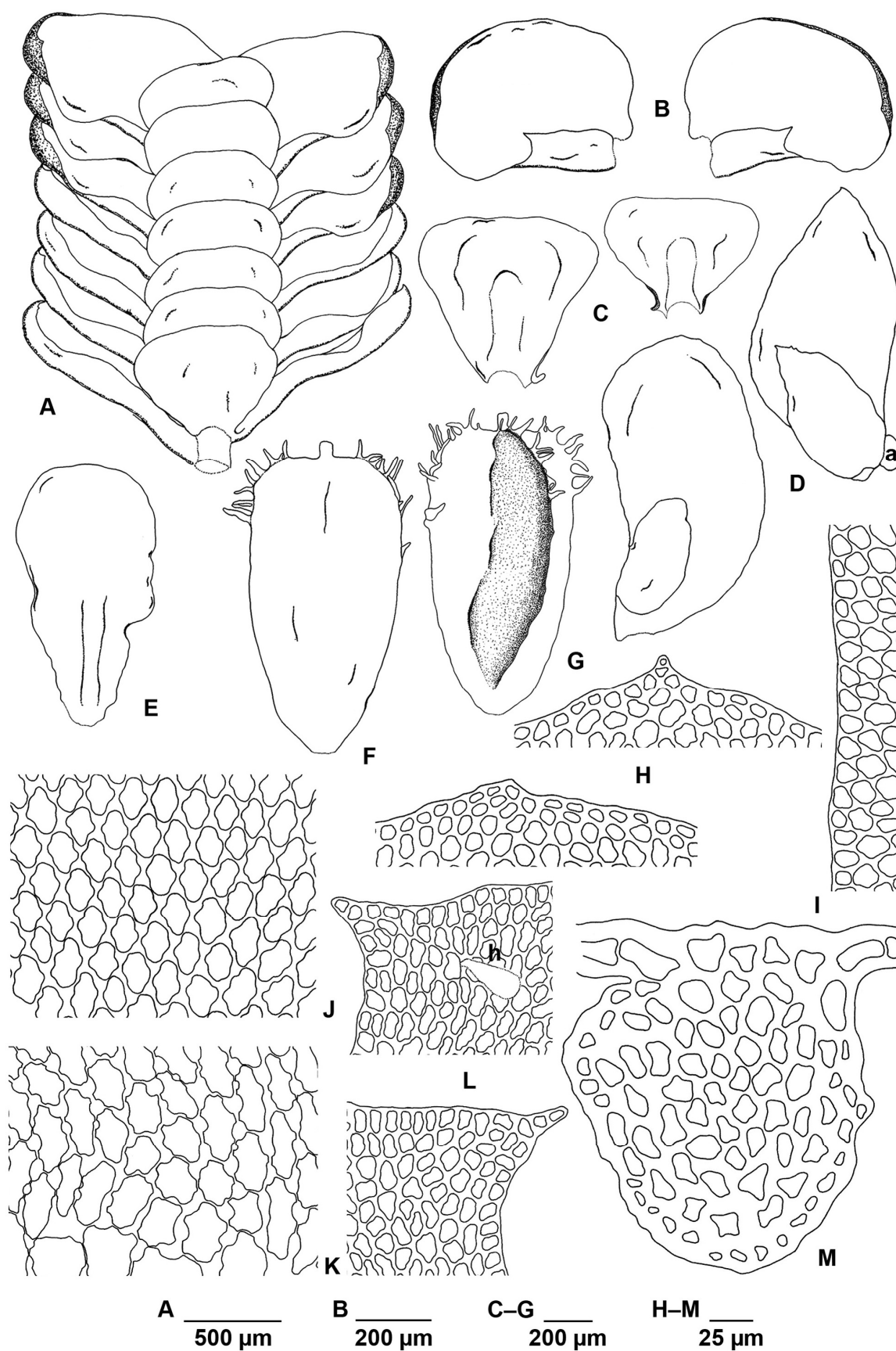


FIG. 21. *Thysananthus pancheri* (Steph.) Hürl. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apices. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices: h = hyaline papilla. M. Cross section of stem. (All from the lectotype).

