A TAXONOMIC REVISION OF ORTHOTRICHACEAE (MUSCI) WITH CONTRIBUTIONS TO THE BIOSYSTEMATICS OF *MACROMITRIUM* BRID. IN MALAYSIA

YONG KIEN THAI

INSTITUTE OF BIOLOGICAL SCIENCES
FACULTY OF SCIENCE
UNIVERSITY OF MALAYA
KUALA LUMPUR, MALAYSIA

2010

A TAXONOMIC REVISION OF ORTHOTRICHACEAE (MUSCI) WITH CONTRIBUTIONS TO THE BIOSYSTEMATICS OF *MACROMITRIUM* BRID. IN MALAYSIA

YONG KIEN THAI

A THESIS SUBMITTED IN FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

INSTITUTE OF BIOLOGICAL SCIENCES
FACULTY OF SCIENCE
UNIVERSITY OF MALAYA
KUALA LUMPUR, MALAYSIA

2010

ABSTRACT

Macromitrium (Orthotrichaceae) is a large genus variously divided into infrageneric groups by different authors, resulting in a complex classification which has not included many Malaysian species. This study reviews the taxonomy of Malaysian taxa and extent of morphological variation in relation to the type group. A molecular phylogenetic study was carried out to determine if Malaysian *Macromitrium* species represented a homogeneous taxonomic grouping. A cladistic analysis of morphological characteristics was attempted for identifying well-defined groups and their key character states. Molecular studies included Maximum Parsimony and Bayesian Inference analyses of two chloroplast DNA regions (*rps*4 gene and *trn*L-*trn*F interspecific region) for an Orthotrichaceae ingroup including representative Orthotrichoideae and Macromitrioideae, the latter comprising various genera and ten Malaysian, and two extra-Malaysian, species of *Macromitrium*. The outgroup included Bartramiaceae, Bryaceae, Calymperaceae, Dicranaceae, Hedwigiaceae, Pottiaceae and Rhizogoniaceae from other orders. A total of 27 species and three varieties in six genera were enumerated for the Orthotrichaceae. The majority (17 species including 3 varieties) are in *Macromitrium*. An identification key, species descriptions, notes and illustrations are provided. Two new species (*Desmotheca mohamedii* ined. and *Groutiella kelantanense* ined.) and two new varieties (*Macromitrium longipilum* var. *ligulatum* ined. and *M. longipilum* var. *rugosum* ined.) are proposed. All Orthotrichaceae taxa in Malaysia (including seven endemics) are tropical in origin, with nearly half restricted to Malesia. The remainder are mainly Asiatic, except a paleotropical species and three pantropical species. The molecular analyses resolved both subfamilies Orthotrichoideae and Macromitrioideae as sister clades, with *Leratia* basal to them in the Maximum Parsimony analysis and hence of uncertain position in the current subfamilial classification. Both large genera, *Orthotrichum* (Orthotrichoideae) and *Macromitrium* (Macromitrioideae) were paraphyletic, with several species-groups (including the type group) being resolved by the molecular analyses as different clades. The morphological cladistic analysis identified the same monophyletic type group with a divided peristome and sparsely hairy calyptra as shared group characters but it was not possible to regard these as true synapomorphies because two other putative Macromitrioideae genera (*Macrocoma* and *Matteria*) that also had these character states were not included in the analysis. In the molecular study, *Zygodon* (including *Pleurorthotrichum*) and *Schlotheimia* were resolved as monophyletic groups. The relationships among *Desmotheca*, *Groutiella* and *Macromitrium*, as well as other related genera, remain unclear, as there was generally poor resolution in the molecular phylogenetic study. Overall, it was possible to affirm the distinctness of the two subfamilies of Orthotrichaceae, the basal uncertain position of *Leratia*, the heterogeneous nature of both *Orthotrichum* and *Macromitrium*, and the apparent distinctness of the smaller genera *Zygodon* (including *Pleurorthotrichum*) and *Schlotheimia*. The positions of *Sehnemobryum*, *Stoneobryum*, *Nyholmiella*, *Ulota*, *Desmotheca* and *Groutiella* remain unclear. There was insufficient resolution in both morphological and molecular analyses to support any of the infrageneric groups proposed for *Macromitrium* thus far. The present study provides only a regional perspective of this speciose pantropical genus, so that a more complete understanding of the phylogeny and classification of *Macromitrium* would only be possible with a wider taxon sampling and the use of more informative gene regions.

ABSTRAK

Macromitrium (Orthotrichaceae) merupakan genus yang besar merangkumi beberapa kumpulan infragenerik dan pengelasan yang kompleks, akan tetapi kedudukan spesiesnya yang terdapat di Malaysia masih kurang difahami. Kajian ini memberi satu tinjauan taksonomi jenis-jenis yang terdapat di Malaysia dan variasi morfologi berbanding dengan kumpulan tipnya. Kajian filogenetik molekul dilakukan untuk menentukan sama ada spesies *Macromitrium* Malaysia mewakili pengelompokan taksonomi yang homogenus. Kajian kladistik ke atas ciri morfologi juga dilakukan untuk mengenalpasti kumpulan yang jelas dan ciri penyifatnya. Kajian molekul dilakukan menurut analisis "Maximum Parsimony" dan "Bayesian Inference" ke atas dua kawasan DNA kloroplas (gen rps4 dan kawasan interspesifik trnL-trnF) untuk kumpulan dalaman Orthotrichaceae termasuk Orthotrichoideae dan Macromitrioideae, juga pelbagai genus Macromitrioideae bersama sepuluh spesies *Macromitrium* dari Malaysia dan dua spesies luar negara. Kumpulan luaran termasuk Bartramiaceae, Bryaceae, Calymperaceae, Dicranaceae, Hedwigiaceae, Pottiaceae dan Rhizogoniaceae dari pelbagai order yang lain. Sejumlah 27 spesies dan tiga varieti dalam enam genus Orthotrichaceae dapat dicamkan. Dari jumlah ini kebanyakannya (17 spesies termasuk 3 varieti) merupakan *Macromitrium*. Kekunci pengecaman, keterangan spesies, nota dan ilustrasi diberikan. Dua spesies baru (*Desmotheca mohamedii* ined. dan *Groutiella kelantanense* ined.) dan dua varieti baru (*Macromitrium longipilum* var. *ligulatum* ined. dan *M. longipilum* var. *rugosum* ined.) dikemukakan. Segala takson Orthotrichaceae di Malaysia (termasuk tujuh jenis yang endemik) berasal dari wilayah tropika dan hampir separuhnya terhad di Malesia. Yang lain merupakan jenis Asiatik, kecuali satu spesies paleotropika dan tiga spesies pantropika. Kajian molekul dapat mengecamkan subfamili Orthotrichoideae dan Macromitrioideae sebagai klad jiran yang jelas, manakala *Leratia* berkedudukan pangkal di sampingan mereka dalam analisis "Maximum Parsimony" maka kedudukannya masih kurang jelas dalam pengelasan subfamili. Kedua-dua genus yang besar iaitu *Orthotrichum* (Orthotrichoideae) dan *Macromitrium* (Macromitrioideae) disahkan sebagai parafiletik, juga beberapa kumpulan spesies *Macromitrium* (termasuk kumpulan tip) menduduki klad-klad yang berlainan menurut analisis molekul. Analisis kladistik morfologi juga mengecamkan kumpulan monofiletik tip yang khas dicirikan oleh peristom terbahagi dan kaliptra yang berbulu jarang, akan tetapi ciri-ciri tersebut tidak terus dianggap sebagai ciri sinapomorfi yang benar sebab ia juga hadir dalam dua lagi takson (*Macrocoma* dan *Matteria*) yang dianggap sebagai genus Macromitrioideae. Akibat kajian molekul, *Zygodon* (termasuk *Pleurorthotrichum*) dan *Schlotheimia* disahkan sebagai kumpulan monofiletik. Hubungan antara *Desmotheca*, *Groutiella* dan *Macromitrium* serta genera berkaitan yang lain masih kurang jelas kerana resolusi analisis filogenetik molekul tidak mencukupi. Pada keseluruhannya kedua-dua subfamili Orthotrichaceae dapat disahkan sebagai kumpulan yang jelas, kedudukan *Leratia* adalah sebagai takson pangkalan yang masih belum difahami dengan baik, kedua-dua *Orthotrichum* dan *Macromitrium* adalah heterogenus, dan genus kecil seperti *Zygodon* (termasuk *Pleurorthotrichum*) dan *Schlotheimia* boleh diterima sebagai takson yang jelas. Kedudukan taksonomi *Sehnemobryum*, *Stoneobryum*, *Nyholmiella*, *Ulota*, *Desmotheca* dan *Groutiella* masih kurang pasti. Resolusi dari analisis morfologi dan molekul tidak memadai untuk menyokong sebarang pengelasan infragenerik *Macromitrium* yang ada. Kajian pada masa ini cuma memberikan satu perspektif serantau untuk genus pantropikal tersebut yang mengandungi banyak spesies. Maka kefahaman yang lebih lengkap mengenai filogeni dan pengelasan *Macromitrium* hanya akan diperolehi dengan penyampelan takson yang lebih meluas dan penggunaan kawasan gen yang lebih banyak memberi maklumat.

ACKNOWLEDGEMENTS

I would like to express my utmost gratitude to my supervisors, Professor Dato Haji Mohamed Abdul Majid and Professor Amru Nasrulhaq Boyce for their guidance, advice and patience throughout the study. I would also like to express my gratitude to Professor Wong Khoon Meng who provided me with much critical advice and suggestions, and to Professor Phang Siew Moi for allowing me to use her laboratory facilities to carry out the molecular work. Many thanks to Dr. Paulo Camara from Universidade de Brasilia, Brazil, Dr. Ho Boon Chuan, Mr. Hiroaki Masuzaki and Ms Sim Mei Chia who have provided me much invaluable advice for the molecular work.

I would also like to express my appreciation to Professor Robbert Gradstein, Professor Datin Lim Ah Lan, Emeritus Professor Yong Hoi Sen, Mdm. Patricia Low, Ms. Gan Hui Hoon, Ms. Cheng Pei Leng, Mr. Low Yee Wen, Mr. Sugumaran Manickam and others in the Institute of Biological Sciences who have helped me in one way or another.

I thank the curators of the following herbaria for the loan of specimens: BM, BORH, HIRO, KLU, NICH, NY, PC, S, SING, SINU, TNS, and UKMB. This research was financially supported through grants from the University of Malaya and the Malaysia Toray Science Foundation. I also wish to acknowledge the Faculty of Science, University of Malaya for providing me with a teaching position in the Institute of Biological Sciences.

Last but not least, I would like to thank my friends for all their encouragement and most importantly, my family, for all the support they have provided.

TABLE OF CONTENTS

Page

Chapter 1: Introduction

Chapter 2: Literature review

Chapter 3: Material and methods

Chapter 4: Morphology and anatomy

Chapter 5: Taxonomic treatment

Chapter 6: Molecular phylogenetic analyses and a cladistic morphological study

Chapter 7: General conclusions

LIST OF FIGURES

LIST OF TABLES

ABBREVIATIONS

The abbreviations for authority and publication in the nomenclature follow that of Brummit & Powell (1992) for names and authors, and Stafleu & Cowan (1976-1988) for literature citation. Common abbreviations used in the thesis are listed as below:

alt.	altitude
DNA	deoxyribonucleic acid
e.g.	for example
excl.	excluding
Fig.	Figure
Gg.	*Gunung* (Malay word for mountain)
i.e.	that is
Kg.	*Kampung* (Malay word for village)
Mt.	Mount
p.	page
pl.	plate
Prov.	Province(s)
Rd.	Road
s.coll.	*sine collector* (without collector)
s.date	*sine date* (without date)
s.lat.	*sensu lato* (in a broad sense)
s.n.	*sine numero* (without number)
s.str.	*sensu stricto* (in a strict sense)
sect.	section
SEM	Scanning Electron Microscope
Sg.	*Sungai* (Malay word for river)
sp. nov. ined. prop.	proposed new species, unpublished
sp.	species
syn.	synonym
tab.	tabula
var. nov. ined. prop.	proposed new variety, editing
var.	variety
viz.	namely

CHAPTER 1

INTRODUCTION

1.1 General introduction

Members of the Orthotrichaceae are usually found growing on exposed rock or as epiphytes on tree trunks or, more often, on tree branches at the canopy level, where there is most exposure to sunshine and wind. Thus, these mosses are more-or-less xerophytic and relatively well adapted to dry habitats compared to many other bryophytes, which only thrive well in constantly damp or moist habitats. Members of the Orthotrichaceae can be found in a wide range of elevation, from sea level to highlands but are more diverse in highland areas. The family is nearly cosmopolitan in distribution, represented by nearly 600 species in 22 genera of two subfamilies (Goffinet & Vitt, 1998). Among the two subfamilies, namely Orthotrichoideae and Macromitrioideae, the former is mainly distributed in temperate countries, whereas the latter subfamily is chiefly found in the tropics.

The Orthotrichaceae are characterized by an acrocarpous or cladocarpous habit (bearing capsules at stem or branch tips), numerous subperichaetial (beneath the perichaetia) branches, and leaves that are variously twisted-contorted to strongly inrolled when dry, but plane and spreading to squarrose-recurved when wet. Cells in the more distal parts of the leaf are usually small and often papillose, leaf base cells are usually longer and more hyaline, and alar cells are not differentiated. The erect capsules are often ribbed, either emerged or immersed, and usually have mitriform, smooth or hairy calyptrae. The peristome is diplolepidous (with jointed teeth, where the outer face of each segment is formed from remnants of the walls of two cells) and highly modified, and highly diverse in morphology across the family (Shaw, 1986); it often appears single due to the suppression of either the exostome or the endostome teeth.

Regional revisions for a number of genera in the Orthotrichaceae have been completed for Australasia, Japan, Southern China (particularly Hunan Province), South Africa and North America (Guo et al., 2004, 2007; Iwatsuki, 1959; Lewinsky, 1984, 1992; Noguchi, 1967, 1968; Rooy & Wyk, 1992; Vitt, 1973, 1983, 1989, 1990; Vitt & Ramsay, 1985; Vitt et al., 1993, 1995). Notwithstanding these, a significant number of the taxa in this study require reference to the published floras for Eastern India and adjacent areas (Gangulee, 1976), the Phillipines (Bartram, 1939), Java (Dozy & Molkenboer, 1861; Fleischer, 1904) and Malesia in general (Eddy, 1996). There is still no proper monograph of the Orthotrichaceae of Malaysia (including Sabah and Sarawak), a significant part of West Malesia (Steenis, 1950).

Lewinsky (1992) pointed out that revision of the genera of Orthotrichaceae has normally resulted in a reduction of recognized species of at least 50%. For the Australasian *Orthotrichum*, 74 species and two variety names in the literature have been reduced to a mere 9 species and 3 varieties after revision (Lewinsky, 1984). Also a total of 95 names for the Australasian *Macromitrium* has been assigned to just 33 taxonomically distinct taxa (Vitt & Ramsay, 1985). In the case of New Zealand, 15 taxonomically recognizable species of *Macromitrium* have had 47 different names applied to them (Vitt, 1983). Hence, because of the existence of an extensive number of published names, there is a need for careful work in order to know the real number of species of Orthotrichaceae in Malaysia.

Recently, Goffinet and his team published a series of works (1998, 2004) addressing the generic classification in the Orthotrichaceae, based on the molecular phylogeny and a comparative morphological study. A few changes have been proposed that affect some of the genera reported for Malaysia. However, due to the inclusion of only three out of 42 reported taxa for Malaysia in these studies, there remain many uncertainties about this group in Malaysia. Correspondingly, it would be worthwhile to extend such studies to understand the circumscription and phylogeny of taxa reported for Malaysia.

1.2 Objectives

The present study aimed mainly to revise the Orthotrichaceae of Malaysia, comprising the territories of Peninsular Malaysia, Sabah and Sarawak. Material of Malaysian taxa that also occur outside of the country but still within Malesia was included for study, contributing to verification of their geographical distribution and assessment of possible variation.

Another objective of this study was to discover general taxonomic characters that may reflect the phylogeny of the group. Related to this is the possible use of an improved classification as the basis for a workable identification key for Malaysian Orthotrichaceae.

These objectives are supported by cladistic studies utilizing both DNA sequence data and morphological data, performed in an attempt to identify evolutionary trends among Malaysian Orthotrichaceae.

CHAPTER 2

LITERATURE REVIEW

2.1 Taxonomic history and geographical distribution of the Orthotrichaceae

The Orthotrichaceae is among the earliest recognized moss families, with the name first used by Arnott (1825). This was derived from the type genus *Orthotrichum* established by Hedwig (1790) and which was later included in his *Species Muscorum Frodonsorum* (Hedwig, 1801), the first comprehensive work on the nomenclature of mosses. With a long history of study and cosmopolitan distribution, the Orthotrichaceae now includes many taxa showing a wide variety of form and structure, and is known as one of the most diverse families of mosses (Vitt, 1982a; Goffinet & Vitt, 1998).

Brotherus (1925) enumerated 14 genera and 939 species of mosses for the Orthotrichaceae. Sixty years later, in a general account of the genera of Orthotrichaceae, Vitt (1982a) also listed 14 genera but with only about 550 species. Later in 1984, Vitt expanded the family to include 21 genera, and soon after that, 27 genera, after additional genera were transferred from Pottiaceae (Vitt, 1993; Zander, 1993) and several new genera were established by various authors (Norris & Robinson, 1981; Lewinsky-Haapasaari, 1994; Lewinsky-Haapasaari & Crosby, 1996). More recently, after extensive generic revision (Goffinet, 1997a) and guided by related molecular evidence (Goffinet et al., 1998; Stech, 1999), the family is now accepted as having 20 genera with about 600 species worldwide (Goffinet & Vitt, 1998).

Brotherus (1925) was the first person to subdivide the Orthotrichaceae into four subfamilies; this was also adopted by Vitt (1982a) with little modification. The division into subfamilies was based on the characters of calyptra shape, stem growth direction and the perichaetial position. However, recent phylogenetic findings based on molecular evidence and comparative morphology (Goffinet, 1998; Gofinet et al., 1998) have led to the conclusion that a better classification would include only two subfamilies, each composed of two tribes (Goffinet & Vitt, 1998), viz., the Orthotrichoideae (with tribes Zygodonteae and Orthotricheae), and the Macromitrioideae (with tribes Schlotheimieae and Macromitrieae).

Subfamily Orthotrichoideae is represented by taxa with orthotropic stems and sympodial branching, of dioicous (producing antheridia and archegonia on separate plants) or monoicous (producing antheridia and archegonia on the same plant) sexuality, or both (but never phyllodioicous (with dwarf male plants growing on the leaves of female plants)), and mostly of acrocarpous (bearing sporophytes at the tips of main stems) habit. In contrast, Subfamily Macromitrioideae is characterized by plagiotropic stems and frequently monopodial branches, a phyllodioicous (rarely dioicous or monoicous) condition, and a mostly cladocarpous (bearing sporophytes at the tips of branches) habit. The apparently markedly different life forms of these two subfamilies has led Churchill and Linares (1995) to recognize the Macromitrioideae as a distinct family. However the concept is not widely accepted and recent cladistic analysis based on rbcL sequences (Goffinet et al., 1998) support a monophyletic Orthotrichaceae as earlier defined. As such, a broader family concept, Orthotrichaceae *sensu lato*, is followed in the present study.

The Orthotrichoideae are nearly cosmopolitan, occupying a wide diversity of habitats from the tropics to sub-polar regions, with most members found in the temperate regions. On the other hand, the Macromitrioideae are mainly tropical to subtropical in distribution, with some representatives in temperate areas, and do not extend far towards sub-polar regions. In Malesia generally, as well as in Peninsular Malaysia and Borneo, the family representation is predominantly of subfamily Macromitrioideae (about 88%, unpublished data). Presently, there are less than 15 Orthotrichoideae members reported for Malesia, all from highland forest of the upper montane to alpine elevation zones. Many of them are local endemics, with most records from New Guinea (Lewinsky, 1992; Vitt et al., 1993; Eddy, 1996).

The two largest genera of the family are *Macromitrium* Brid. and *Orthotrichum* Hedw., which contribute more than 2/3 of the taxa. *Macromitrium* (with 368 accepted specific names fide Crosby et al., 1999) is mostly tropical to subtropical in distribution, and is more common in the southern hemisphere. Meanwhile, *Orthotrichum* (145 species) is mainly found in temperate regions with more representatives from the northern hemisphere. The other three major genera in the family are *Schlotheimia* (121 spp.), *Ulota* (57 spp.) and *Zygodon* (91 spp.). *Schlotheimia* is pantropical, *Ulota* is mainly temperate, and *Zygodon* has a wide distribution in the tropics and subtropics, extending to temperate regions. Eight out of the 20 Orthotrichaceae genera have been recognized for the Malesian region (Lewinsky, 1992; Vitt et al, 1993, 1995; Eddy, 1996). Besides the five major genera mentioned above, there are also representatives of *Desmotheca* (endemic to Southeast Asia), *Groutiella* (pantropical) and *Macrocoma* (widespread from tropical to temperate areas of both hemispheres) in Maleisa. These latter three are the smaller genera in the family that include only a small number of species overall.

2.2 Taxonomic position

Orthotrichaceae is the type family for the order Orthotrichales, in which it was formerly grouped with four other families, i.e., Erpodiaceae Broth., Helicophyllaceae Broth., Microtheciellaceae Miller & Harrington, and Rhachitheciaceae Robinson. All these families were later excluded from the Orthotrichales and transferred to different orders or even subclasses (Goffinet, 1998; Goffinet & Buck, 2004). The result was that the Orthotrichaceae remained as the sole family in the Orthotrichales of Subclass Bryidae, Class Bryopsida. By excluding the four other families, this order is now restricted to taxa with an acrocarpous or cladocarpous habit, stems without central conducting tissue, typically papillose lamina cells, erect capsules, diplolepidous peristomes and recurved exostomes.

Peristomial morphology and ornamentation characters have long been considered as taxonomically useful and have been extensively used in moss classification (Mitten, 1859; Fleischer, 1904; Brotherus, 1925). The peristome of the Orthotrichales is known to be diplolepideous, i.e., with the following characters: "an endostome with segments that alternate with exostome teeth; lack of basal membrane and with segments, which are not or are rarely keeled; and an exostome that has a thick, outer layer and a thin, inner layer" (Vitt, 1982a). Based on a study of 21 Orthotrichaceae species, Shaw (1986) proposed a peristome formula for the Orthotrichaceae of 4: 2: 2-4, a diplolepideous arrangement. He also suggested that the high frequency of rudimentary peristomes in the family might have resulted from the evolutionary modification of an ancestral diplolepideous type, most possibly from the typical bryoid type (Shaw & Rohrer, 1984).

Based on this consideration, *Drummondia* and *Amphidium*, genera displaying haplolepideous affinity morphologically (Crum, 1972; Vitt, 1972; Edward, 1979; Shaw, 1986; Crum, 1987; Goffinet, 1997a) or even in molecular analyses (Goffinet et al., 1998; Stech, 1999), were excluded from the Orthotrichaceae. *Amphidium* had been a long-standing controversy and had been transferred in and out from the Orthotrichaceae many times due to its gymnostomous feature (Brotherus, 1925; Sainsbury, 1955;

Anderson & Crum, 1958; Lewinsky, 1976; Vitt, 1973, 1993). Likewise, the Erpodiaceae and Rhachitheciaceae, two families that include some gymnostomous members, have been excluded from the Orthotrichales because of their haplolepideous affinity (Goffinet, 1997b; Goffinet et al., 1998).

The convergence of habit and growth form in the Orthotrichaceae with phylogenetically distant families has been noted by various authors. For example, *Zygodon* species and some Pottiaceae are extremely similar (Zander & Vitt, 1979) or highly similar with some members of Dicranaceae Schimp. (Malta, 1926). *Orthotrichum* is often confused with species of Grimmiaceae Arn. (Grout, 1903) or Rhabdoweisiaceae Limpr. (Anderson & Crum, 1958). Meanwhile, members of *Macromitrium* may also resemble some species of the Meteoriaceae Kindb. (Vitt, 1982a). Vitt (1982a) has called for more studies to resolve the apparent convergence of growth forms in the Orthotrichaceae with other distantly related families of mosses. That may help in better understanding the circumscription of arthrodontous mosses.

2.3 Ecology

The Orthotrichaceae have been reported from a wide range of habitats, with preferences ranging from saxicolous to corticolous, in urban environments in temperate areas to the temperate and tropical forests, with an elevation range from sea level to mountain peaks; as an extreme, there are species reported from rocks near sea level on subantarctic islands (*Muelleriella* spp.; Vitt, 1976). Vitt & Ramsay (1985) gave an account of the seven different forest types in Australia where *Macromitrium* species were collected, including subtropical ravine forest, temperate *Nothofagus*-dominated forest, tropical vine forest, tropical montane forest, gallery forest, littoral forest, and temperate *Podocarpus-Dacrydium-Nothofagus*-dominated forest.

In Malaysia, the Orthotrichaceae have only been reported from inland forests, ranging from lowlands to mountains, in various dry-land forest types, from the dominant mixed dipterocarp forest to vegetation over limestone, quartz-derived soils, and sandstone plateau (Mohamed, 1987; Mohamed et al., 2003; Mohamed et al., 2004; Yong et al., 2006; Mohamed & Yong, 2007). There is no report or collection of Orthotrichaceae from either the coastal belt or mangrove swamps. This suggests that Malaysian Orthotrichaceae may not be able to tolerate high salinity and cannot survive in coastal areas.

In the lowlands of Malaysia, the Orthotrichaceae are mostly confined to the forest environment, flourishing in pristine conditions, and are almost absent from urban areas. In wet climax forest, they are commonly found on the higher parts of tree trunks or on tall branches at the canopy level, where there is sufficient sunlight. However in relatively open sites, such as the fringes of forest gaps or by water bodies, they often occur at relative low portions of tree trunks, but never quite reach the base. Occasionally they can also be found at ground level, growing on boulders, rocks or even cement structures in open but still moist areas. In the man-made environment, the Orthotrichaceae have only been found growing profusely on the trunks and branches of old and big trees in the Taiping Lake Garden, Perak, a well-known recreation site in Peninsular Malaysia by the forested foothills of the Main Range.

The species diversity of the Orthotrichaceae increases with elevation and reaches a maximum in the lower and higher montane zones. At damper, higher elevations, Orthotrichaceae species become more common and inhabit both forest and man-made environments. In places like the Genting Highlands, Cameron Highlands (in Peninsular

Malaysia) or the Kinabalu National Park (in Sabah), they are usually found in open and sunny environments, and even rather close to man-made structures. They are likely to be found on roadside trees, especially on those with rough bark surface, or on tree ferns, where the trunk is densely covered by decaying leaf bases, and where sufficient nutrient is available and competition is scarce. These environments are regularly visited by mist and fog, and Orthotrichaceae are occasionally found there on rocks, large boulders on cut slopes or even concrete structures. Although Malaysian Orthotrichaceae are predominantly represented by epiphytic species, the facultatively saxicolous or terricolous species have been noted to increase along the hiking trek up to the higher part of Mount Kinabalu (at 2500-3000 m). However, similar observations are not available for Peninsular Malaysia, where the highest summit, Mount Tahan, reaches only 2187 m.

The Orthotrichaceae are extremely rich in the canopy of montane forest. However, due to shorter tree heights in montane forest, Orthotrichaceae species are more frequently found at ground level, even forming thick cushions at tree bases, such as in the highland heath forest of the Maliau Basin (Sabah) and Mount Jerai (Kedah state, Peninsular Malaysia). They are profusely abundant in the upper montane to subalpine zones, where the vegetation is generally dwarfed and discontiguous in many areas. At this elevation on Mount Kinabalu, Orthotrichaceae species are found on almost every mature tree and usually occur in yellow-brown patches the size of a human palm to around a metre across on trunks or branches. As noted by Holttum (in Dixon, 1935), *Macromitrium* spp. are the most common mosses growing among branches of *Leptospermum* spp. (Myrtaceae) and conifers (Gymnospermae, mainly Podocarpaceae) at elevations above 9000 ft. (about 2743 m) to the tree line. However, the number of Orthotrichaceae species decrease drastically to almost absent in thick highland forest where conditions are densely shaded and extremely moist. Many other bryophyte species grow profusely in this condition, where they often occur as an extensive cover found almost all over the ground and tree surfaces, giving rise to the term ‘mossy forest’, although, in fact, there are more liverworts than mosses.

Some of the common lowland forest species are also adapted to xeric conditions on limestone, quartz or sandstone. Most of the time, these species occur as epiphytes and only grow on calcareous or sandstone rocks by chance. As with the case among higher plants, this extreme environment may have encouraged the evolution of endemic Orthotrichaceae species, such as an unnamed *Groutiella* species on a limestone outcrop at Gua Musang (Kelantan state, Peninsular Malaysia).

2.4 Geographical distribution of Orthotrichaceae in Malaysia

Six out of the eight genera reported for Malesia (i.e., with the exception of *Macrocoma* and *Orthotrichum*), are found in Peninsular Malaysia and Borneo, where Borneo has the richer flora than the Peninsular Malaysia and many taxa have been reported from Mount Kinabalu (Frahm et al., 1990; Akiyama et al., 2001). In a revised moss checklist for Borneo, Suleiman et al. (2006) listed 28 species in six genera of Orthotrichaceae, while in Peninsular Malaysia, Mohamed & Tan (1988) listed 17 species in three genera.

2.4.1 Borneo, especially Malaysian Borneo

Dozy & Molkenboer (1844) established five species, viz., *Cryptocarpon apiculatum*, *Macromitrium angustifolium, M. elongatum, M. semipellucidum* and *Schlotheimia teres*, based on material collected from Borneo as well as from Java or Sumatra. This represents the very first report for Orthotrichaceae in the study area. However, most of the Bornean material studied by Dozy and Molkenboer were collected by P.W. Korthals from Mount Sakoembang in southern Borneo (see Fleischer, 1904; Touw, 2007), which belongs to Indonesia-Kalimantan politically.

These species were later included in *Bryologia Javanica* (Dozy & Molkenboer, 1861), the first comprehensive moss flora of Java island (with illustrations) that serves as a very important resource in studying the mosses of Indonesia and adjoining regions. In this important publication, Mitten established *Macromitrium striatum* based on a collection by Hugh Low from Mount Kinabalu. Besides this, Dozy and Molkenboer reported *M. reinwartii* based on Korthal's collection from Borneo but with no exact locality.

In 1892, G.D. Haviland, the curator of the Museum at Kuching, Sarawak, collected extensively on Mount Kinabalu and sent his botanical collections to Kew for determination. Different workers were assigned to work on the collected materials, and the bryophytes were determined by W. Mitten and C.H. Wright. All their identification was published in O. Stapf's flora of Mount Kinabalu (1894), where he included two new *Schlotheimia* species: *S. splendida* described by W. Mitten and *S. rubiginosa* described by C.H. Wright. *Macromitrium cuspidatum* was reported for the first time for Borneo in this publication.

Fleischer (1904), in his work on the moss flora of Buitenzorg, included Borneo in the distribution range for *M. sulcatum* but no specimens were cited. Fleischer examined all the Bornean taxa recognized by Dozy & Molkenboer (1844, 1861) and listed them in his flora, noting that he followed the concept of Cardot (1897) and using the name *Desmotheca apiculata* instead of *Cryptocarpon apiculatum* as first published in Dozy & Molkenboer (1844).

Macromitrium winkleri was described by Brotherus (1912) based on a collection by Winkler from Hayup, South Borneo. And later in 1916, Dixon reported *M. merrillii* as new to Borneo based on a collection from Kota Belud by Rev. C.H. Binstead. In fact, both *M. winkleri* and *M. merrillii* reported by these authors actually referred to *M. falcatulum* Müll. Hal., according to the synonymy in Vitt et al. (1995). Similarly, the species *M. hallieri* and *M. rubricuspis* that were described by Brotherus (1925, 1928) and *M. clemensiae* by Bartram (1936), all based on material collected from different parts of Borneo, turned out to be later synonyms of *Macromitrium ochraceum* (Dozy & Molk.) Müll. Hal. (Touw, 1978; Vitt et al., 1995), a species common in highland forest.

In 1935, Dixon published the first moss flora of Borneo. There, he listed 12 species in four genera of the Orthotrichaceae. Among these, *Macromitrium goniorrhynchum* (Dozy & Molk.) Mitt., *M. minutum* Mitt., *M. longicaule* Müll. Hal., and *M. zollingeri* Mitt. *ex* Bosch & Sande Lac., were newly reported for Borneo. In the same publication, Dixon also described several new species: *Leptodontiopsis orientalis* (later transferred to *Zygodon orientalis* by Goffinet et al., 2004), *Macromitrium papillisetum*, *M. perdensifolium*, and *M. ochraceoides*.

Fröhlich (1962) studied some material collected by W. Meijer from Mount Kinabalu and published *M. kinabaluense* and *M. stephanodictyon* as new to science. Iwatsuki (1969) published *Ulota hattori*, an endemic epiphyte found at the alpine vegetation on Mount Kinabalu. Also, two *Zygodon* species were later reported from Borneo: Frahm et al. (1990) reported *Zygodon reinwardtii* (Hornsch.) A. Braun, and Akiyama et al. (2001) reported *Z. intermedius* Bruch & Schimp., both collected from Mount Kinabalu. Adding to the species known, Akiyama et al. (2001) collected and reported *Macromitrium* *aspericuspis* Dixon from Mount Kinabalu. The latest addition was *M. incurvifolium* (Hook. & Grev.) Schwägr., reported by Mohamed et al. (2004) from a limestone site near Bau, Sarawak. Thus, at present, a total of 28 taxa in six genera have been reported for the Orthotrichaceae of Borneo (Suleiman et al., 2006).

2.4.2 Malay Peninsula

In the case of Malay Peninsula, the very first record of Orthotrichaceae was published by Möller (1919), who reported *Macromitrium goniorrhynchum* (Dozy & Molk.) Mitt. from the Singapore Botanic Gardens. Holltum (1927) collected the same species from the same garden but reported it as *Groutiella goniorrhyncha* (Dozy & Molk.) E.B. Bartram.

Dixon (1924) published a new species, *Macromitrium magnirete* based on material collected from Mount Tahan by M. Haniff and M. Nur. Brotherus (1925) cited "Malacca" in the distribution range of *M. orthostichum* Nees without providing further detail; however, Dixon (1926) doubted the existence of this species in Peninsular Malaysia.

Dixon (1926) published the very first account of the mosses of Malay Peninsula and listed 13 records in two genera of Orthotrichaceae, based on material collected throughout Peninsular Malaysia and Singapore. He listed *M. brevirete* as new based on I.H. Burkill's collection from Jerantut, but failed to provide a diagnosis or description of that species, so that this is a *nomen nudum* according to the International Code for Botanical Nomenclature (ICBN) (Mohamed & Tan, 1988). Among the species reported in Dixon (1926) are *Desmotheca apiculata*, *Macromitrium blumii*, *M. incurvifolium*, *M. minutum*, *M. ochraceum*, *M. semipellucidum* and *M. zollingeri*, so that, apparently, Dixon would have noticed the high similarity among the Orthotrichaceae of the Malay Peninsula (essentially Peninsular Malaysia) and Borneo Island.

In 1988, Mohamed and Tan updated the Malay Peninsula moss checklist published by Dixon (1926) as well as the generic moss flora of Manuel (1981). In this account, Mohamed & Tan (1988) listed 17 taxa in three Orthotrichaceae genera for Peninsular Malaysia. Among the additions are four records from Fraser's Hill, viz., *M. cumingii* Müll. Hal. and *M. reinwardtii* (Tixier, 1971), *M. micropoma* M. Fleisch. and *M. salakanum* (Noguchi, 1973); a record from Cameron Highlands, viz., *M. longicaule* (Tixier, 1980); and two records from limestone throughout Peninsular Malaysia, viz., *M. subtile* and *M. cuspidatum* (Mohamed, 1987). In the revision of New Guinean Orthotrichaceae, Vitt et al. (1995) examined a collection from Peninsular Malaysia and identified it as *M. falcatulum*. Most recently, *M. nepalense* was reported from Belum Forest Reserve (Damanhuri, 2000) and *M. angustifolium* from a lowland forest in Wang Kelian, Perlis (Damanhuri & Maideen, 2001); however, the latter species has never been reported from such a low elevation, so that the identification might be in doubt. Thus, to date there are 20 taxa of three Orthotrichaceae documented for Peninsular Malaysia.

2.5 The genus *Macromitrium*

Macromitrium, named for the long and large calyptra, was established by Bridel in 1819 based on the type species *Macromitrium aciculare* Brid. (synonym of *M. pallidum*). It found acceptance among most bryologists of that time, including Schwägrichen, Hornschuch, Hampe, although Hooker & Greville (1824) included it under their very broad concept of *Orthotrichum sensu lato.*

Müller (1845) presented a synopsis of 79 known *Macromitrium* taxa of that time and was the first to recognize infrageneric categories in *Macromitrium.* He placed the 79 taxa in the following five sections: I. *Macrocoma* (3 spp.), II. *Chaenomitrium* (1 sp.), III. *Macromitrium* (47 spp.), IV. *Schlotheimia* (26 spp.), and V. *Cryptocarpon* (1 sp.). All five sections were later elevated to genera by different authors, among these *Schlotheimia* and *Cryptocarpon* (=*Desmotheca*) are found in Malaysia.

Fleischer (1920a) proposed a classification system based largely on peristome features that was probably influenced by Philibert's tedious work on the variations of the peristome found within the Bryopsida (see translation by Taylor, 1962). Differring from Müller, Fleischer (1904) established two subgenera for *Macromitrium*, i.e. Subgenus *Diplohymenium* with double peristome and Subgenus *Haplodontiella* with single peristome. Under each subgenus, he further segregated the members of *Macromitrium* into sections and subsections. Just like Brotherus (1925), he accepted *Schlotheimia* and *Desmotheca* (placed under subgenus Cryptocarpon in Müller) as distinct genera, but he placed *Schlotheimia* in Subfamily Macromitrieae and *Desmotheca* in Subfamily Pseudo-Macromitrieae.

Many more new names were introduced by Müller, Mitten, Cardot, Thériot and others during the late 1800's and the early 1900s. Until the first version of Musci for *Die Natürlichen Pflanzenfamilien,* Brotherus (1909) had listed 384 names in five different subgenera established by himself (1909), Müller (1845) and Mitten (1873). *Drummondia* and *Schlotheimia* were accepted as distinct genera in his treatment. The list was later increased to 415 names in his second volume of the same work (Brotherus, 1925).

From time to time, other small genera have been segregated from *Macromitrium*. Besides *Desmotheca*, *Drummondia* and *Schlotheimia* mentioned above, other examples are *Leiomitrium* Mitt. (1879), *Macrocoma* (Hornsch. ex Müll. Hal.) Grout (1944), *Groutiella* Crum & Steere (1950) based on *Micromitrium* Schimp. ex Besch. (1872) non *Micromitrium* Aust., *Cardotiella* Vitt (1981b), and others. In the *Index Muscorum* published during 1959-69, about 460 names were listed, but by the time of the latest account by Crosby et al. (1999), only 368 names were retained in their list after considering much synonymy.

The great variation among many *Macromitrium* species has been noted by Eddy (1996). He considered this as being due to the prevalent obligately out-breeding nature of the plant, where active exchange of genetic information contributes to plasticity in morphological features. After a thorough revision of the Australasian *Macromitrium* (Vitt, 1983; Vitt & Ramsay, 1985), Vitt & Ramsay (1985) made an attempt to categorize the 33 species of Australian *Macromitrium* into seven groups based on their phylogenetic relationships. However, they did not formalize the groups as distinct taxonomic entities due to the close relationships among Australasian taxa that cause difficulties in grouping. In spite of this, the groups somehow reflect the sections and subsections created by Fleischer (1904) in his revision of Javan *Macromitrium*.

Vitt & Ramsay (1985) suggested that the genus *Macromitrium* is Gondwanan in origin, and further commented that the high species endemism in the neotropics, paleotropics and Australian region is due to recent infrageneric diversification after the breakup of Gondwanaland, with only limited distribution to the northern hemisphere (Vitt, 1982a, 1982b; Vitt & Ramsay, 1985).

CHAPTER 3

MATERIAL AND METHODS

3.1 Study material

The present study is based on the examination of herbarium material as well as fresh material collected from various locations in Peninsular Malaysia, Sabah and Sarawak. Over 2800 dried specimens, including type specimens, were carefully examined. Herbarium material used in this study were loaned from 12 institutional herbaria (abbreviations according to Holmgren & Holmgren, 1998): BM, BORH, HIRO, KLU, NICH, NY, PC, S, SING, SINU, TNS, and UKMB.

3.2 Fieldwork

New fieldwork was undertaken in order to gain a better understanding of studied taxa, and to provide a population perspective for data obtained by studying herbarium material. Fieldwork was carried out in Peninsular Malaysia, Sabah and Sarawak to observe species habitat and ecology, as well as to collect fresh and herbarium specimens. The fieldwork localities included (for Peninsular Malaysia) Kedah (Ulu Muda Forest Reserve), Penang (Penang Hill), Perak (Belum Royal Park, Taiping Hill, Taiping Lake), Selangor (Batang Kali, Batu Cave, Gombak Forest Reserve, Gunung Bunga Buah, Gunung Nuang, Gunung Ulu Kali), Negeri Sembilan (Kenaboi), Johor (Endau-Rompin), Pahang (Cameron Highland, Fraser’s Hill, Taman Negara), Terengganu (Gunung Mandi Angin), Kelantan (Gunung Stong); (for Borneo) Sabah (Maliau Basin, Mount Kinabalu), Sarawak (Bau, Mulu National Park, Gunung Santubong); (for neighbouring regions) Java (Bogor Botanical Garden, Cibodas Botanical Garden, Gunung Halimun National Park, Gunung Patuha), Sumatra (Gunung Sago). Information about the growth substrate, altitudinal range and other ecological data for each species was obtained through field observation and collated with that retrieved from herbarium specimen labels.