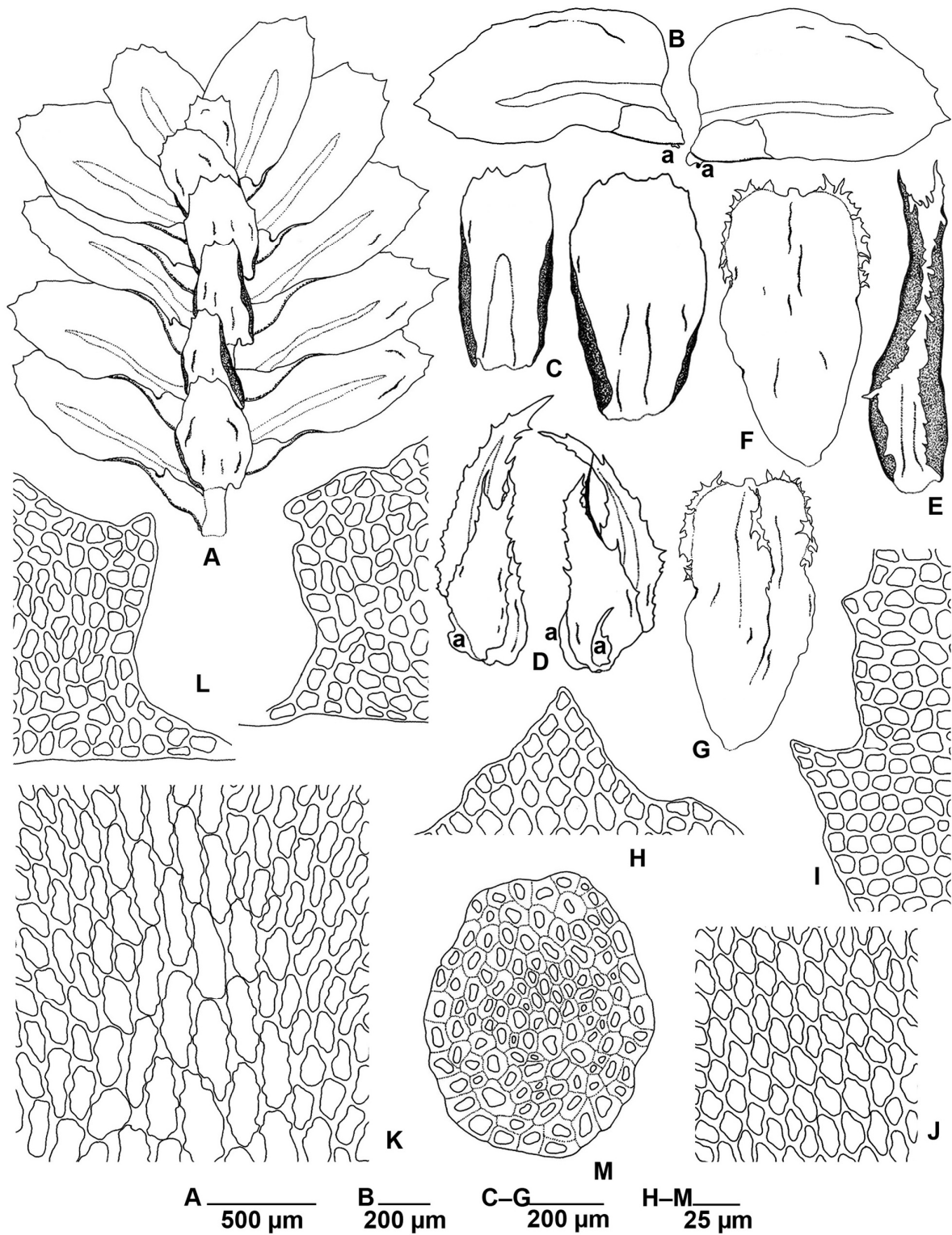


FIG. 22. *Thysananthus fruticosus* (Lindenb. & Gottsche) Schiffn. A. Portion of shoot, ventral view. B. Leaves, ventral view: a = appendage. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apex. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe, showing the vitta. L. Leaf lobule apices. M. Cross section of stem. (A–C, H–M from the lectotype; D–G from *Brass* 22185 (JE)).

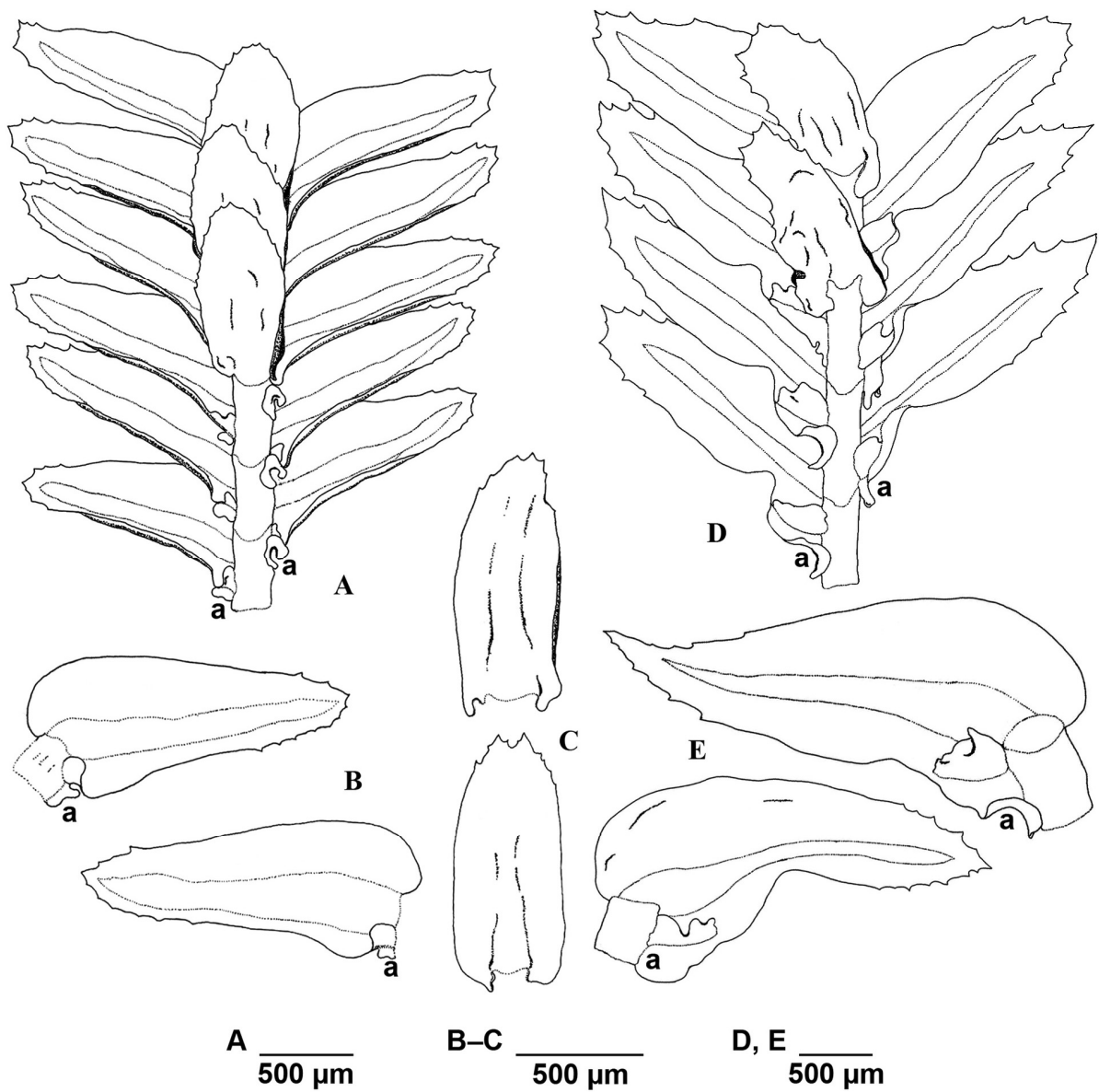


FIG. 23. *Thysananthus fruticosus* (Lindenb. & Gottsche) Schiffn. A–B. Portion of shoot, ventral view: a = appendage. C–D. Leaves, ventral view: a = appendage. E. Underleaves, ventral view. (A, C, E from *Beccari s.n.* (JE); D, E from *Streimann 25733* (JE)).