3.3 Light microscopy and measurements

Morphological and anatomical information of studied taxa were obtained through the use of a Nikon Flashlens 5.6 mm 'Megascope' dissecting microscope; and with a Nikon Alphaphot 2 compound microscope. The specimens were first examined in its dried form to gain an overall view of the plants. A few stems with complete branches, preferably with sporophytic materials, were then soaked in water to which a few drops of Teepol (a detergent, to reduce surface tension of water) has been added, for one minute. When the plant has fully expanded to its original form, the material was examined again for gross features under the same microscope, after which a few mature branches or stems (preferably with sporophytic structures) were detached for further examination under a compound or light microscope. Part of the detached branches or stems, together with leaf material were dissected and mounted on a glass slide with water (temporary preparation) or fixed with glycerine jelly (semi-permanent preparation). The glycerine jelly was prepared beforehand according to the protocol given in Zander (1997). Cross-sections of stem, leaf, seta and capsule were made using the free-hand cutting technique, followed by fixing in the mounting medium mentioned above. The leaf morphology and other microscopic features, as well as anatomical details of the plant, were then observed and measured using a compound microscope.

In order to produce accurate morphological descriptions and to ascertain variations among different populations of a particular taxon, five plants of every herbarium specimen were selected for detailed measurement. The important features documented included the vegetative leaf and perichaetial leaf size, upper-middle-lower lamina cell size, and other characters specific to certain taxa, such as the arista (long excurrent costa growing out from the leaf lamina) length. Likewise, important sporophytic characters, such as seta length, urn size (excluded the operculum), exothecial cell size and spore size, were measured. In addition to these, a search for morphological features that are often overlooked in taxonomic research was carried out. Thus, information such as paraphysis length, vaginula length, and perichaetium length were also recorded.

3.4 Scanning electron microscopy studies

To search for additional diagnostic taxonomic characters, observation of the minute peristomatic features, lamina cell surfaces and other potentially useful microscopic structures was carried out with a scanning electron microscope. A short branch or stem with mature capsule was separated from the dry herbarium material and soaked in water. The moist and fully expanded sample (with both sporophytic and gametophytic structures) was later transferred to a glass slide and the mature capsule with peristome teeth was cut into half. A coverslip was placed over the sample and pressed down with slight pressure, in order to minimize the curvature of peristome teeth upon drying. The prepared material was then dried at room temperature for approximately three days.

The completely air-dried material was then transferred from the glass slide and placed on an aluminium stub already mounted with dark-coloured two-sided adhesive tape. The two halves of the capsule were gently arranged on the stub with the first half showing the ventral side of the peristome teeth, facing upward, and the second half showing the dorsal side of the teeth, exposed. Some spores were distributed evenly next to the capsule, and a few vegetative leaves (detached from the branch) were also mounted on the stub. The sample was coated with gold to ensure a uniform electrical charge and then viewed with a JEOL JSM-6400 scanning electron microscope at an accelerating voltage of 6-10 kV and a working distance of 10-15 mm.

3.5 Description and illustrations

The scientific description of every taxon studied was based on critical examination of mainly herbarium specimens and, where available, fresh material. Descriptive terminology followed Malcom & Malcom (2007) unless otherwise stated. The revision of the family included detailed nomenclatural and taxonomic discussions, species descriptions, identification keys to taxa, lists of specimens examined, habitat information and distributional comments for each taxon.

Representative examples of different parts of the morphological range for each taxon were selected to produce line drawings. The inked line illustrations of leaves, cells and unique features of every taxon recognized in this work were prepared based on glycerine jelly mounted specimens with the aid of a camera lucida. The habit, calyptrae and capsules were photographed from dry specimens unless otherwise indicated. The dry state of the plants was chosen because most of the time these photophylic plants were encountered in dry conditions in the field; additionally, they also resembled the dried herbarium material. For close-up images, a Leica MZ9.5 Automated Stereomicroscope with digital camera attachment was used. Photographs taken in the field of selected taxa were also provided whenever available.

3.6 Cladistic analysis of morphological characters

The evolutionary relationships among the taxa studied, particularly among *Macromitrium* species, was analyzed by cladistic methods. As many morphological characters as possible were used in the analysis, some unique to a taxon, and others shared by a few or many taxa. Cladistic analysis was carried out using using maximum parsimony (MP) performed in winPAUP 4.0b10 (Swofford, 2002). In the present study, ten random addition cycles of 200 ratchet iterations each were used. Each iteration comprised two rounds of tree-bisection-reconnection (TBR) branch swapping; one on a randomly reweighted data set (25% of the positions), and the other on the original matrix by saving one shortest tree. Shortest trees collected from different tree islands were used to compute a strict consensus tree. Heuristic bootstrap searches (BS; Felsenstein, 1985) were performed with 1000 replicates. In addition, 10 random cycles per bootstrap replicate were run to boost accuracy.

3.7 Molecular phylogenetic analysis

3.7.1 DNA isolation and amplification

Phylogenetic inferences were made based on variation in small ribosomal protein 4 (rps4) sequence data, a chloroplast DNA-coding gene. This region has been surveyed for green plants and was shown to be useful for phylogenetic reconstruction at the subfamily and generic levels for bryophytes (e.g., Cox & Hedderson, 2003; Werner et al., 2004). Total DNA was extracted from fresh material or dried herbarium specimens according to the modified Doyle & Doyle (1990) protocol by using CTAB (cetyltrimethylammonium bromide) as solvent (Tsubota et al., 1999, 2000). When dried herbarium materials were used for this purpose, only specimens stored less than three years were chosen. Some specimens with older storage age have been tried for DNA extraction; however, the yield is usually of poor quality and is insufficient for subsequent amplification.

A few short branches or stems, preferably with sporophytic structures, were removed from the specimens and ground in a 1.5 ml microcentrifuge tube using a mini plastic pestle. The sample yield, in powder form, was incubated with extraction buffer and then purified through a series of precipitating and cleaning processes. The pure genomic DNA product was then used directly for polymerase chain reaction (PCR) amplification. The primer set (forward and reverse primers) rpsa [5'ATG TCC CGT TAT CGA GGA CCT3'] (Nadot et al., 1994) and trnas [5'TAC CGA GGG TTC GAA TC3'] (Buck et al., 2000) was used to amplify the *rps4* region, while primer set trnC [5'CGA AAT CGG TAG ACG CTA CG3'] and trnF [5'ATT TGA ACT GGT GAC ACG AG3'] (Taberlet et al., 1991) was used to amplify the *trnL-trnF* region. The PCR reactions were performed in 0.2 ml microcentrifuge tubes using 1 unit of Taq DNA polymerase (FinnZymes), 0.2 mM dNTP mix (FinnZymes), 1x Taq buffer (FinnZymes), 2.5 mM $MgCl_2$, 1.25 µM of each forward and reverse primer in 25 µl final working volume. A sample of 100 ng genomic DNA was used as template and loaded into the working solution.

Thermocycling profile for PCR reaction was set as follows: initial denaturation at 94°C for 4 minutes; 35 cycles of 94°C for 1 minute, annealing temperature (varied from 52°C to 60°C) for 1 minute and 72°C for 2 minutes; final elongation and tailing at 72°C for 7 minutes. In general, an annealing temperature at 52°C was employed to amplify recently obtained genomic DNA, but a higher annealing temperature (up to 60°C) was used for genomic DNA stored more than six months in Tris-EDTA buffer at -20°C. The amplified PCR products were purified using a QIAquick Purification Kit (Qiagen) following the manufacturer's instructions. The double-stranded DNA was sequenced on an ABI PRISM® 3100 Genetic Analyzer (Applied Biosystems) with the BigDye® Terminator ver. 3.1 Sequencing Kit in the following cycle sequencing conditions: 25 cycles of 96°C for 10 seconds, 50°C for 5 seconds and 60°C for 4 minutes, at rapid thermal ramp for 1°C/second.

3.7.2 DNA sequence alignment and analysis

Newly obtained sequences were edited for inaccurate base-calling by prior assemblage of the forward and reverse strands into a consensus sequence in BioEdit ver. 7.0.5.3 (Hall, 1999). Available sequence information for other Orthotrichaceae taxa in the DDBJ/EMBL/GenBank International Nucleotide Sequence Database Collaboration, as well as those of selected outgroup members, was downloaded from the website and incorporated into the dataset. Edited sequences and those downloaded from the DDBJ/EMBL/GenBank were entered into Clustal X ver. 1.8 (Thompson et al., 1997) for preliminary alignment. The pre-aligned sequences were later adjusted manually in BioEdit ver. 7.0.5.3 (Hall, 1999) and MEGA ver. 4 (Tamura et al., 2007) according to the criteria laid out in Borsch et al. (2003) and Quandt & Stech (2005). Those sequences or sites of questionable quality were excluded from the analyses.

Three separate data matrixes have been generated and were employed in later phylogenetic reconstruction of the family. The first two matrices were derived from the characters of each separate locus (either *rps*4 or *trn*L-*trn*F) obtained while the third data set was the combined information of both loci. The data matrixes with many aligned gaps (or indel), such as *trn*L-*trn*F and combined data set, were analyzed employing a Simple Indel Coding (SIC) strategy (Simmons & Ochoterena, 2000) as implemented in SeqState (Müller, 2005). When indel coding was used, indels were incorporated into the analyses as binary data. SeqState generated a ready-to-use nexus file containing the sequence alignment with an automatically generated indel matrix appended. The file could then be analyzed either directly in winPAUP 4.0b10 (Swofford, 2002) or MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003).

The tree-searching method was employed in the current study to estimate phylogeny, while distance methods were avoided. The tree-searching method is actually character-based, where the characters within each column in a multiple alignment are compared leading into the construction of numerous trees. Subsequently, some criteria are used to determine the best tree, or best set of trees (Holder & Lewis, 2003). On the other hand, the distance or algorithmic approach relies on pair-wise differences between sequences in a multiple alignment in order to construct the phylogenetic tree. However, observed differences between DNA sequences may not accurately reflect the evolutionary distances between them, especially if some lineages evolved faster than others (Holder & Lewis, 2003). For instance, multiple substitutions at the same site could introduce several changes to a particular sequence. As a result, that sequence might be artificially close to some other sequences that have apparently evolved at a slower rate; or in other words, it underestimates the changes that have taken place during the evolutionary event. Hence, the tree-searching method using different optimality criteria (i.e. parsimony, maximum likelihood and Bayesian approaches) was preferred in the present study for inferring the phylogenetic relationships in the Orthotrichaceae.

Phylogenetic reconstructions using maximum parsimony (MP) were performed in winPAUP 4.0b10 (Swofford, 2002) as for the morphological analysis (above), except that, in this case, the analysis was conducted in combination with PRAP (Müller, 2004). The latter programme generates command files for PAUP* that allow parsimony ratchet searches as designed by Nixon (1999).

The Akaike Information Criterion (AIC) as implemented in MrModeltest 2.2 (Nylander, 2004) was used to select the best fitting models for later Bayesian analysis. AIC is designed to choose the model that best approximates reality, or which is closest to the truth (but does not indicate the truth or falsity of the chosen hypothesis), and it has been proven to have many advantages over the hierarchical likelihood ratio tests (hLRTs) which form the other model selection method provided by MrModeltest 2.2 (Posada & Buckley, 2004). Bayesian analyses were performed with MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003), applying the General-Time-Reversible model (Rodriguez et al., 1990) with a proportion of invariant sites and a discrete gamma distribution of rates (GTR+I+G) for all the sequence data as proposed by MrModeltest 2.2. However, in the restriction site model for the indel partition, the ascertainment (coding) bias was set to variable (lset coding = variable). Posterior probability (PP) distributions of trees were created using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) method and the following search strategies suggested by Huelsenbeck et al. (2001, 2002). Ten runs with four chains (2,000,000 generations each) were run simultaneously (mcmc nruns=10 nchains=4 ngen=2,000,000). Chains were sampled every 100 generations and the respective trees written into a tree file. Calculations of the consensus tree and of the Posterior Probability (PP) of clades were performed based upon the trees sampled after the chains converged.

Consensus topologies and branch support values from the different methodological approaches were compiled and drawn manually. Branches with bootstrap (BS) value ≥70% are considered well-supported under maximum parsimony inferences, while branches with posterior probability (PP) ≥0.95 are considered well-supported under Bayesian analysis. The cladograms generated based on molecular information were later compared with that from the morphological cladistic analysis by inspection, to see if any identical clusters of taxa were generated.

CHAPTER 4

MORPHOLOGY AND ANATOMY

4.1 General introduction

General information on the morphology of the Orthotrichaceae is usually found in the form of taxonomic enumerations in a number of regional floristic works (e.g., Dozy & Molkenboer, 1861; Fleischer, 1904; Bartram, 1939; Sainsbury, 1955; Vitt et al., 1995). Detailed discussions and general summaries are only available for two genera that have been revised globally and studied intensively, i.e., *Orthotrichum* (Vitt, 1973; Lewinsky, 1977, 1989, 1993) and *Zygodon* (Malta, 1926; Lewinksy, 1990; Calabrese, 2006). More usually, brief summarizing characters are provided in regional generic revisions (e.g., Malta, 1926; Vitt, 1973; Lewinksy, 1990; Calabrese, 2006).

Unlike vegetative habit and gametophytic structures, reproductive behaviour and sporophytic structures of the Orthotrichaceae have been more widely studied and better understood. The members of this family are well known for producing spores of unequal sizes and dwarf male plants that develop epiphytically on the mature female plants (Fleischer, 1920b). Members of *Macromitrium* and *Schlotheimia* have been widely used in experiments investigating the relationship between anisosporous behaviour and sexual dimorphism (Ernst-Schwarzenbach, 1936, 1939, 1943; Ramsay, 1979; Une, 1985a, 1985b). A number of cytological studies of Orthotrichaceae have also been published. These have confirmed the presence sex chromosomes accounting for morphological differences in the anisosporous *Macromitrium* species (Ramsay, 1966) and indicated that sexual dimorphism in *Macromitrium* species are typically genetically driven, although there are exceptions when dimorphic sexual expression can be over-ridden by environmental factors (Ramsay, 1979; Ramsay & Vitt, 1986). However, cytological knowledge of the Orthotrichaceae is still far from complete. Available chromosome counts only reflect a small perspective into the genetic systems of Orthotrichaceae, and tropical examples are poorly represented (Ramsay & Vitt, 1984; Fritsch, 1991; Ramsay, 1993; Ramsay et al., 1995; Maniselvan & Kumar, 1999).

Peristomial architecture and development has also been studied. Philibert (1884, 1888), in his monumental work on the moss peristome architecture, had already noted that the peristome of Orthotrichaceae is unique among the diplolepideous type (Taylor, 1962). Almost a century later, Vitt (1981a) proposed to recognize it as a unique peristome-type among four distinct arthrodontous peristome types (one haplolepideous and three diplolepideous types). In the same communication, Vitt (1981a) discussed three possible mechanisms through which the Orthotrichaceous peristome might have evolved independently from a more ancestral diplolepidous peristome: fusion, reduction and resorption. The usefulness of the Orthotrichaceous peristome as a natural taxonomic character was supported by Lewinsky (1989, 1990, 1993) based on observations of *Orthotrichum* and *Zygodon*; but it was rejected by Shaw & Rohrer (1984), who preferred to interpret it as a reduction of the typical diplolepideous type, i.e., the Bryaceous type, which is apparently also supported by peristomial development characters (Goffinet et al., 1999). However, the direction of peritome evolution remains contentiouos until lately, when a more robust phylogenetic hypothesis became available. Recent molecular findings now indicate that the Orthotrichaceous peristome has indeed, probably derived from an ancestral Bryaceous type (Cox & Hedderson, 1999; Cox et al., 2000; Goffinet & Buck, 2004).

Apart from discussions on the evolutionary development of the Orthotrichaceous peristome, general morphological information about peristomial structures in

Orthotrichaceae species, either as brief descriptions or images, or sometimes both, are available in many regional revisions (e.g., Malta, 1926; Noguchi, 1967, 1968; Vitt, 1973, 1976, 1983, 1989; Vitt & Ramsay, 1985; Lewinsky, 1984, 1990, 1992; Rooy & Wyk, 1992; Vitt et al., 1993, 1995; Calabrese, 2006). Apart from that, detailed discussions of the peristomial features of many *Orthotrichum* taxa are found in Lewinsky (1977, 1993), while peristomial characters of many *Zygodon* species, especially those in Australasia, are given in Lewinsky (1990). A more general discussion of various peristomial characters in the Orthotrichaceae was given by Shaw (1986), who investigated representatives of eight out of 14 Orthotrichaceae genera recognized then.

Thus, the two genera most studied are *Orthotrichum* and *Zygodon* (Orthotrichoideae), with acrocarpic habit and better represented in the temperate regions. Besides taxonomic enumerations in regional floristic works or generic revisions, there is a dearth of morphological accounts of the Macromitrioideae, which is basically cladocarpic in habit and largely tropical. Here I provide a summary of the morphological characters of the tropical Orthotrichaceae treated in this study, based on observations and work carried out for the present investigation.

4.2 Gametophores

4.2.1 Protonemata

Limited studies of protonemal morphogenesis in the Orthotrichaceae have included species of *Macrocoma, Macromitrium, Orthotrichum, Schlotheimia* and *Ulota* (Nishida, 1978; Ramsay, 1979; Goode et al., 1993). After being shed, the spores germinate into filamentous protonemata including a subglobular cell at the proximal end (Nishida, 1978). The spores germinate by forming one or two germ tubes with short side-branches developing close to the spore. The close branching will later form a compact protonemal system with gametophores developing within the centre of such colonies and producing rhizoids with pigmented walls and oblique septa (Ramsay, 1979; Goode et al., 1993). The protonemata are monomorphic; the filaments comprise only short cells with hyaline and transverse end-walls (chloronemal type), but do not normally differentiate into caulonema (with pigmented and oblique cell walls) although caulonema development has been reported by Ramsay (1979) and Goode et al. (1993). This protonema morphology is unique to the Orthotrichales, Isobryales and Thuidiales, whereas typical chloro- and caulonemata are found in most orders of mosses, from Dicranales to Hypnobryales (Duckett et al., 1998).

4.2.2 Habit

Due to their acrocarpic habit, members of Orthotrichoideae form either loose (e.g., *Ulota splendida*) or dense tufts (e.g., all three *Zygodon* species) (Fig. 4.1E-F), whereas members of Macromitrioideae (e.g., genera *Desmotheca*, *Groutiella*, *Macromitrium* and *Schlotheimia*) are commonly loosely to densely mat-forming or cushion-forming due to their cladocarpic habit (Fig. 4.1A-D, 4.2). However, some Macromitrioideae can produce many tall, erect branches that cause the plants to appear tufted, in spite of long-creeping and widely spreading stems.

Plant size varies; smaller species like *Macromitrium densum* and *M. papillisetum* can grow to 5 mm high only, larger species like *Schlotheimia rubiginosa* and *M. ochraceum* can reach 5 to 6 cm high in their natural habitats. However, plants of intermediate size, 1.5–3 cm tall, are most common within the family.