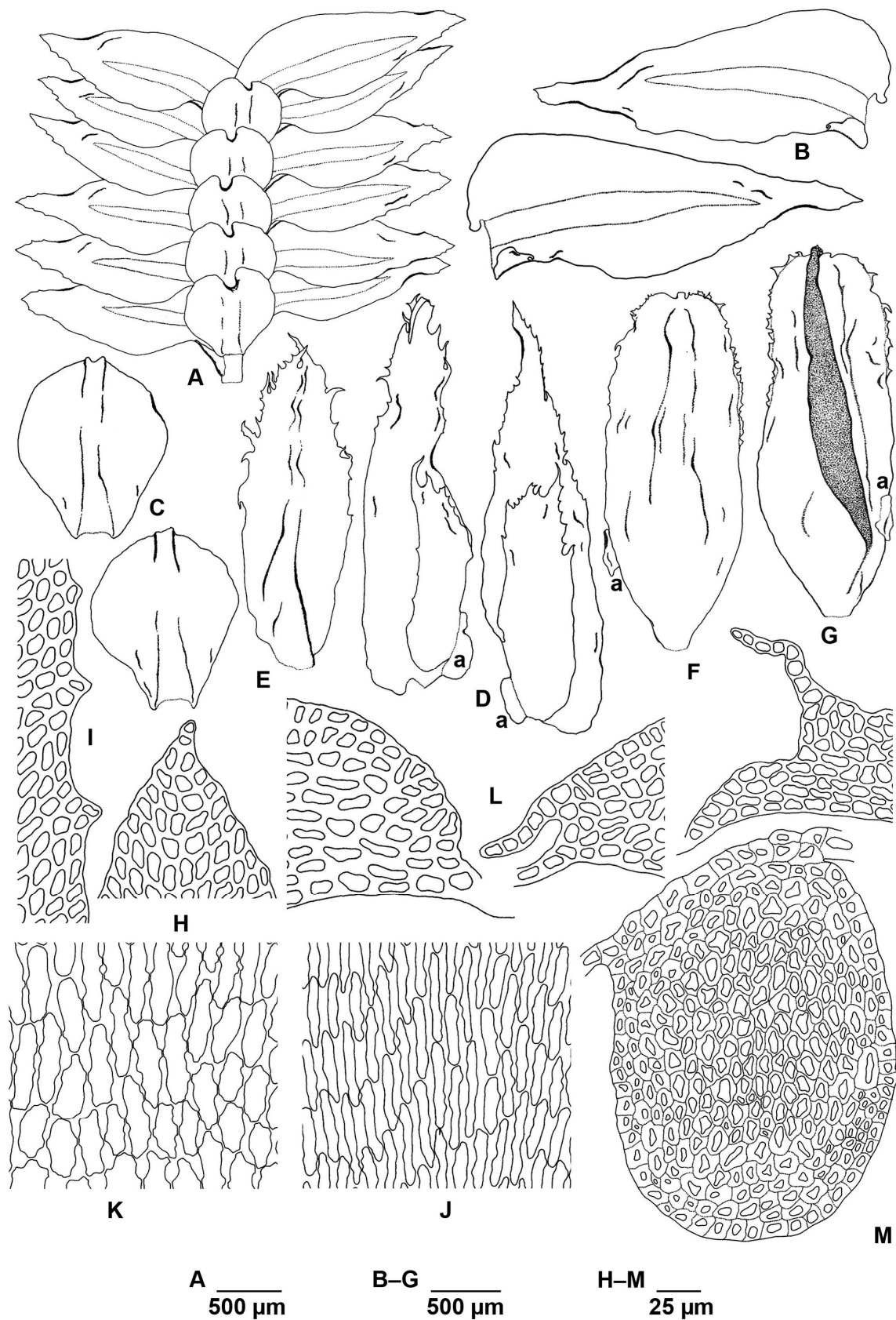


FIG. 24. *Thysananthus mollis* Steph. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view: a = appendage. E. Female bracteole, ventral view. F. Perianth, dorsal view: a = appendage. G. Perianth, ventral view, a = appendage. H. Leaf apex. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apices. M. Cross section of stem. (All the holotype).

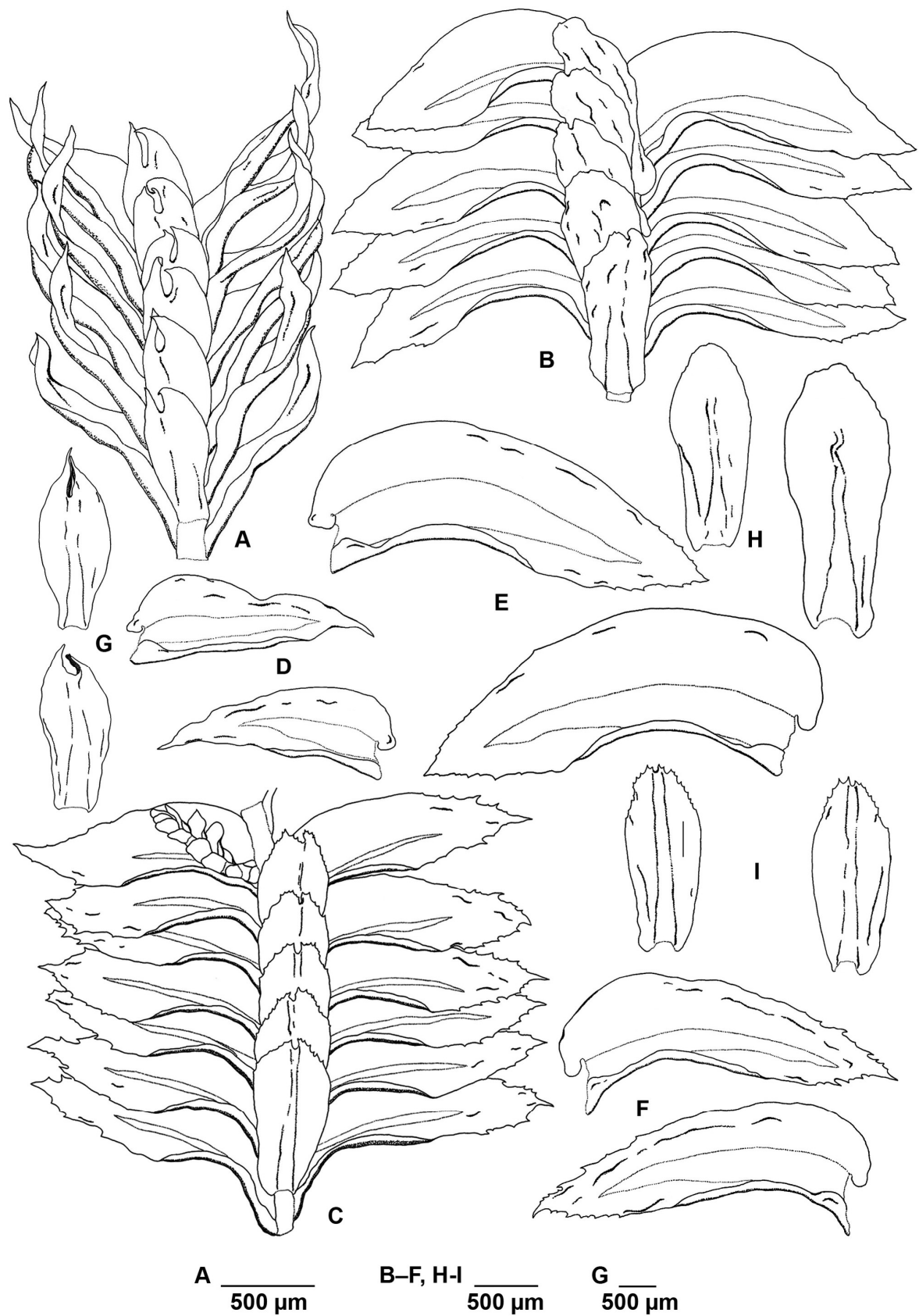


FIG. 25. *Thysananthus mollis* Steph. A–C. Portion of shoot, ventral view. D–F. Leaves, ventral view. G–I. Underleaves, ventral view. (A, D, G from Streimann & Bellamy 13049 (JE); B, E, H from Streimann 26631 (JE); C, F, I from Gradstein 3792 (GOET)).

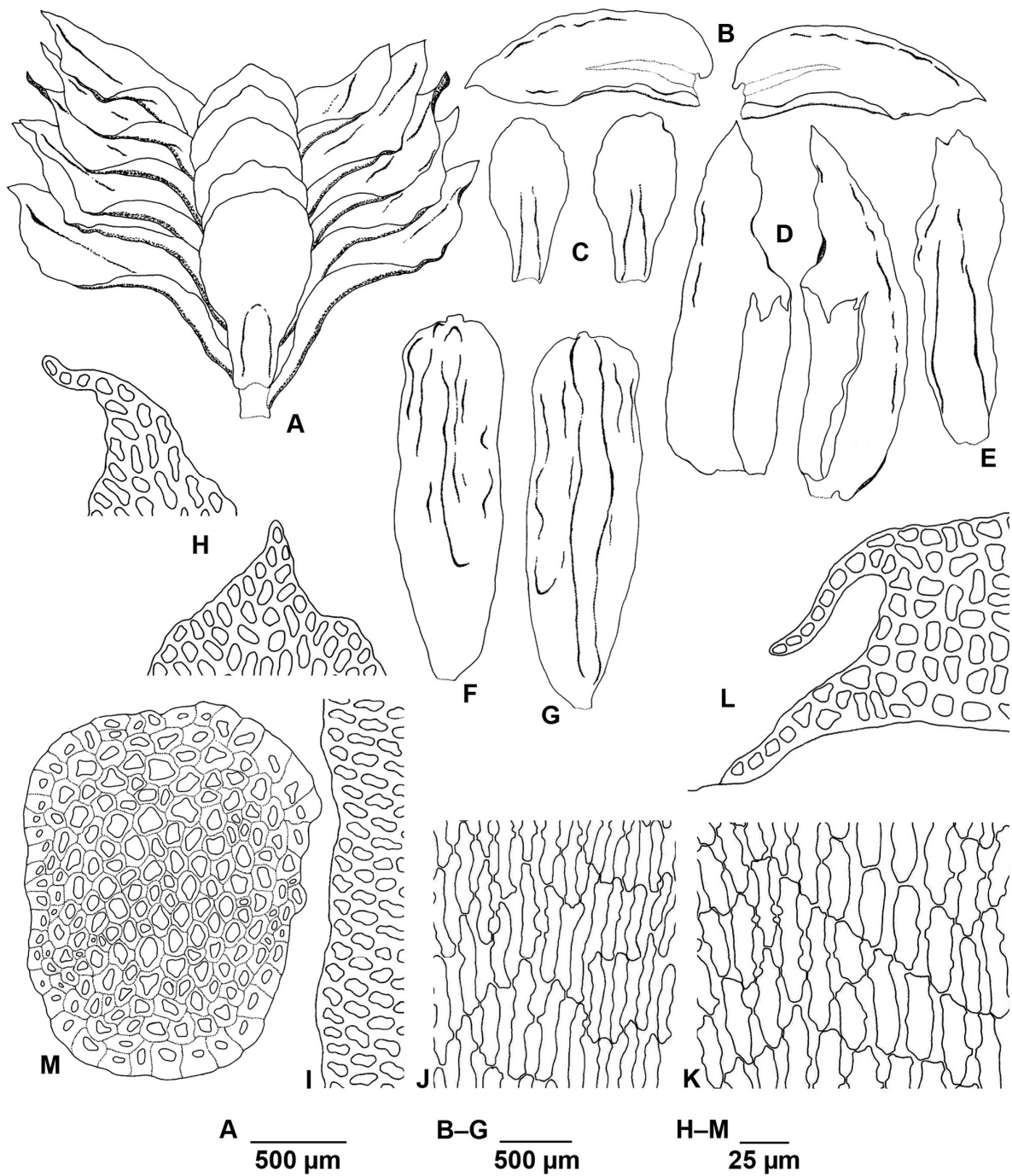


FIG. 26. *Thysananthus montanus* Gradst. et al. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view. E. Female bracteole. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apices. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe. L. Leaf lobule apex. M. Cross section of stem. (All from the holotype).