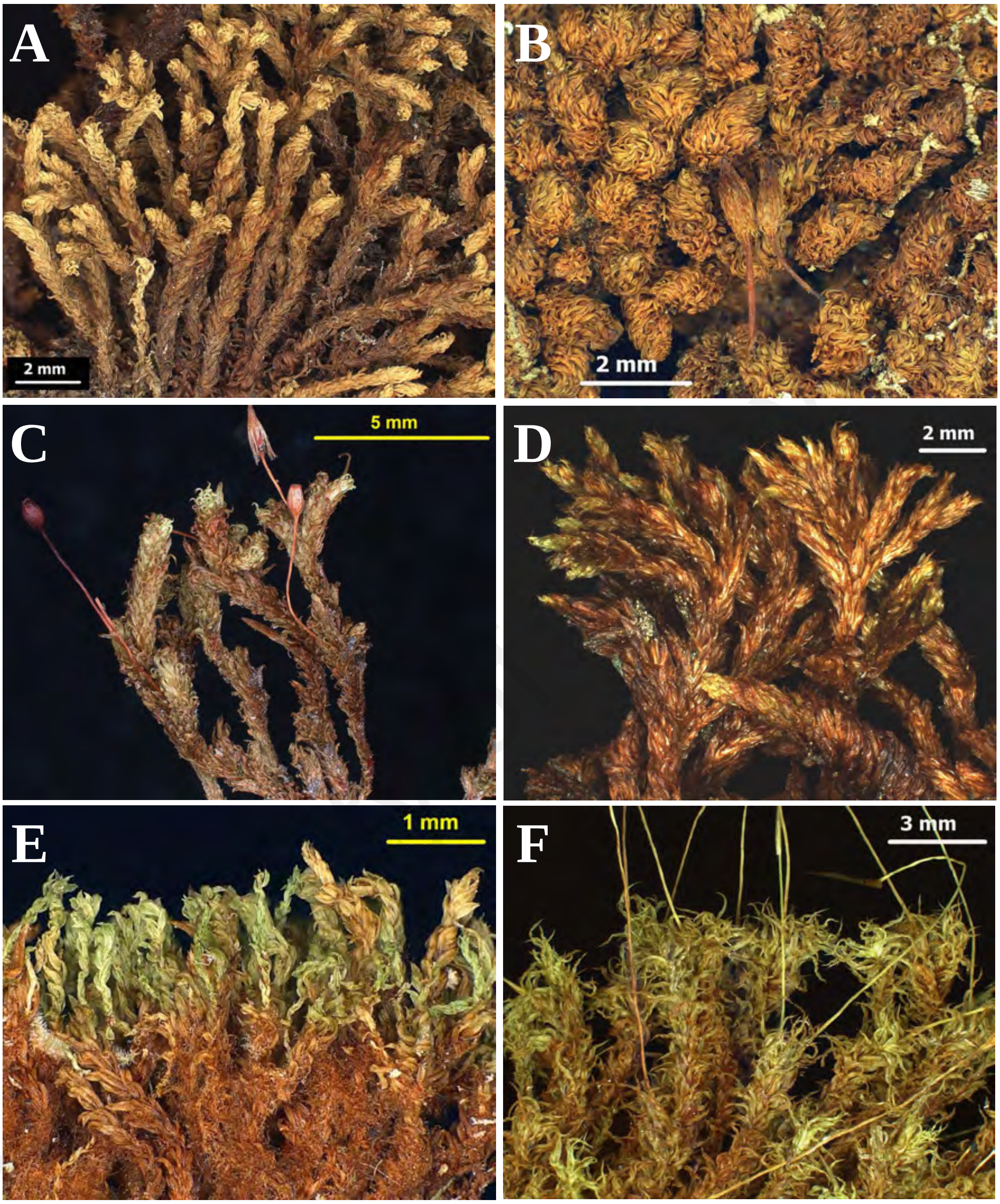

Figure 4.1. Habits I. — **A,** *Macromitrium orthostichum* Nees ex Schwägr.; **B,** *Macromitrium papillisetum* Dixon; **C,** *Macromitrium salakanum* Müll. Hal.; **D,** *Schlotheimia rubiginosa* C.H. Wright; **E,** *Zygodon intermedius* Bruch & Schimp.; **F,** *Zygodon orientalis* (Dixon) Goffinet.

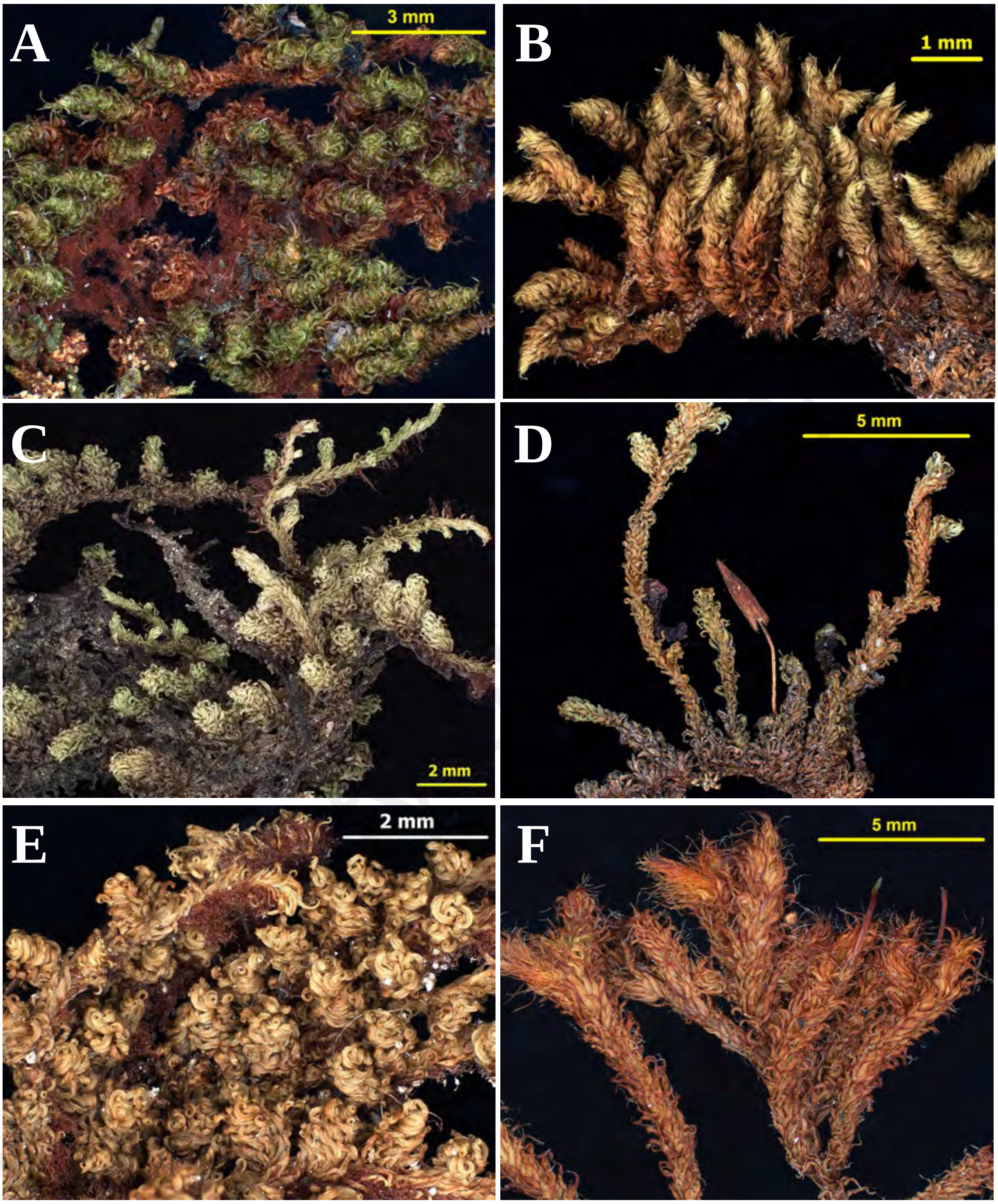

Figure 4.2. Habits II. — **A,** *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **B,** *Macromitrium blumei* Nees *ex* Schwägr.; **C,** *Macromitrium fuscescens* Schwägr.; **D,** *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr.; **E,** *Macromitrium nepalense* (Hook. & Grev.) Schwägr.; **F,** *Macromitrium ochraceoides* Dixon.

The plants are generally green; even so the colour ranges from light green (e.g., in all three *Zygodon* species), through yellowish-green and dark green, to olive-green (most commonly), with a tendency of turning brownish when they grow older (especially in *Desmotheca* and many *Macromitrium* species). Among these, *S. rubiginosa* and *S. wallisii* often appear glossy in nature whereas the others are relatively dull. Sometimes, the older leaves and costa can be strongly pigmented, striking reddish-brown in mature populations of *M. ochraceoides*, *M. ochraceum*, *S. rubiginosa* and *S. wallisii*. The reddish-brown appearance may also be due to rhizoids densely covering the lower to middle parts of erect branches (the so-called "tomentose" character) as seen in *Groutiella tomentosa*, *Zygodon orientalis* and *Z. reinwardtii*. However, in the latter, greenish shoots normally appear on top of the reddish "tomenta".

4.2.3 Stems and branches

The Orthotrichoideae exhibits the typical acrocarpous moss branching pattern, with orthotropic stems or primary modules (usually erect, sometimes ascending) with determinate growth but branching sympodially immediately below the perichaetia (i.e., at a subperichaetial position) (Fig. 4.3A). Usually, only a single new branch will form but once again growth of the relay branch axis will be terminated by formation of a terminal perichaetium. New branches grow vertically but not horizontally and can be of unequal lengths, and generally contribute to increase in plant height.

In contrast, the primary modules of the Macromitrioideae are prostrate or plagiotropic, showing indeterminate growth and sympodial branching, with new branches of metameric origin (Fig. 4.3B). Usually, only a single new horizontal branch will form along each axis. A branch will also grow indeterminately and re-branch sympodially, forming repeated modules. In addition to these, as the stem grows, many lateral

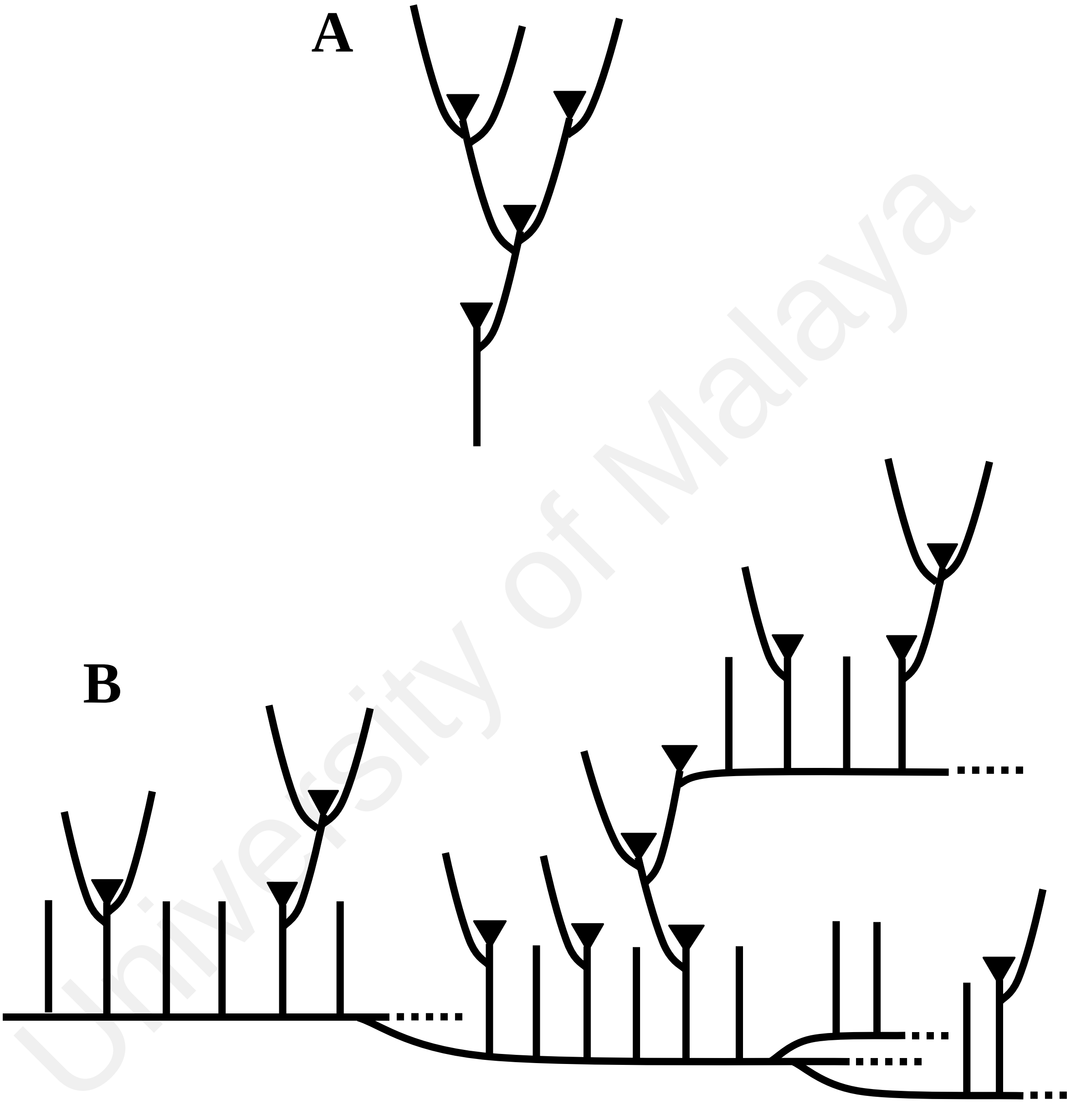

Figure 4.3. Schematic diagram of plant architecture for members of Subfamily Orthotrichoideae (A) and Subfamily Macromitrioideae (B). Sexual organs are represented by solid triangles (either perigonia or perichaetia for the Orthotrichoideae, but usually only perichaetia in the Macromitrioideae).

innovations will be formed. These develop into numerous orthotropic branches that are perpendicular to the plagiotropic axis bearing them. These vertical branches are also metameric in origin and are usually almost similar in height. They are either closely arranged and resemble cushions (e.g., *G. tomentosa*, *M. salakanum*, *S. rubiginosa*), or distantly arranged, causing the plants to appear loose and wiry (e.g., *Desmotheca apiculata* and *M. ochraceum*) (Fig. 4.1A-D, 4.2). The development of gametangia at the apices halts the growth of such monopodial orthotropic branches, on which subsequent sympodial extension growth (or ‘secondary modules’ according to La Farge-England, 1996) later arises through lateral innovations. In *D. apiculata*, the first-order vertical innovation is always the longest, and subsequent orders developed are uniformly short; this may be easily distinguished from other Orthotrichaceae, where higher-order erect innovations are of similar length.

Reiteration is common in members of the Macromitrioideae and initiates irregularly from the orthotropic branches. Occasionally, a lateral innovation on an orthotropic branch grows horizontally instead of vertically. Formation of this new horizontal axis signals the start of the reiteration (Fig. 4.3B). This new reiterative horizontal axis develops following the basic architecture of the original plagiotropic axes, with indeterminate growth and sympodial plagiotropic branching, as well as many determinate monopodial orthotropic lateral branches along each plagiotropic segment.

Both the Orthotrichoideae and Macromitrioideae exhibit similar stem and branch anatomy. Both stems and branches are roughly rounded to pentagonal in transverse section. The epidermis is made of 2–4 rows of small cells with thick, red-brown walls. The cortex is mainly made up of large, isodiametric or oblate cells with moderately thick to rather thin walls, except in *U. splendida* and the genus *Desmotheca*, where cell walls are consistently thick in both epidermal layer and cortex (Fig. 4.4). An additional character in *Desmotheca* is that cells found in the cortex and epidermal layer are not distinctly different in size. In general, the cortex cell wall is weakly yellowish at the outer ring and colourless in the pith region. A central strand is absent in both stem and branch in all Malaysian Orthotrichaceae.

4.2.4 Rhizoids

Rhizoids are stem-borne and always situated on the side facing the substrate, except those forming a tomentose indumentum along erect stems or vertical branches. Rhizoids always appear in abundance and their initials are found just below the leaf insertion along the creeping stem in the Macromitrioideae, and at the lower portion of the erect stem in the Orthotricoideae. Sometimes the plant can be tomentose, with dense rhizoids found either at the lower half position of the vertical branches in the Macromitrioideae (e.g., *G. tomentosa*) (Fig. 4.2A) or stems in respect to the Orthotrichoideae (e.g., *Z. intermedius, Z. orientalis*) (Fig. 4.1E-F). Mature rhizoids are reddish-brown in colour, multicellular and uniseriate with oblique cell wall, and always dichotomously branched. The rhizoids appear to be scabrous with barely visible papillae under the compound light microscope. Under the scanning electron microscope, the papillae appear as very low bumps which are distributed irregularly and are fused together at their bases (Fig. 4.5). This type has been described as ‘verrucate papillae’ according to Hirohama & Iwatsuki (1980). A species of particular interest is *M. orthostichum*, which bears a few short rhizoids on the abaxial surface of leaves, and not just on the stem.

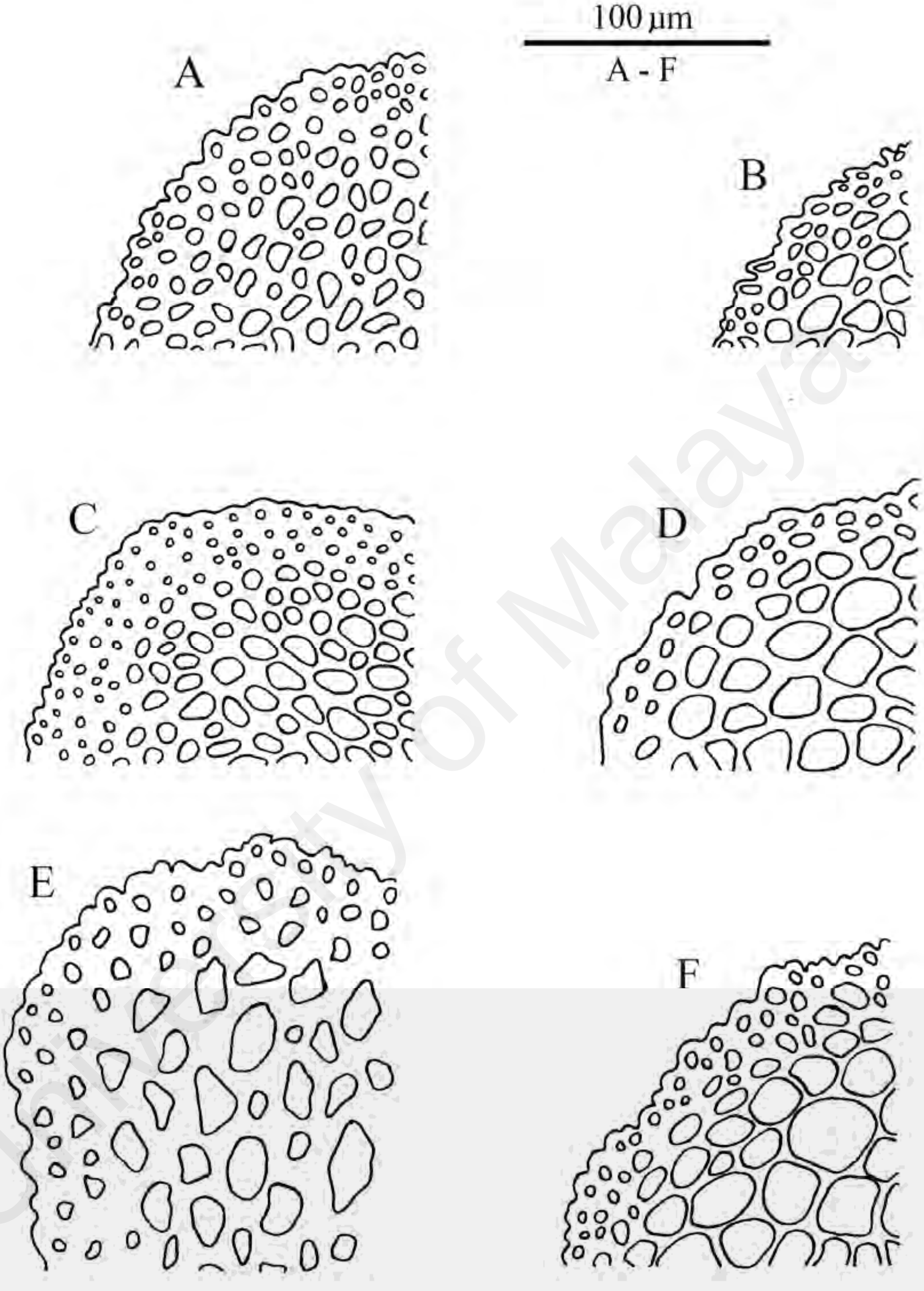

Figure 4.4. Parts of stem cross-sections. — **A,** *Desmotheca apiculata* (Dozy & Molk.) Lindb.; **B,** *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **C,** *Macromitrium longicaule* Müll. Hal.; **D,** *Schlotheimia rubiginosa* C.H. Wright; **E,** *Ulota splendida* E.B. Bartram; **F,** *Zygodon orientalis* (Dixon) Goffinet.

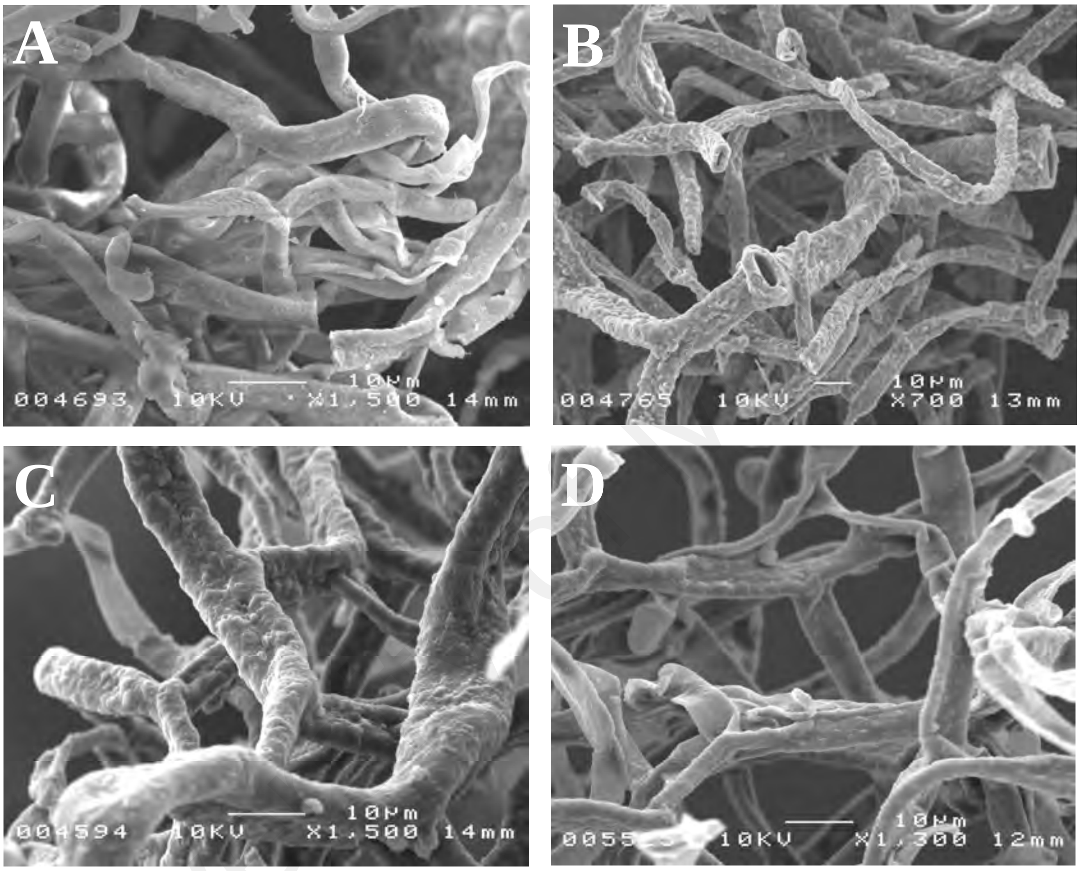

Figure 4.5. SEM images of rhizoids. — **A,** *Groutiella kelantanense* sp. ined.; **B,** *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr.; **C,** *Zygodon orientalis* (Dixon) Goffinet; **D,** *Zygodon reinwardtii* (Hornsch.) A. Braun.

4.2.5 Foliation

Leaves are spirally inserted along the stem and branches in most Orthotrichaceae, except in two *Desmotheca* species and *M. orthostichum*, which show a distinct pentastichous disposition of vegetative leaves, more often referred to as a 5-ranked arrangement (Vitt et al., 1995; Eddy, 1996). In the Macromitroideae, the leaves on the creeping axes are hidden by orthotropic branches and are usually eroded in the mature plant. If leaves are present, they are usually located at the younger portion or the terminal part of the creeping axis, always radially arranged and squarrose-recurved in orientation.

The orientation of the leaves varies according to the state they are in. When dry, the leaves can be erect and appressed (e.g., *D. apiculata*, *Z. intermedius*) (Fig. 4.6A-C); weakly flexuose (e.g., *M. cuspidatum*) to flexuose-undulate (e.g., *M. ochraceum*, *M. ochraceoides*); or flexuose-contorted, which is the most common orientation observed for most Orthotrichaceae (Fig. 4.6D-F, 4.7A-C). In many species, the upper laminae are strongly deflexed, curved or twisted when dry. There are also extreme cases where most or all leaves are typically twisted. In many taxa, they are often irregularly twisted except in a group where the leaves are tightly twisted around the branch axis (in *G. tomentosa*, *M. blumei*, *M. blumei* var. *zollingeri*, *M. densum*, *S. rubiginosa*, *S. wallisii*) (Fig. 4.7D-F).

When wet, leaves vary from erect, erect-spreading to wide-spreading in most of the species. One common observation for many species is that leaves at the upper portion of stems or branches have a tendency to recurve or squarrose-recurve, whereas they are wide-spreading and straight at the proximal position of stems and branches (e.g., *M. cuspidatum*, *M. ochraceum*, *M. salakanum*).

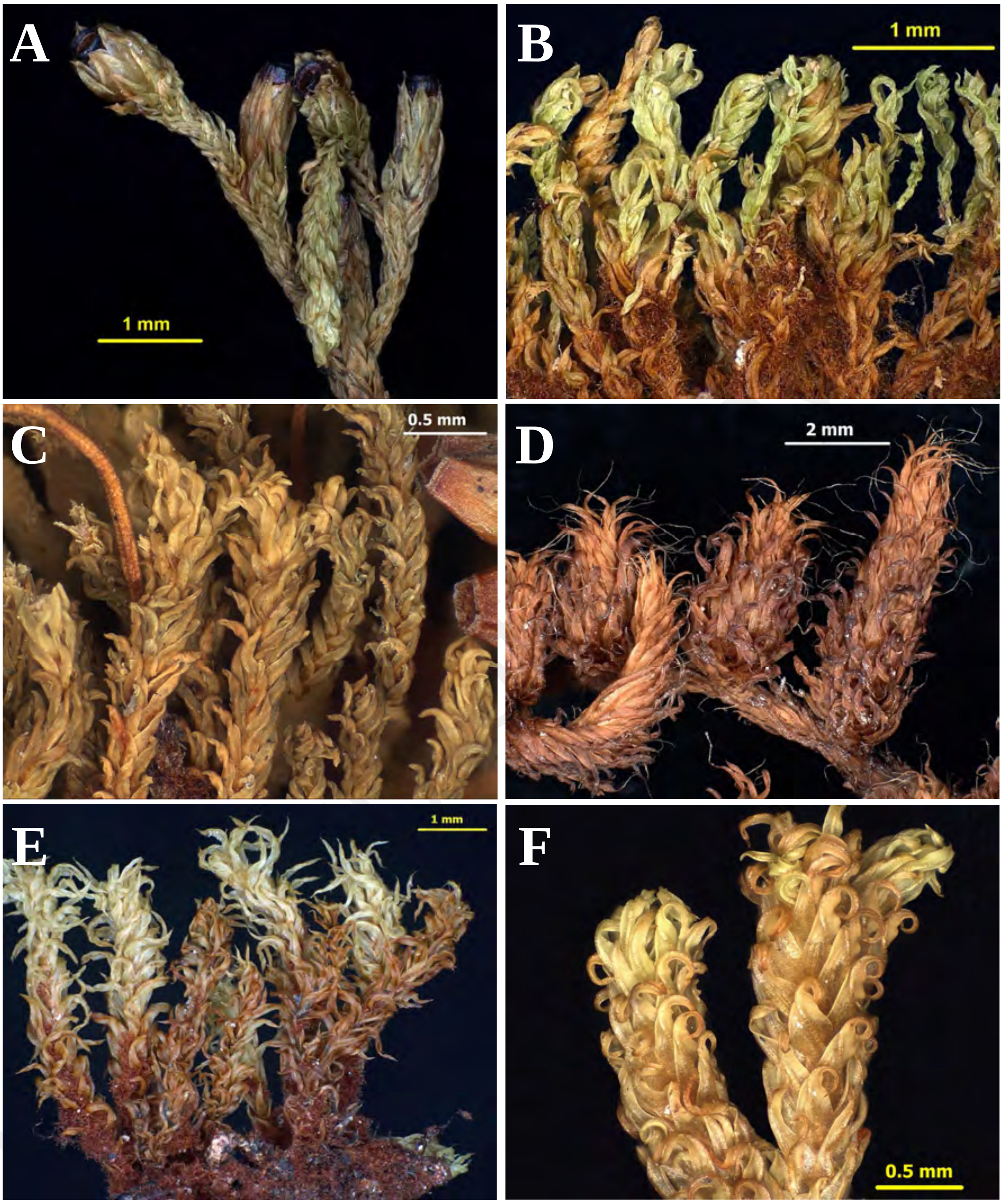

Figure 4.6. Foliate arrangement I. — **A,** *Desmotheca apiculata* (Dozy & Molk.) Lindb.; **B,** *Zygodon intermedius* Bruch & Schimp.; **C,** *Macromitrium orthostichum* Nees ex Schwägr.; **D,** *Macromitrium longipilum* A. Braun *ex* Müll. Hal.; **E,** *Zygodon orientalis* (Dixon) Goffinet; **F,** *Macromitrium salakanum* Müll. Hal.

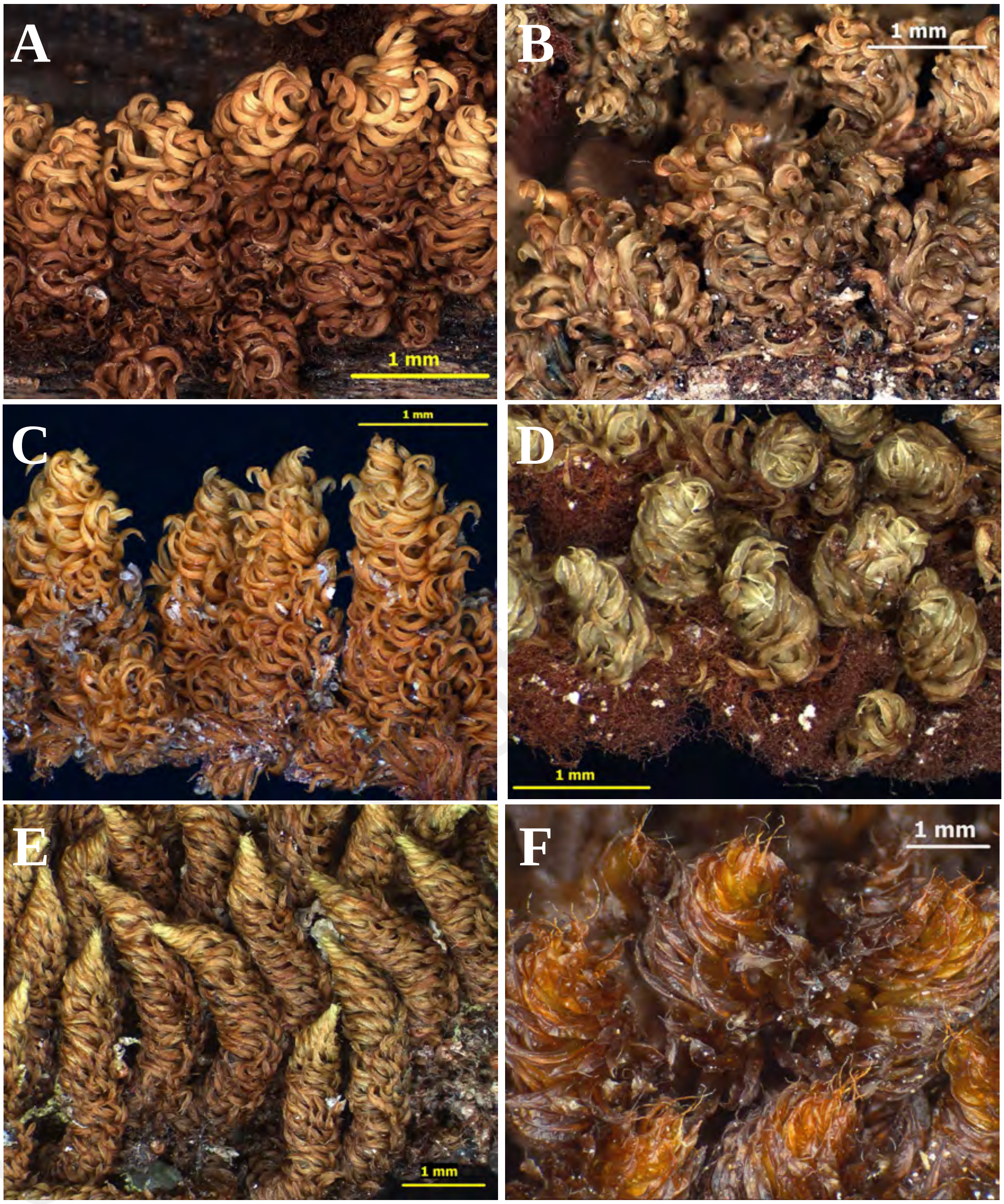

Figure 4.7. Foliate arrangement II. — **A,** *Macromitrium falcatulum* Müll. Hal.; **B,** *Macromitrium nepalense* (Hook. & Grev.) Schwägr.; **C,** *Macromitrium parvifolium* Dixon; **D,** *Macromitrium densum* Mitt.; **E,** *Macromitrium blumei* var. *zollingeri* (Mitt. *ex* Bosch & Sande Lac.) S.L. Guo, B.C. Tan & Virtanen; **F,** *Schlotheimia wallisii* Müll. Hal.

4.2.6 Leaf characters

Members of Orthotrichaceae exhibit a wide range of leaf sizes and shapes, and often the leaf shapes are associated with plant size. In the smaller species, leaves vary from ovate to short-elliptic (e.g., *D. apiculata*), wide or slender long-elliptic to elliptic-lanceolate (e.g., *M. blumei*, *M. densum*, *M. orthostichum*), or broadly lingulate (e.g., *M. falcatulum* Müll. Hal., *M. papillisetum*, *Z. intermedius*) to slender lingulate (e.g., *M. parvifolium* Dixon). In the medium to large-sized plants, leaves are usually elliptic-lanceolate (e.g., *M. longipilum* A. Braun *ex* Müll. Hal., *S. rubiginosa*, *S. wallisii*), or lanceolate to slender lanceolate from an oblong base (e.g., *M. macrosporum* Broth., *M. ochraceum*, *M. salakanum*). There are also species with lingulate leaves that are much more elongated compared to the smaller species (e.g., *M. incurvifolium* (Hook. & Grev.) Schwägr., *M. nepalense*), as well as lingulate-lanceolate leaves (e.g., *G. tomentosa*). Linear-lanceolate leaves are rare among Malaysian Orthotrichaceae. It is only found in *U. splendida* and an extreme form of *Z. orientalis*. *Z. reinwardtii* demonstrates another uncommon leaf shape in the family, a subspathulate shape, with upper leaves slightly broader apices (however, lower leaves are not distinctly basally narrowed).

Although many species exhibit a great variety of leaf sizes (e.g., *M. angustifolium*, *M. fuscescens*, *M. ochraceiodes*, *M. orthostichum*, *S. wallisii*, *Z. orientalis*), these variations are usually overlapping and therefore cannot be categorized into different states. Leaf dimorphism only occurs in *Desmotheca,* where the leaves at the basal portion of vertical branches are long-lingulate, but the rest of the leaves along vertical branches are ovate to short-elliptic and are roughly three quarters of the length of the earlier leaves.

Leaf lamina—The leaf lamina for most Orthotrichaceae is mostly flat and rarely undulate, and occasionally pleated at the leaf base next to the margin. Rugose laminae, usually found at the apical part of leaf, has only been observed in *G. kelantanense*, *S. rubiginosa* and, occasionally, among *M. longipilum* varieties. The leaf laminae of all the Orthotrichaceae are deeply channelled along the costa, with the groove beginning from a short distance below the apex. Therefore, the leaves appear keeled especially at its basal lamina in both dorsal and side views. For convenience, here I adopt the terms 'basal lamina' and 'upper lamina' to refer to the proximal portion and the distal portion, respectively, of the leaf lamina.

Apex—Variations in the leaf apices of Malaysian Orthotrichaceae can be generally classified into two groups. In the first group, the upper lamina is long, distinctly slender, tapers off gently from a broad basal lamina, and then ends in an acute to acuminate apice (e.g., *M. angustifolium*, *M. macrosporum*, *M. ochraceum*, *U. splendida*). In the second group, the upper lamina can be either long or short, but is as wide as the basal lamina. It then ends in a rounded to obtuse apex, or more often, tapers abruptly to a mucronate or cuspidate end. An excurrent costa is present in species with a cuspidate apex and can be either short or long (e.g., *M. blumei*, *S. wallisii*). Emarginate or retuse apices are not common in the family; thus far this has only been observed in *M. densum* and occasionally in *S. rubiginosa*. Two species of particular interest are *G. tomentosa* and *M. angustifolium*, where the apices of their mature leaves are always fragile and are easily broken off even by a gentle touch. Although the purpose of producing these fragile leaf tips is unknown at the moment, this character has become a useful tool in identifying these two species in the field.

Margin—In general, the leaf margins are plane and flat at the upper lamina for all the taxa studied. Recurved or weakly recurved margins are common at the basal lamina for most of the taxa. However, the magnitude of curvature is largely variable due to the strongly carinate leaf base and is not persistent in any particular taxon. Upper laminal margins are mostly to almost entire with irregular and indistinct undulation due to cell projections, or are often scabrous due to the lateral projection of cell papillae. Toothed and serrulate margins are only found in a handful of taxa in the family, and has only been seen in *M. orthostichum*, *M. ochraceum*, *M. ochraceoides* and *Z. orientalis*. Among Orthotrichaceae, *U. splendida* exhibits the most elaborate leaf margin with denticulate teeth appearing irregularly along the margin. The leaf margin of *Z. reinwardtii* is decorated with pronounced dentations, sometime of two to three cells wide, distantly arranged on the upper laminal margin. The basal laminal margins are rather simple in all Orthotrichaceae, and they are either entire or weakly crenulate due to lamina cell projections.

Border—In most cases, marginal cells of Orthotrichaceae leaf laminae are not differentiated and, therefore, the margins are not bordered. An exception is the genus *Groutiella*, with noticeable borders occurring on both sides of the basal laminal margin. The border consists of two to five rows of hyaline, thin-walled, long-rectangular and smooth cells, that contrast sharply with the chlorophyllose, thick-walled, short oval to oblong, and tuberculate basal laminal cells. The existing hyaline border is very distinctive and thus, the genus *Groutiella* is easily distinguished from other Orthotrichaceae under the compound microscope.

Costa—All laminae are unicostate, and the costa is stout. The costa is usually as long as the leaf itself and reaches the leaf tips (i.e., is percurrent, e.g., *M. angustifolium*, *M. ochraceum*, *U. splendida*, *Z. orientalis*), or is slightly shorter and not reaching the leaf tips (e.g., *G. tomentosa*, *Z. intermedius*). However, in a number of species the costa exceeds the leaf (i.e, it is shortly excurrent, e.g., *D. apiculata*, *M. falcatulum*, *M.*

orthostichum, *M. salakanum*, to long excurrent, e.g., *M. cuspidatum*, *M. longipilum*, *S. wallisii*). The costa surface is generally smooth, except for the excurrent portion which often bears minute teeth, scattered on its ventral surface (Fig. 4.8). Those teeth are due to the prosenchymatous stereid cells found at the apical portion of the costa. On the whole, the costa are generally stout, but in a number of species (e.g., *M. cuspidatum*, *M. longipilum*), the laminal cells are integrated with the costa cells, especially at the narrow strip of lamina that has extended together with the excurrent arista.

Anatomy—The leaf lamina is typically unistratose (single-cell thick) for all Malaysian Orthotrichaceae (Fig. 4.9A, C-I), except *G. tomentosa*, where the leaf apex is 2–3-cells thick (Fig. 4.9B). In the other Malaysian Orthotrichaceae, the only structure that is multi-layered is the costa. Viewed in cross-section, the costa is made of two ventral guide cells in a single band and 1–3 bands of substereid and stereid cells (Fig. 4.9). Due to the absence of epidermal chlorophyllose cells, the ventral guide cells are exposed on the leaf adaxial surface.

Areolation—Lamina cells are parenchymatous in most Orthotrichaceae except in the genus *Schlotheimia*, where the cells are strictly prosenchymatous.

Upper laminal cells—Upper laminal cells are usually small, and the length-width ratio is normally 1:1, at the most 2:1 or 3:1 for some larger species (e.g., *S. rubiginosa*, *S. wallisii*, *U. splendida*, *M. longipilum* and its varieties). Cells are mostly rounded or oblate, to wide rectangular; rhombic only in the larger species mentioned above. Cell walls are moderately thick to incrassate, not pitted except occasionally in *Schlotheimia*. The surfaces are either smooth, prorate, or more commonly pluripapillose with obscure to distinctly seen papillae. There are usually 2–4 simple papillae on each cell, but they

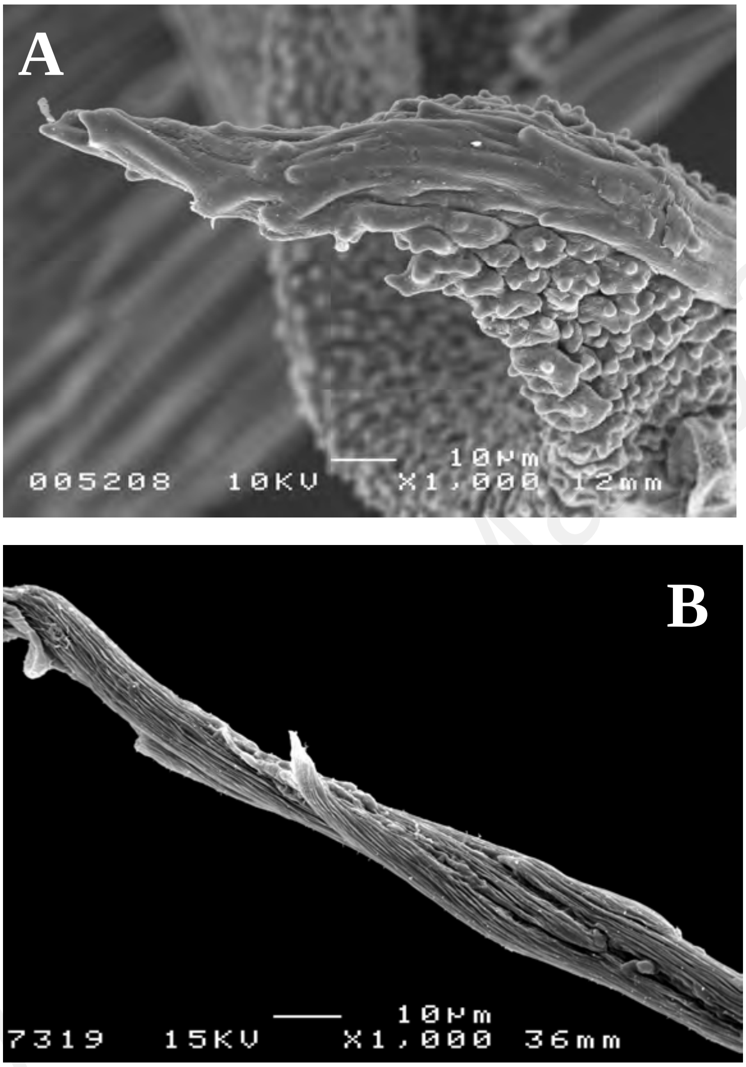

Figure 4.8. SEM images of the excurrent costa in *Macromitrium orthostichum* Nees ex Schwägr. (A), and *Macromitrium ochraceoides* Dixon (B). Note costal cells with prorate ends that appear toothed under compound microscope.