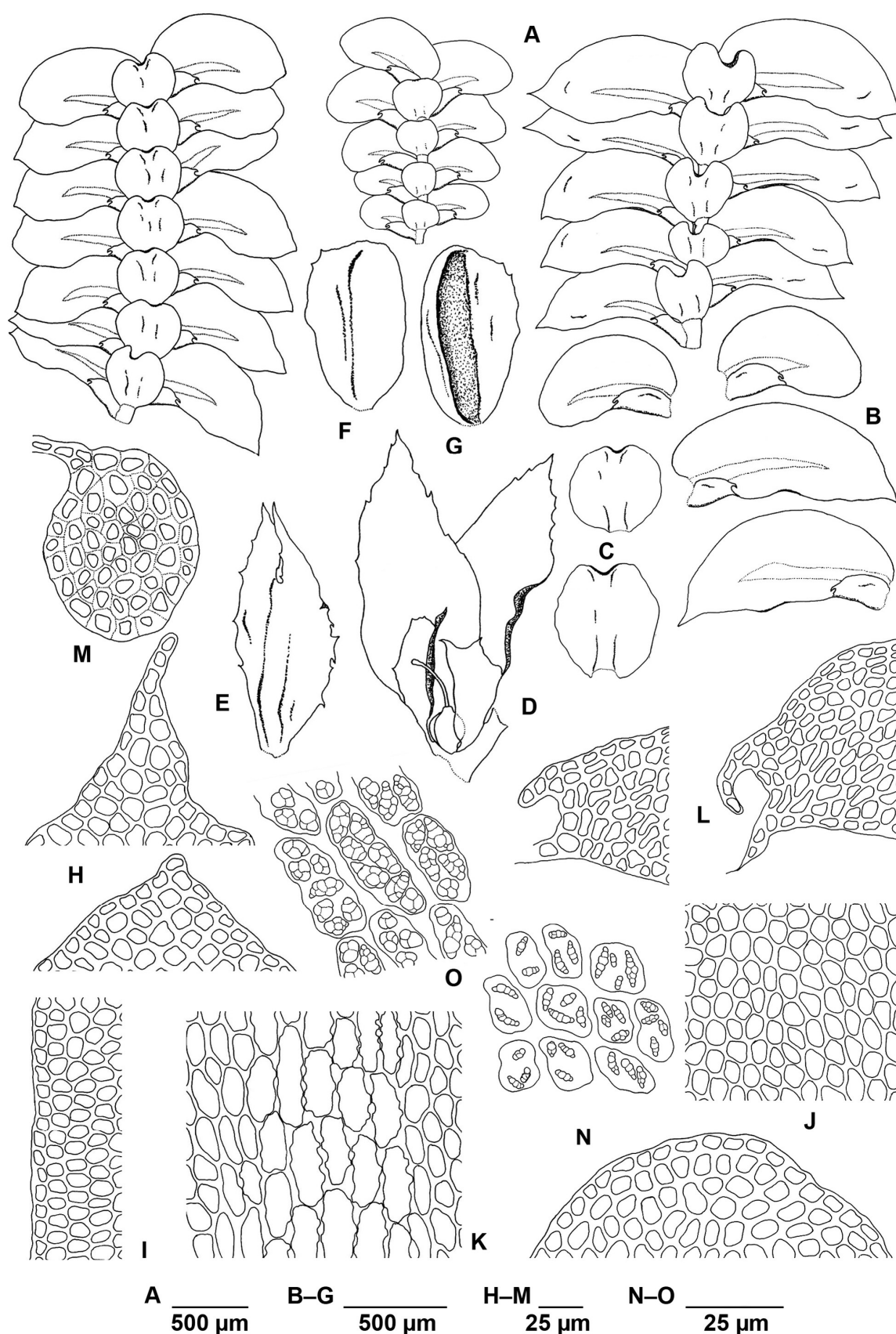


FIG. 27. *Thysananthus retusus* (Reinw. et al.) B. Thiers & Gradst. A. Portion of shoot, ventral view. B. Leaves, ventral view. C. Underleaves, ventral view. D. Female bracts, ventral view. E. Female bracteole, ventral view. F. Perianth, dorsal view. G. Perianth, ventral view. H. Leaf apices. I. Margin cells of leaf lobe. J. Median cells of leaf lobe. K. Basal cells of leaf lobe, showing the vitta. L. Leaf lobule apices. M. Cross section of stem. N. Oil bodies, non-vittate cells. O. Oil bodies, vittate cells. (A-M from the holotype; N-O from *Sukkharak 733* (BKF, GOET)).

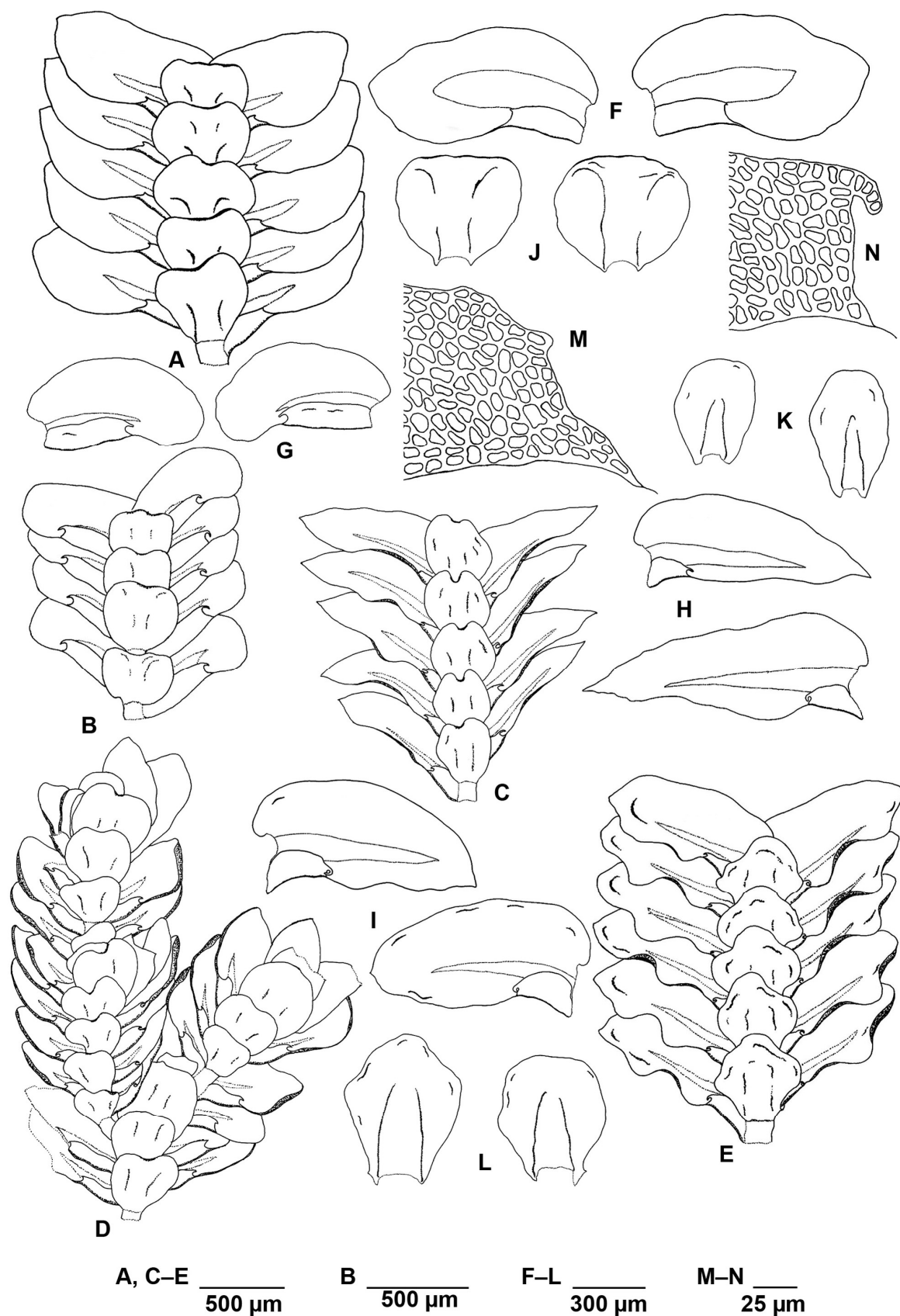


FIG. 28. *Thysananthus retusus* (Reinw. et al.) B. Thiers & Gradst. A–E. Portion of shoot, ventral view. F–I. Leaves, ventral view. J–L. Underleaves, ventral view. M–N. Leaf lobule apices. (A, F, J, M from the holotype of *T. australis*; C, H, K, N from *Gradstein 3963* (GOET); D, from the holotype; E, I, L from *Degelius 223* (JE).—*T. retusus* subsp. *sellingii* (Hürl.) comb. nov. B. Portion of shoot, ventral view. G. Leaves, ventral view. (All from the holotype).