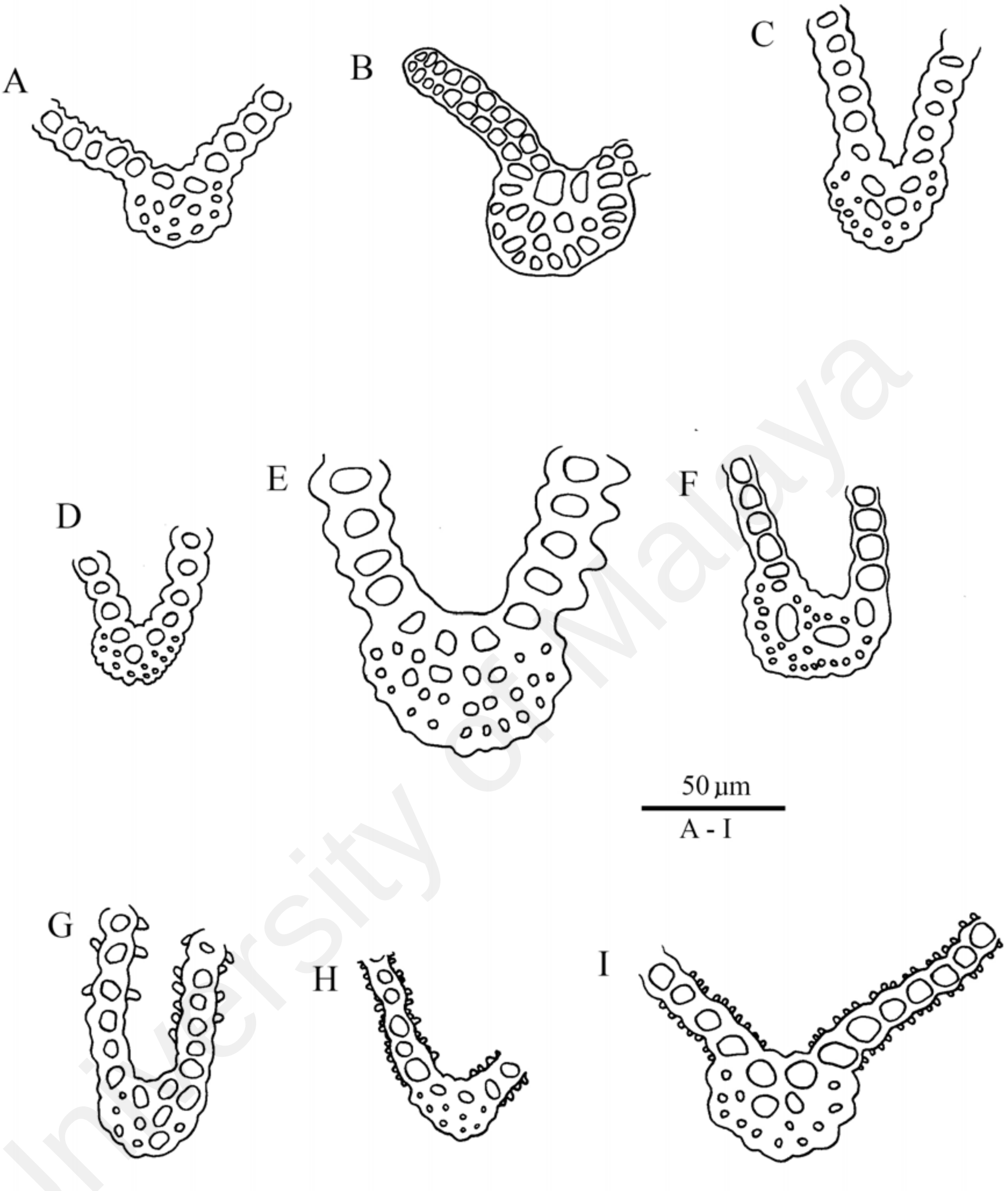

Figure 4.9. Cross-sections of leaf costae. — **A,** midleaf of *Desmotheca apiculata* (Dozy & Molk.) Lindb.; **B,** upper lamina of *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **C,** lower lamina of *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **D,** midleaf of *Macromitrium blumei* Nees *ex* Schwägr.; **E,** midleaf of *Macromitrium ochraceoides* Dixon; **F,** midleaf of *Schlotheimia rubiginosa* C.H. Wright; **G,** midleaf of *Ulota splendida* E.B. Bartram; **H,** midleaf of *Zygodon intermedius* Bruch & Schimp.; **I,** midleaf of *Zygodon orientalis* (Dixon) Goffinet.

often occur in a bigger number in the genus *Zygodon*. In the genus *Zygodon*, there are 5–8 papillae on a single cell, usually smaller in size and located on the cell wall instead of on the cell lumen as in other Orthotrichaceae. These small, thick-walled and papillose lamina cells are purported to play a role in trapping water and, thus, protect the plants from dessication (Grout, 1908). On the other hand, it may also create an external carpillary system that enhances superficial water movement, keeping the plant well wetted (Proctor, 1981).

Normally, there is a gradual change of the size and shape of lamina cells, beginning from the midleaf or more proximally, down towards the base. Nearing the midleaf or just below, longer cells are found. However, cell lengths usually increase gradually until they match those of the basal laminal cells. The only exception is in *M. fuscescens*, where cell length only changes abruptly at midleaf, thus resulting in a demarcation line between the upper and basal laminal cells (Fig. 4.10A).

Basal laminal cells—Basal laminal cells are normally longer, but not much wider than the upper laminal cells. The length-width ratios attained are 4–6:1 while the maximum is 7–9:1 (for *U. splendida*). However there are a few with cells of similar length or that are slightly longer than the upper laminal cells. Such cells are normally short-rectangular with a length-width ratio of 2:1 or less than 1.5:1 (e.g., *D. apiculata*, *M. densum*, *M. orthostichum*, *M. papillisetum*, *Z. intermedius*). Cell walls are all incrassate, and are often as thick as, or thicker than, the lumen. In extreme cases, the thickness of cell walls can cause the lumen to appear slender and linear. The cell wall thickening can either be even or uneven on both sides; in the latter, the lumen is curved or sigmoid. Cells are mostly not pitted; pitted cells are only found near to the insertion, especially at

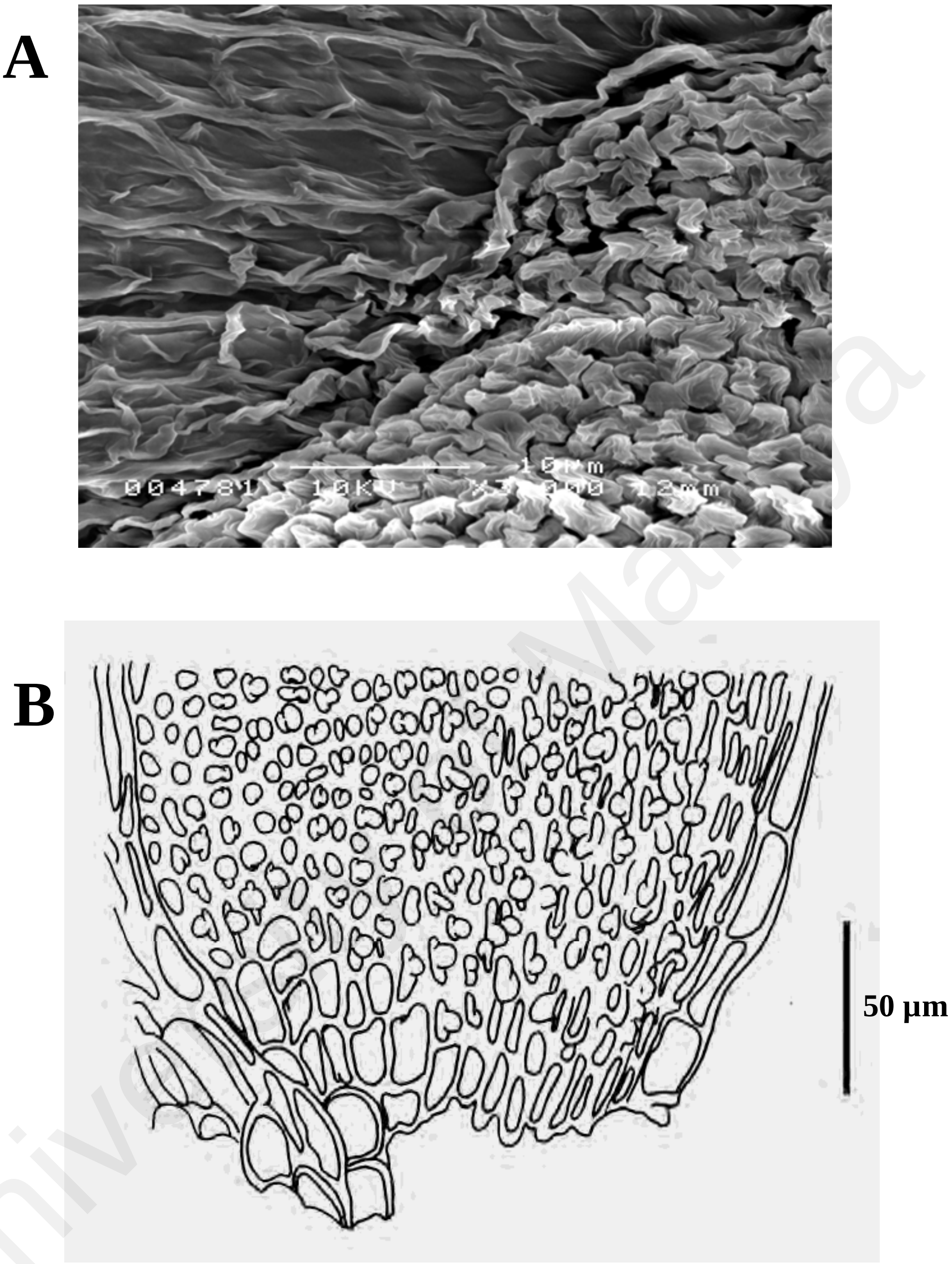

Figure 4.10. Laminal cells in Orthotrichaceae. — A, SEM image of *Macromitrium fuscescens* Schwägr. at its midleaf region, showing the sudden change of laminal cell types, from short and pluripapillose cells in the upper lamina (right) to long and smooth cells in the lower lamina (left), leaving a demarcation line between them; **B,** Basal lamina of *Groutiella tomentosa* (Hornsch.) Wijk & Margad., note that leptodermous tissue of large, smooth and thin-walled rectangular cells found at the juxtacostal region, right before the leaf insertion.

the juxtacostal region. The surface of basal laminal cells can be smooth and flat, or convex or papillose. If papillae are present, they are always unipapillose. The papillae may be strong and tall, like tubercles (the surface often referred to as ‘tuberculate’).

Basal laminal leptodermous tissue—This refers to a group of thin-walled, smooth, large, square or rectangular cells distinctly different from the thick-walled, thin lumen basal laminal cells. This group of cells only occurs at the juxtacostal-insertion region. However, this leptodermous tissue is mostly very small and at times is absent from Malaysian Orthotrichaceae. Exceptions are in *Z. orientalis* and both of the *Groutiella* species, where the leptodermous tissue is distinct and sometimes pigmented, as in *Z. orientalis*. This is easily seen under the compound microscope (Fig. 4.10B).

4.2.7 Vegetative propagules

Propagules are not common in the Orthotrichaceae, except in *Zygodon* (Malta, 1926). The propagules are often found at the leaf axils and can be abundant in *Z. intermedius* and *Z. reinwardtii* (Calabrese, 2006). For these two species, propagules are always fusiform to fusiform-clavate, and consist of 4–6 hyaline cells with transverse septa only (Calabrese, 2006). However, in Malaysian *Z. intermedius* and *Z. reinwardtii*, propagules are rarely produced. No other vegetative reproductive structure has been reported and observed for Malaysian Orthotrichaceae.

4.2.8 Sexual condition

Most species are phyllodioicous; the male plant often much smaller in size and epiphytic on the female plant. There are also free-living dioicous species that produce male (perigonia) and female (archegonia) organs on different individuals (e.g., *Z. intermedius, Z. orientalis* and the two *Groutiella* species). Only two species were found to be autoicous (a form of the monoicous condition) in this study, i.e., *Ulota splendida* and *Z. reinwardtii*. An interesting observation about the position of the gametangia on these two species is that the perigonia are always located just beneath the perichaetia in *U. splendida*, while the perigonia are located further down below the perichaetia in *Z. reinwardtii*. However the usefulness of this character for distinguishing these two genera will require further investigation of more taxa.

A species of particular interest is *M. blumei*, which displays both the autoicous and phyllodioicous conditions. The ability of producing normal males or dwarf males in this species has also been noted by Dening (1935), but the reason for this particular species being heteroicous remains unknown. It has been long known that the anisosporous condition is correlated with the presence of a dwarf male (Ernst-Schwarzenbach, 1939; Mogensen, 1981; Ramsay, 1979; Une, 1985b). Therefore it appears possible to determine the sexual condition of species with anisosporous spores even in the absence of dwarf or normal male plants within a population. Consequently, the sexual conditions of *M. densum*, *M. longipilum* var. *ligulatus*, *M. longipilum* var. *rugatus*, *M. ochraceum*, *M. ochraceiodes*, *M. papillisetum* and *M. parvifolium* are treated as phyllodioicous in this study, although only female plants were encountered.

4.2.9 Perigonia

In the Orthotrichaceae, the perigonia are either bud-like (growing on the highest position of stems and branches in dioicous species, and below the terminal perichaetia in monoicous species) or are epiphytic dwarf male plants in phyllodioicous species (Fig. 4.11). Among the Orthotrichaceae, the occurrence of dwarf male plants was first observed in *Macromitrium s. l.* (including *Groutiella*) by Dozy and Molkenboer (1861), and later was also reported in *Schlotheimia* by Ramsay (1979). In a study of the

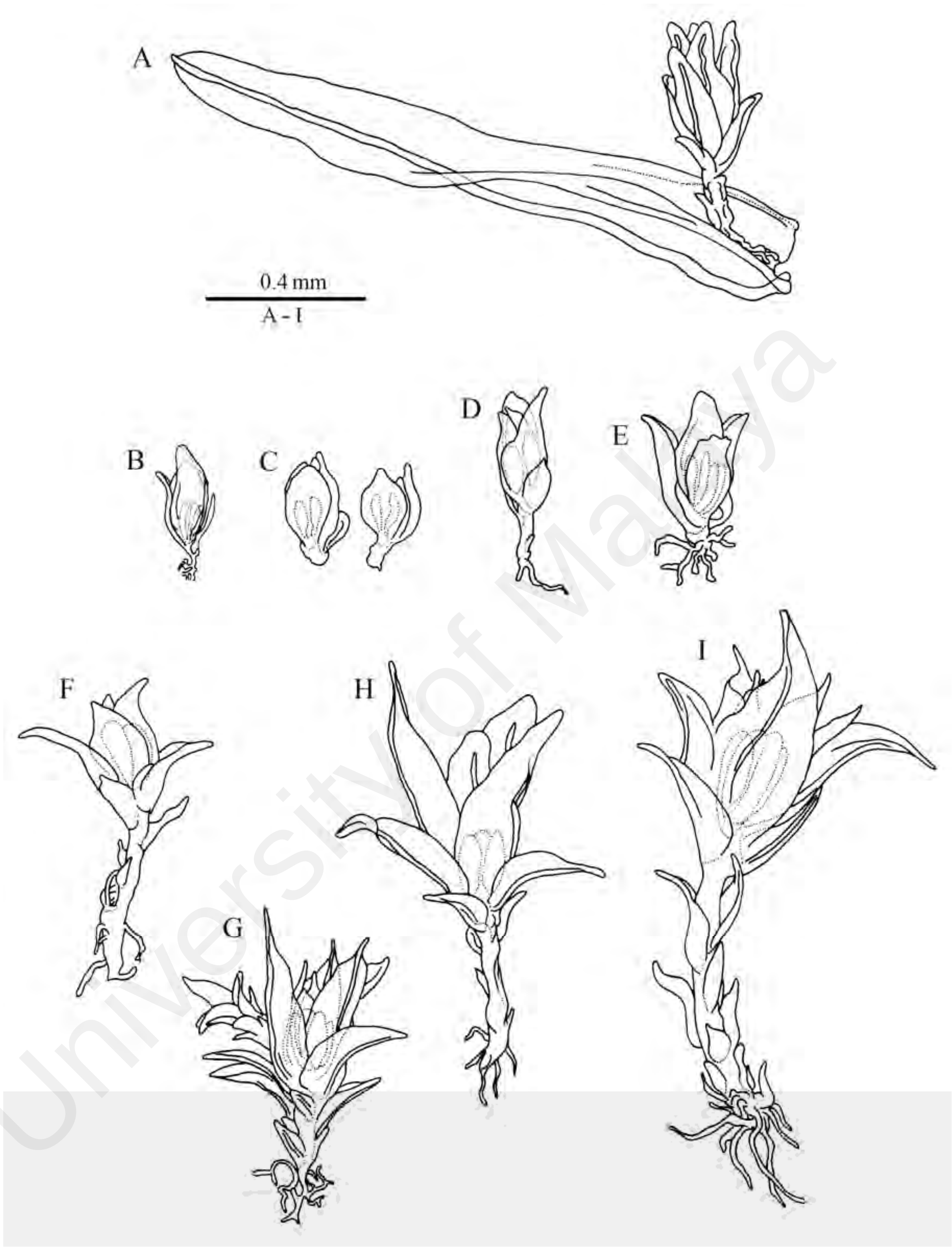

Figure 4.11. Epiphytic dwarf males of Orthotrichaceae. — A, *Macromitrium nepalense* (Hook. & Grev.) Schwägr. with epiphytic dwarf male found at the branch leaf axil; **B,** *Macromitrium orthostichum* Nees ex Schwägr.; **C,** *Desmotheca apiculata* (Dozy & Molk.) Lindb.; **D,** *Macromitrium fuscescens* Schwägr.; **E,** *Macromitrium longicaule* Müll. Hal.; **F,** *Macromitrium cuspidatum* Hampe; **G,** *Macromitrium blumei* Nees *ex* Schwägr.; **H,** *Macromitrium angustifolium* Dozy & Molk.; **I,** *Macromitrium longipilum* A. Braun *ex* Müll. Hal.

distribution of different sexual plants of Japanese *Macromitrium*, Une (1985a) correlated the increase in frequency of sporophyte production with the occurrence of dwarf male plants. He observed that the distance between sperm and egg has been minimized by having epiphytic dwarf males on female plants.

The perigonia consist of a few antheridia with numerous paraphyses and are protected by a few leaves. The perigonial leaves are usually ovate to ovate-lanceolate, mostly concave, 0.2–0.5 mm, with acute to broadly acuminate apices and a faint costa reaching or ending before the leaf tips.

4.2.10 Perichaetia

In Orthotrichaceae, the perichaetia are located at the termini of both stems and vertical branches in the acrocarpous species (subfamily Orthotricoideae) but are found at the termini of vertical branches only in cladocarpous species (subfamily Macromitrioideae). A perichaetium consists of 10–20 archegonia with many paraphyses and are protected by a few leaves. The archegonia are either shorter (e.g., *M. angustifolium*, *M. falcatulum*, *Z. intermedius*) or as long as the paraphyses (e.g., *D. apiculata*, *G. tomentosa*, *M. longipilum*) and vary in length (0.3–1.0 mm). Paraphyses are linear, generally shorter (Fig. 4.12), rarely the length of the vaginula (e.g., *M. angustifolium, M. cuspidatum, M. fuscescens, M. incurvifolium, S. rubiginosa, S. wallisii*), made of hyaline, short to long rectangular cells, and have pointed apical cells (Fig. 4.13). Paraphyses are filamentous and have a uniseriate cell arrangement. They are never branched, although they may occur very closely together. The exception occurs in both species of *Schlotheimia*, where many paraphyses actually arise from (or join into) a common base (Fig. 4.13M). The perichaetial leaves, at least the inner ones are usually erect and ensheath the vaginula. The sheathing behaviour is believed to be an adaptation to epiphytic habitats

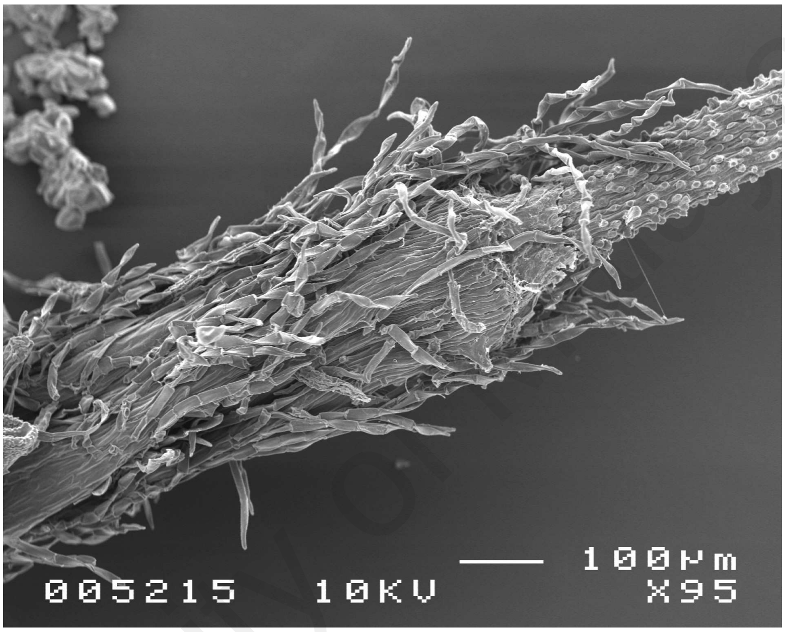

Figure 4.12. SEM image showing vaginula densely covered by paraphyses in *Macromitrium orthostichum* Nees ex Schwägr.

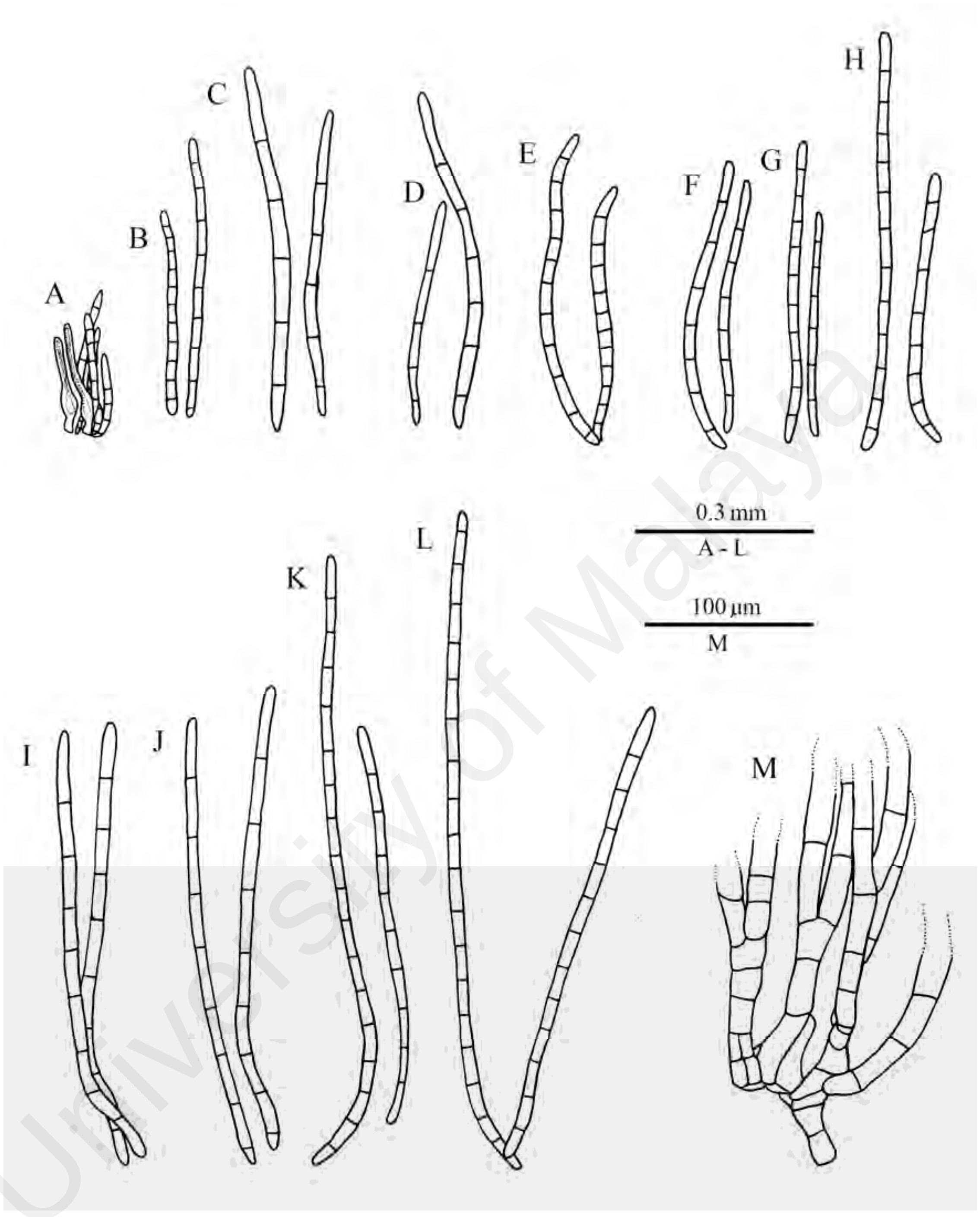

Figure 4.13. Forms of paraphyses in the Orthotrichaceae. — A, *Macromitrium orthostichum* Nees ex Schwägr.; **B,** *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **C,** *Macromitrium angustifolium* Dozy & Molk. ; **D,** *Macromitrium parvifolium* Dixon; **E,** *Macromitrium falcatulum* Müll. Hal.; **F,** *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr.; **G,** *Macromitrium longicaule* Müll. Hal.; **H,** *Macromitrium fuscescens* Schwägr.; **I,** *Macromitrium macrosporum* Broth.; **J,** *Zygodon orientalis* (Dixon) Goffinet; **K,** *Macromitrium cuspidatum* Hampe; **L,** *Schlotheimia rubiginosa* C.H. Wright; **M,** paraphyses join into a single entity at the basal portion in *Schlotheimia rubiginosa* C.H. Wright.

(Vitt, 1981a). Perichaetial leaves may be not, slightly, or distinctly differentiated from vegetative leaves. Leaf shape ranges from oblong, oblong-lanceolate, lanceolate to linear-lanceolate. In a few species, perichaetial leaves are larger than vegetative leaves (e.g., *D. apiculata*, *M. angustifolium*, *S. rubiginosa*). However, species with shorter and smaller perichaetial leaves are more common among Malaysian Orthotrichaceae. Perichaetial leaves are usually distinguishable from vegetative leaves by the upper lamina of the former, which is either slender and long, or broad and short, with a percurrent to long-excurrent costa. The upper laminal cells of perichaetial leaves are also mostly similar to those of vegetative leaves, but basal laminal cells of the former are often distinctly differentiated. These basal laminal cells vary from rhombic to rectangular, are consistently smooth, hyaline and often extend far up the lamina.

Variation in perichaetial leaves has long been accepted as a character useful for distinguishing among closely related species (Bartram, 1939; Vitt & Ramsay, 1985; Vitt et al., 1995; Eddy, 1996). The current study has also examined and expanded on the use of perichaetial characters in the taxonomy of Malaysian Orthotrichaceae.

4.2.11 Vaginulae

The base of the seta is always sheathed by the vaginula which is derived from the venter of the archegonium. The vaginula is generally smooth in all taxa studied, without an ocrea (the flaring upper portion of the vaginula). Traditionally, the ratio of vaginula to perichaetial leaf length has been used to identify members of *Macromitrium* sect. *Cometium* (Mitten, 1873), subsequently known as *Macromitrium* sect. *Cometium* subsect. *Micro-cometium* (Fleischer, 1904; Eddy, 1996). However the present study has found that vaginula length is variable within Malaysian species and, therefore, it is proposed that vaginula-perichaetial leaf length ratio might have little value in taxonomic distinction.

4.2.12 Calyptrae

Members of Orthotrichaceae are characterized by their large, mitrate or campanulate, and hairy calyptrae (Fig. 4.14A-E, 4.15D-F). However, there are also species with naked calyptrae and the degree of hairiness varies among different taxa. *Zygodon* is the only genus with cucullate calyptrae among Malaysian Orthotrichaceae, and its calyptrae are relatively narrow when compared to the others. Within Malaysian Orthotrichaceae, the calyptra shape varies from short-conic, enveloping the operculum only (in genera *Desmotheca* and *Groutiella*) (Fig. 4.14A, 4.15A), or partially enclosing the capsule, leaving the lower half of the urn and neck exposed (in genus *Zygodon*), to long-conic, covering the whole capsule (in genus *Schlotheimia*, *Ulota* and most of the *Macromitria*) (Fig. 4.15B-F).

The calyptra is non-hairy or naked in nearly half of Malaysian Orthotrichaceae (Fig. 4.14 F, 4.15A-C). They are found in all *Zygodon*, *Groutiella* and *Schlotheimia*, and also in eight species of *Macromitria*. The calyptra surface is smooth in both *Schlotheimia* and *Zygodon*, but plicate in *Groutiella* and *Macromitrium* (in species both with naked or pilose calyptrae). In species with pilose calyptrae (*Desmotheca*, *Ulota* and the remaining *Macromitria* species), the abundance and distribution of hairs vary among the taxa. The hairs are generally rough, about 3–5 cells thick at their base to 1–2 cells thick on top. These cells have protruding distal ends and appear scabrous under the compound light microscope. The hairs are abundant and variously pointed or spreading (e.g., *M. orthostichum*, *M. ochraceum*, *U. splendida*) (Fig. 4.14C, 4.15E-F), mostly erect

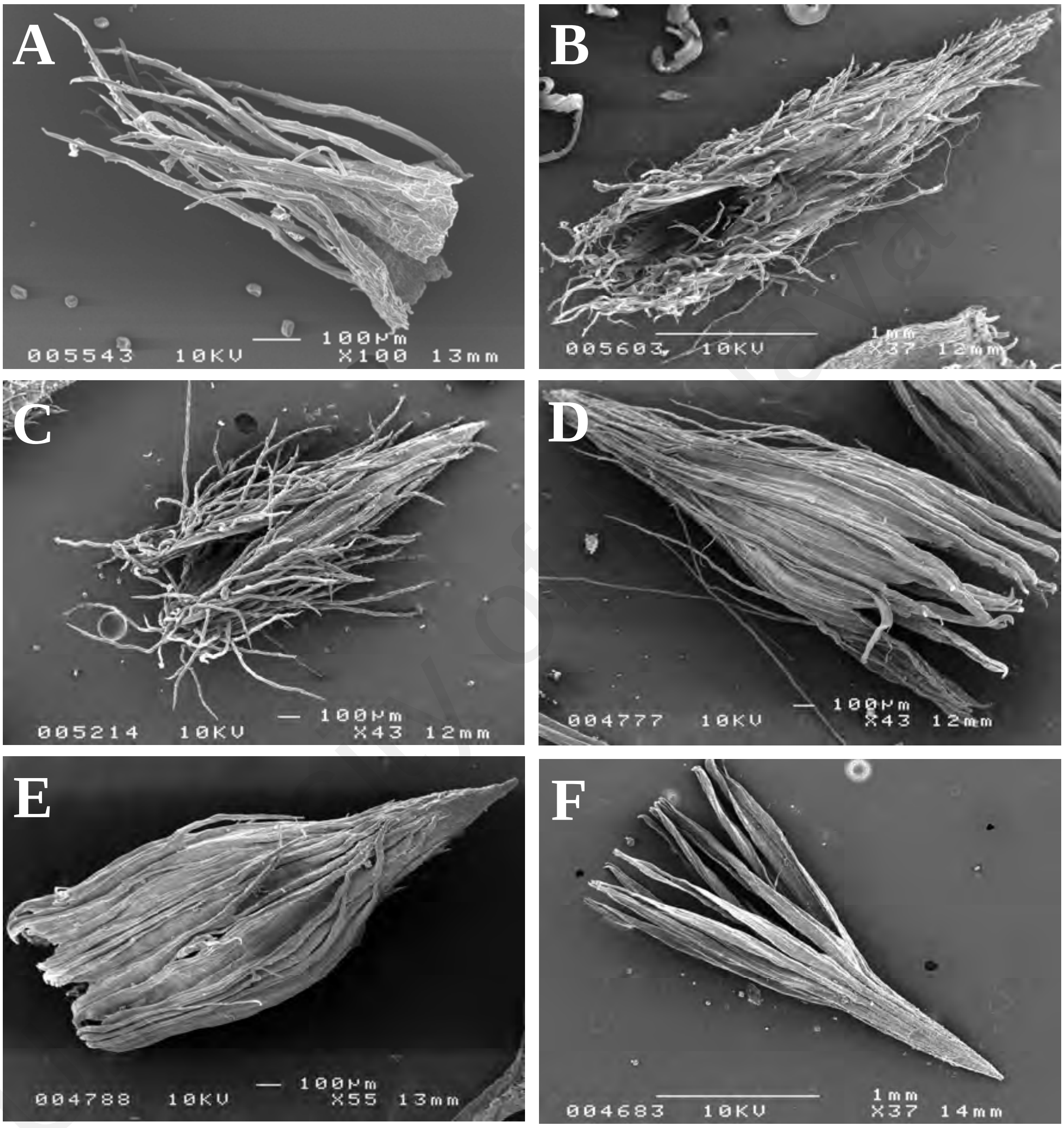

Figure 4.14. Various calyptra forms in Orthotrichaceae. — A, *Desmotheca mohamedii* sp. ined.; **B,** *Macromitrium falcatulum* Müll. Hal.; **C,** *Macromitrium orthostichum* Nees *ex* Schwägr.; **D,** *Macromitrium fuscescens* Schwägr. ; **E,** *Macromitrium longicaule* Müll. Hal.; **F,** *Macromitrium parvifolium* Dixon.

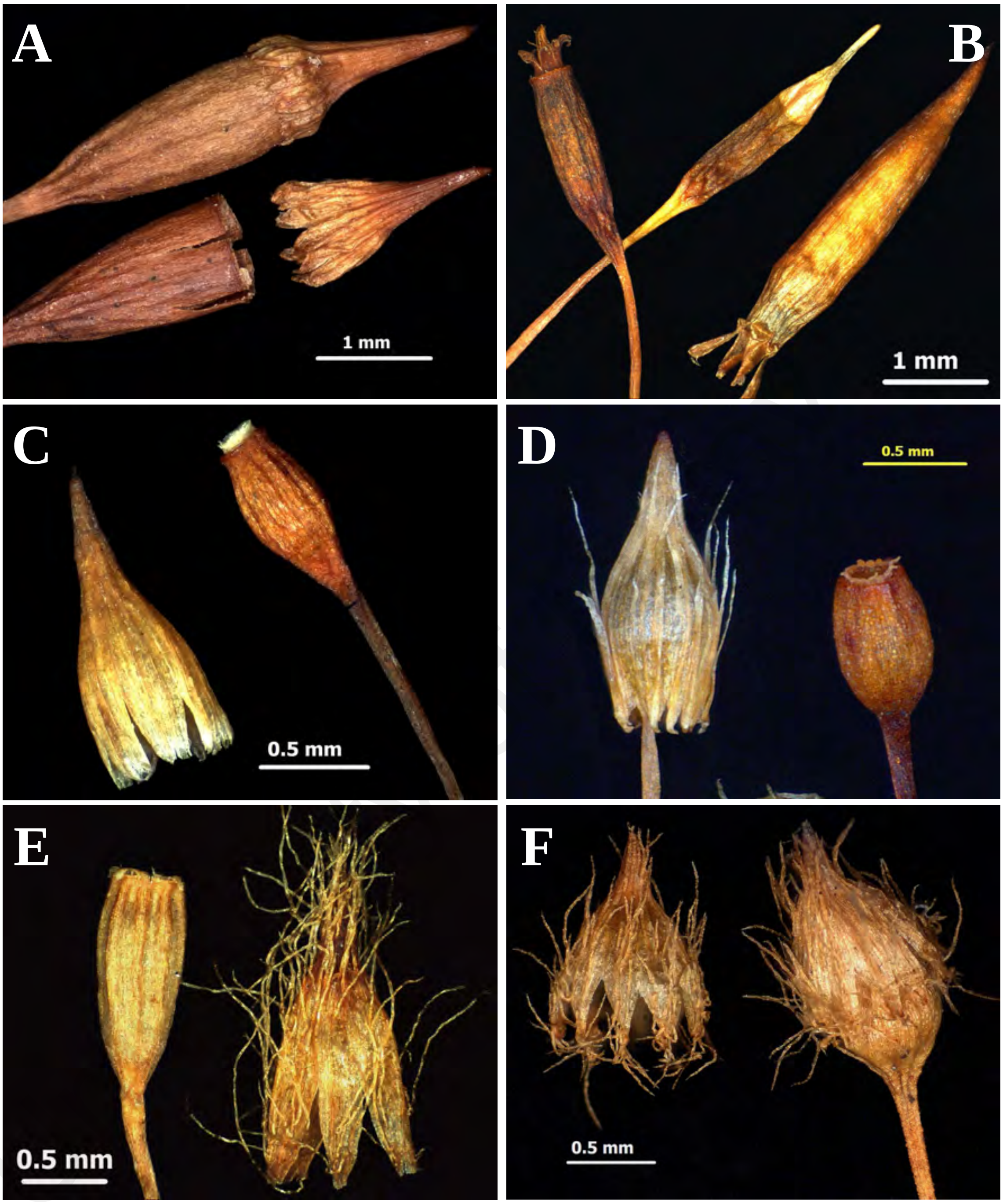

Figure 4.15. Detailed views of the capsules and calyptrae. — A, *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **B,** *Schlotheimia rubiginosa* C.H. Wright; **C,** *Macromitrium blumei* var. *zollingeri* (Mitt. *ex* Bosch & Sande Lac.) S.L. Guo, B.C. Tan & Virtanen; **D,** *Macromitrium longicaule* Müll. Hal.; **E,** *Ulota splendida* E.B. Bartram; **F,** *Macromitrium orthostichum* Nees ex Schwägr.

although some are contorted-twisted or point backwards (e.g., *M. falcatulum*, *M. nepalense*, *M. papillisetum*) (Fig. 4.14B), or just simply erect (e.g., *D. apiculata*, *M. angustifolium*, *M. cuspidatum*) (Fig. 4.14A, D, E, 4.15D). The hairs are mostly developed from the lower portion of the calyptra, especially on the ridges resulting from the strongly pleated calyptra surface (Fig. 4.14A, C-E). However, this is not the case in *M. falcatulum* and *M. nepalense* where the hairs are freely distributed all over the calyptra (Fig. 4.14B). Among the Malaysian taxa of Orthotrichaceae, the hairs are normally as long as or slightly shorter than the calyptra. Exceptions are found in *Desmotheca* and *M. orthostichum, M. ochraceum* and *M. ochraceoides*, where the hairs are usually longer than the calyptra. *Macromitrium falcatulum* is the sole species with short hairs only half of the calyptra length.

Except in the genera *Schlotheimia* and *Zygodon*, the calyptra is lacerated at the proximal end. In *U. splendida*, the proximal end of the calyptra is deeply lacerated (up to a quarter of the calyptra length) at four places, forming four broad parts with tapering ends. However, in *Groutiella*, the base of the calyptra is shallowly lacerated into 8–10 rounded serrations. The calyptra in *Desmotheca* and *Macromitrium* can either be shallowly or deeply lacerated (up to half of the calyptra length) at irregular intervals along the base, and the resultant narrow strips are either incurved or flared at the free ends (e.g., *M. angustifolium, M. cuspidatum, M. salakanum*). However, in the species of *Macromitrium* and *Desmotheca*, the calyptra is characterized by a single deep cleft of more than half the calyptra length (Fig. 4.14A-C). This observation suggests that the calyptra of *Macromitrium* and *Desmotheca* might be cucullate in origin, and the lacerated calyptra is a derived character. However, further examination of the calyptrae of all Orthotrichaceae genera is essential prior to any firm conclusion.

The calyptra base is complete and not lacerated among members of *Zygodon*. The proximal end is almost horizontal with only a single cleft, reaching up to two thirds of the calyptra length, which, in turn, causes the basal part of the urn to be exposed, and the operculum to be totally enclosed in the tubular distal end part. The calyptra bases of the two *Schlotheimia* species are always flanged near the base, lobed, with 4–8 elongated ears attached onto it (Fig. 4.15B). The cells toward the distal part of the calyptra are generally smooth except in *Macromitrium*. In *Macromitrium*, the cells are smooth to prorate at the middle part of the calyptra to distinctly prorate at the distal end and only the prorate cells appear to be scabrous under the compound light microscope.