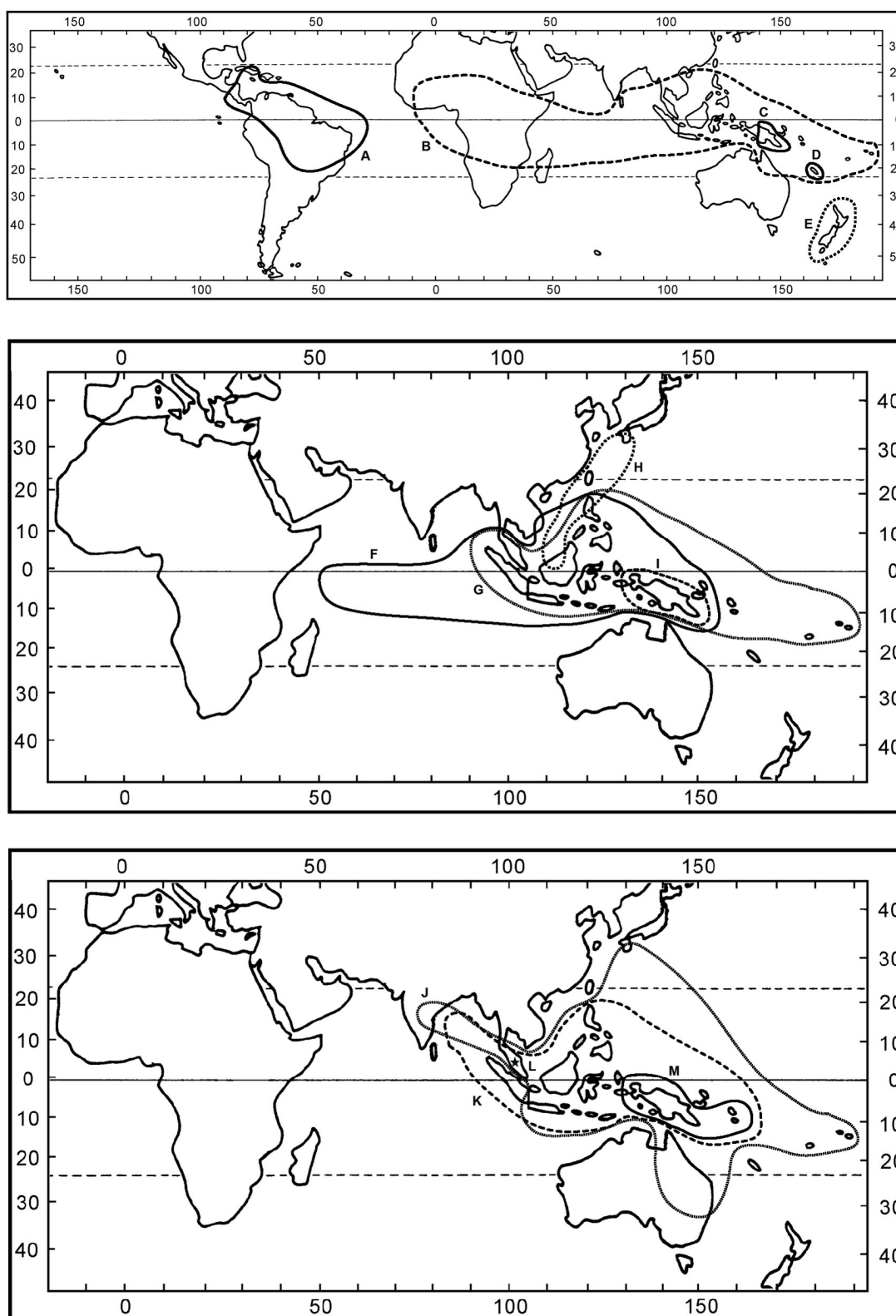


FIG. 29. Distribution of subg. *Thysananthus* species. A. *Thysananthus amazonicus* (Spruce) Schiffn. B. *Thysananthus spathulistipus* (Reinw. et al.) Lindenb. C. *Thysananthus mollis* Steph., *Thysananthus montanus* Gradst. et al. D. *Thysananthus pancheri* (Steph.) Hürl. E. *Thysananthus anguiformis* (Hook. f. & Taylor) Steph. F. *Thysananthus comosus* Lindenb. G. *Thysananthus fruticosus* (Lindenb. & Gottsche) Schiffn. H. *Thysananthus aculeatus* Herzog. I. *Thysananthus appendiculatus* Steph. J. *Thysananthus retusus* (Reinw. et al.) B. Thiers & Gradst. K. *Thysananthus convolutus* Lindenb., *Thysananthus gottschei* (Jack & Steph.) Steph. L. *Thysananthus combinatus* sp. nov. M. *Thysananthus discretus* Sukkharak & Gradst

DECLARATION OF THE AUTHOR'S OWN CONTRIBUTION TO THE PAPERS

I am the overall author of all manuscript presented in this thesis. I did not use any other sources as the ones indicated in the chapters. This thesis has not been submitted previously in any form for another degree at any university or institution.

Phiangphak Sukkharak
Göttingen, 27 April 2011

CURRICULUM VITAE

Name	Phiangphak Sukkharak
Born	7 March 1982, Nan, Thailand
05/1998 – 03/2001	Yupparaj Wittayalai School, Chiang Mai, Thailand supported by the Development and Promotion of Science and Technology talents project (DPST), a Royal Thai government scholarship.
05/2001 – 03/2005	B.Sc. in Biology, Chiang Mai University, Chiang Mai, Thailand. (2 nd Class Honors) supported by the Development and Promotion of Science and Technology talents project (DPST), a Royal Thai government scholarship.
05/2005 – 03/2008	M.Sc. in Botany, Chulalongkorn University, Bangkok, Thailand supported by the Development and Promotion of Science and Technology talents project (DPST), a Royal Thai government scholarship.
08/2008 – 06/2011	Ph.D in Biodiversity and Ecology, University of Göttingen supported by a Royal Thai government scholarship in cooperation with the German Academic Exchange Service (DAAD).
07/2011 onwards	Lecturer at Faculty of Science, Burapha University, Chonburi, Thailand.