4.3 Sporophytic structures

4.3.1 Setae

The seta is always straight, but twisted at the upper portion in all Malaysian Orthotrichaceae. The torsion of the seta has been thought to have taxonomic importance (Vitt et al., 1993 &, 1995). In half of the taxa studied, the seta is consistently twisted in a single orientation; it is either dextrorse (twisting upwards in a counter-clockwise spiral) or sinistrorse (twisting upwards in a clockwise spiral) under both wet and dry conditions. However, there are also a number of taxa which exhibit both sinistrorse and dextrorse seta within a single population. In this regard, this character can only be used with great caution and not generally applied to all taxa.

Seta length varies among taxa, ranging from being almost absent in *D. apiculata*, to 2–3 cm long for *M. longipilum* (Fig. 4.16). The seta surface is smooth (Fig. 4.17A-D) in most taxa, except those in or related to *Macromitrium* sect. *cometium* (sensu Fleischer, 1904). In this group, the seta is usually coarsely prorate to papillose (Fig. 4.17E-H). The upper portion of the seta where it joins the neck is regularly grooved into four angles in

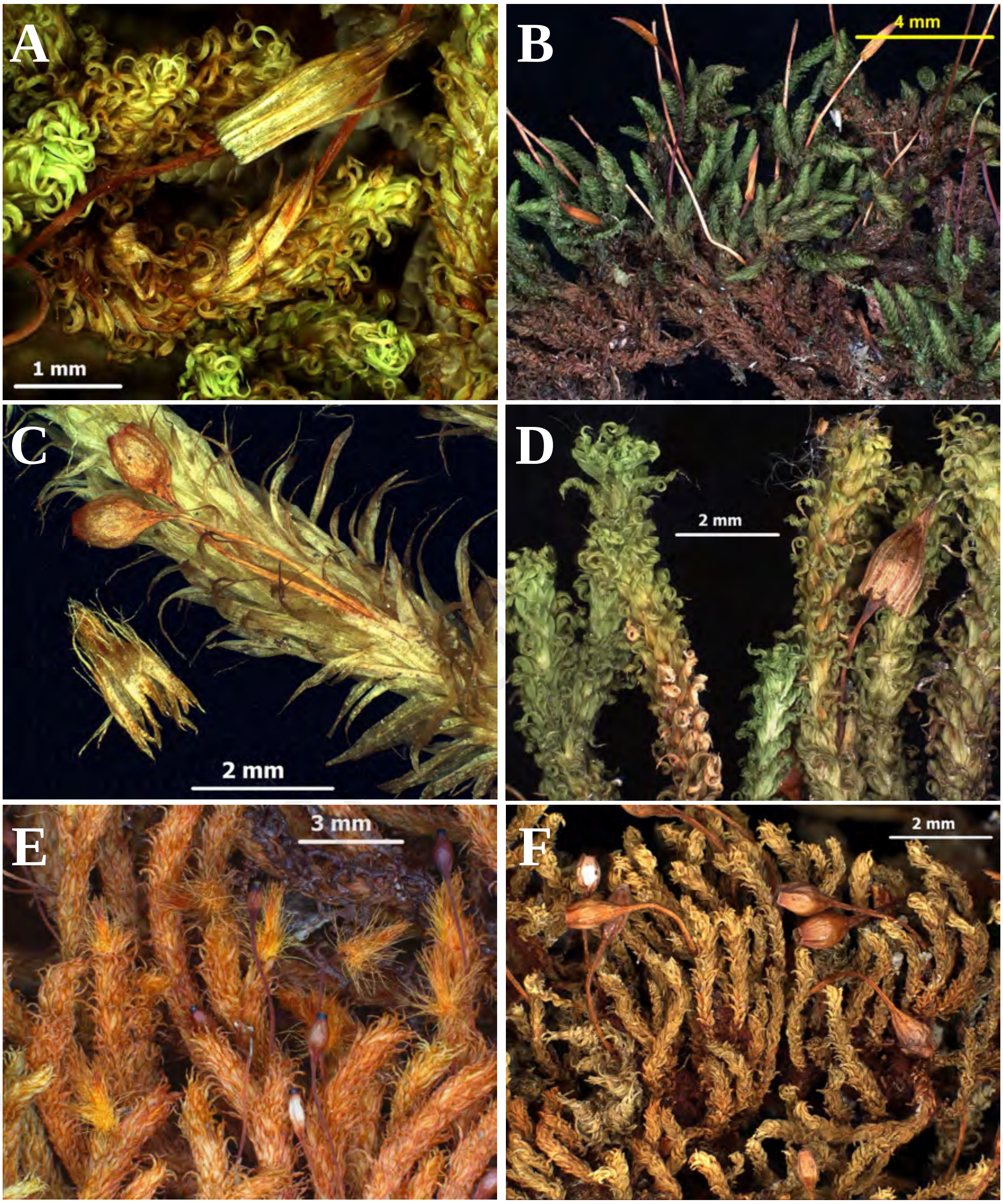

Figure 4.16. Fertile branches with sporophytes. — **A,** *Macromitrium angustifolium* Dozy & Molk.; **B,** *Macromitrium blumei* Nees *ex* Schwägr.; **C,** *Macromitrium cuspidatum* Hampe; **D,** *Macromitrium longicaule* Müll. Hal.; **E,** *Macromitrium ochraceum* (Dozy & Molk.) Müll. Hal.; **F,** *Macromitrium orthostichum* Nees ex Schwägr.

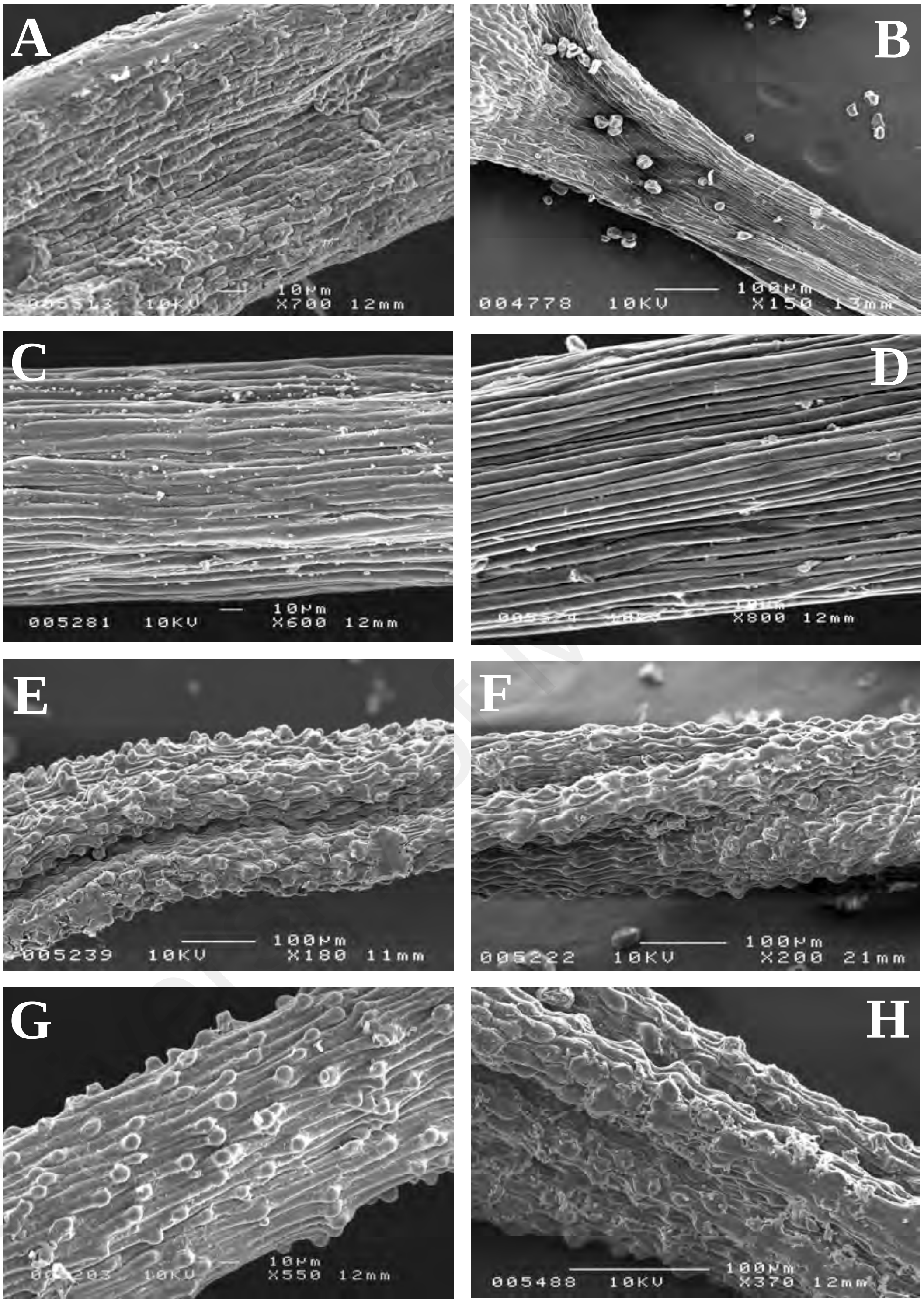

Figure 4.17. SEM images of setae in some taxa of Orthotrichaceae, showing smooth (A-D) and papillose (E-H) surface ornamentation. — A, *Macromitrium angustifolium* Dozy & Molk.; **B,** *Macromitrium fuscescens* Schwägr.; **C,** *Schlotheimia rubiginosa* C.H. Wright; **D,** *Zygodon reinwardtii* (Hornsch.) A. Braun; **E,** *Macromitrium ochraceoides* Dixon; **F,** *Macromitrium ochraceum* (Dozy & Molk.) Müll. Hal.; **G,** *Macromitrium orthostichum* Nees ex Schwägr.; **H,** *Macromitrium papillisetum* Dixon.

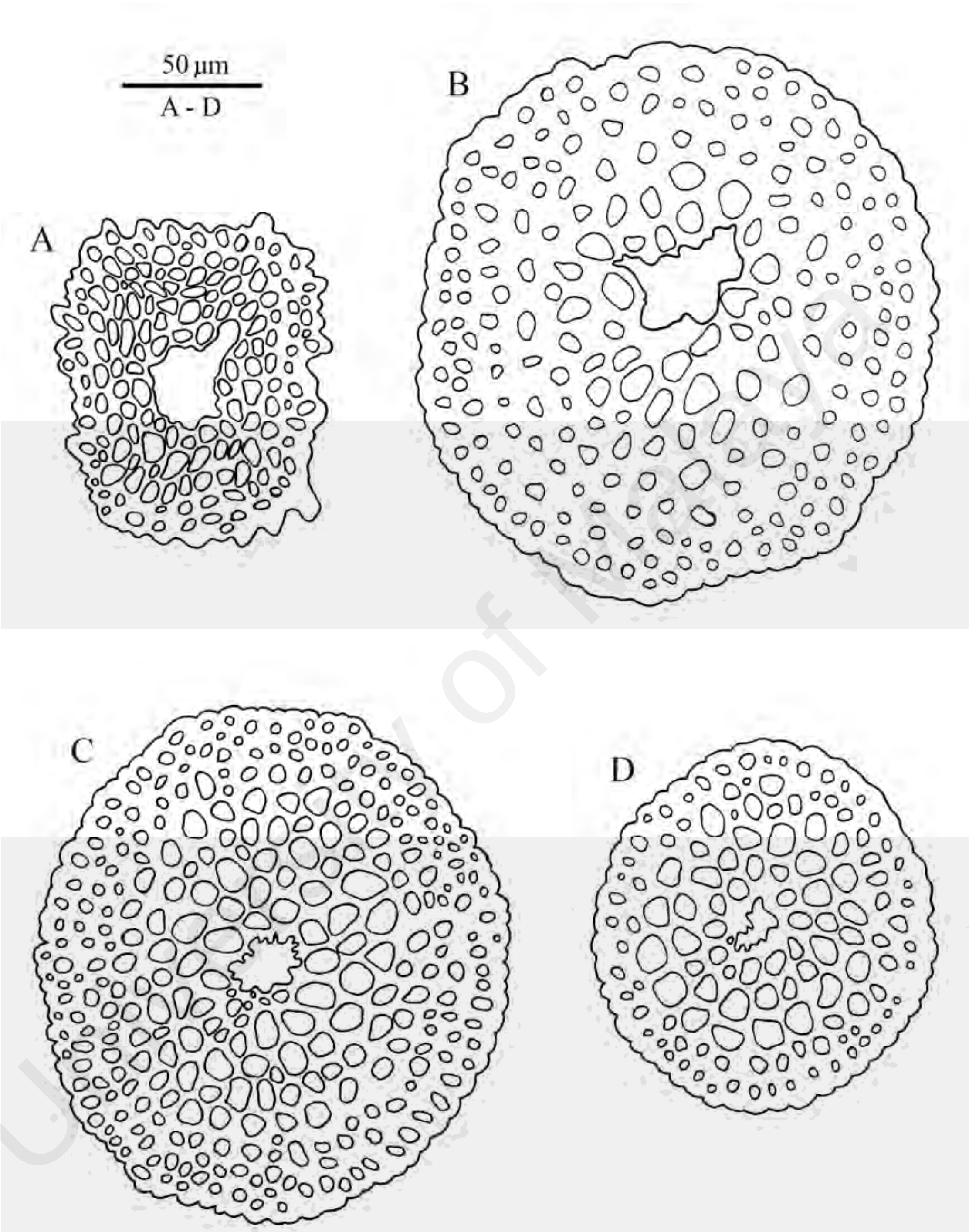

Figure 4.18. Cross-sections of setae. — A, *Macromitrium orthostichum* Nees ex Schwägr.; **B,** *Schlotheimia rubiginosa* C.H. Wright; **C,** *Zygodon orientalis* (Dixon) Goffinet; **D,** *Zygodon reinwardtii* (Hornsch.) A. Braun

association with the twisting (Fig. 4.17B, E, F, H). In cross-section, the seta is mostly rounded to quadrate (Fig. 4.18), its width ranges from 120–240 µm, but usually larger plants have thicker seta. The outermost layer of the seta is made of thick-walled epidermis cells that are usually reddish-brown to orange, the cortex is made of moderately to very thick-walled parenchyma cells, and the centre portion consists of thin-walled hydroid cells that are usually eroded when mature.

4.3.2 Capsules

The capsules are erect in all Malaysian Orthotrichaceae. The capsules are mostly exserted and usually only one capsule will develop from each perichaetium. Immersed capsules are only found among members of *Desmotheca*. The capsules are normally short and vary from slender to broadly cylindrical (in genera *Groutiella*, *Schlotheimia, Ulota* and *Zygodon*), and ovoid-ellipsoid, globose to almost cup-shaped (in genera *Desmotheca* and *Macromitrium*) (Fig. 4.15, 4.19). Both Grout (1908) and Vitt (1981a) have suggested that the short, erect and sometimes ribbed capsules with reduced peristome in Orthotrichaceae are the result of adaptation to an epiphytic habit, which is less humid and subjected to alternate dry and moist periods.

The mouth parts usually are smaller than the middle urn, brown, and are either rounded or constricted into four or eight angles. However, the constrictions are usually indistinct at the mouth. The surface of the capsule may be smooth, slightly to deeply 8-ribbed, especially in the Orthotrichoideae. It is believed that the strong longitudinal ribs regulate spore liberation in those species with greatly reduced peristomes (see Lara et al., 1999). The urn usually narrows gradually, or sometimes abruptly, as it joins the seta through a long neck, which is often also 4-grooved.

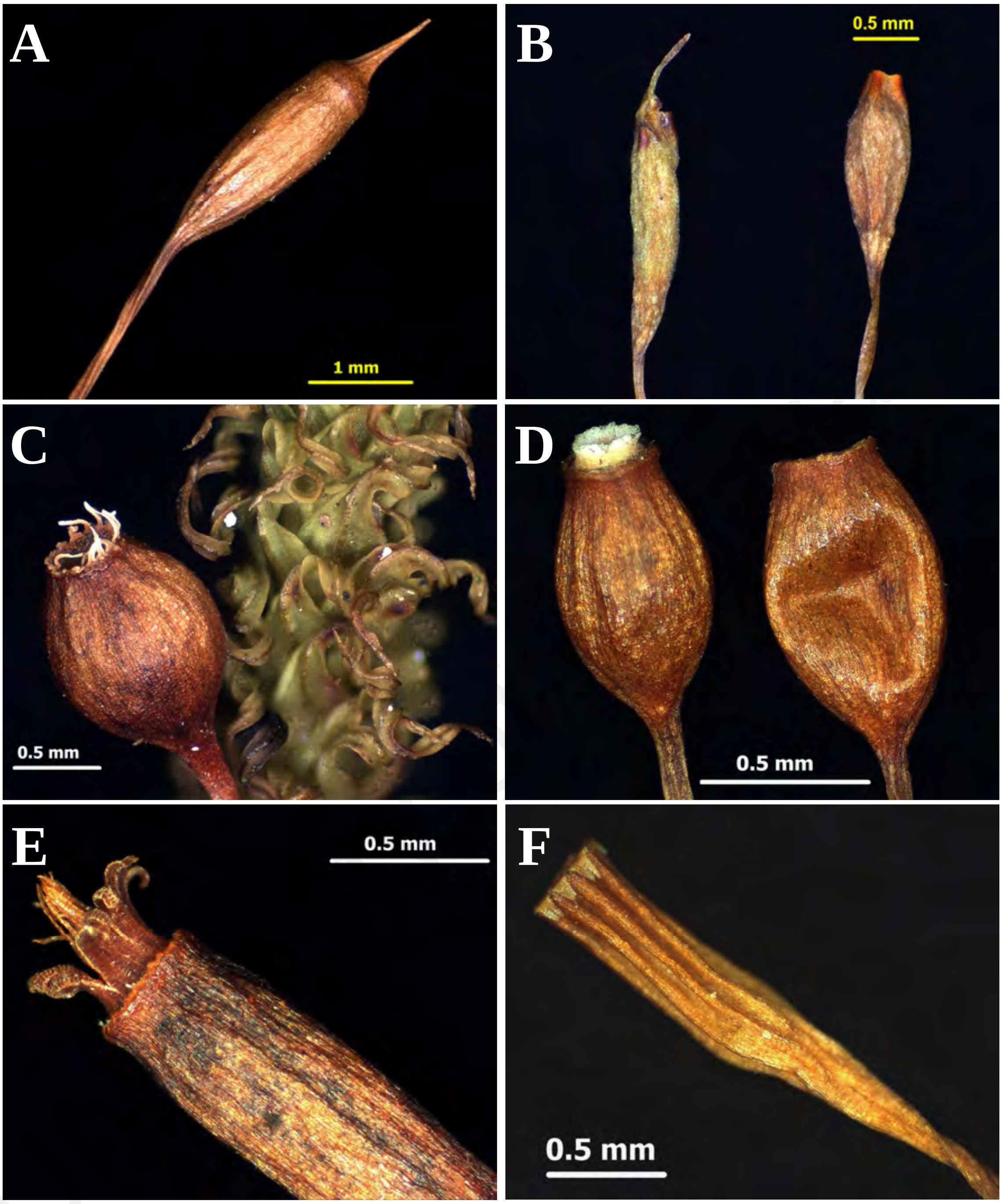

Figure 4.19. Detailed views of capsules. — **A,** capsule with rostrate operculum and erect beak in *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **B,** capsules of *Zygodon orientalis* (Dixon) Goffinet: capsule on the left has a rostrate operculum with oblique beak, while operculum has been removed from the capsule on the right; **C,** capsule of *Macromitrium longicaule* Müll. Hal. showing its single and divided peristome teeth; **D,** capsules of *Macromitrium blumei* Nees *ex* Schwägr.: on the left is a capsule with peristome teeth fused into a peristomial membrane, while the capsule on the right has lost its peristome teeth; **E,** capsule of *Schlotheimia rubiginosa* C.H. Wright showing its well-developed double peristome teeth; **F,** capsule of *Ulota splendida* E.B. Bartram showing exostome teeth that are strongly recurved from the capsule mouth when dry.

The exothecial cells are variable in shape and generally thick-walled (Fig. 4.20 A-I, K-L), except in two *Desmotheca* species with consistently thin-walled exothecial cells (Fig. 4.20J). Normally, a few rows of wide-rectangular to oblate cells are found near the mouth and these cells gradually elongate into long rectangular, broad oblong or polygonial shapes toward the proximal end, with length-width ratios of approximately 3:1 or more (Fig. 4.20). The exothecial cells are all smooth, not collenchymatous and rarely pitted.

4.3.3 Stomata

Stomata are only found at the base of the urn in this family, mostly located close to the neck or occasionally on the neck itself. Stomata are usually sparse or infrequent, often less than six per capsule in *Desmotheca*, *Groutiella* and *Macromitrium*, but on the other hand they can be abundant, 16–20 per capsule in *Schlotheimia*, *Ulota* and *Zygodon*. The stomata of all Malaysian Orthotrichaceae are consistently made up of two morphologically similar guard cells. The stomatal pore is elongate and the main axis of the stomate is parallel to the longitudinal axis of the capsule in all species examined. The cells surrounding the stomata are referred to as ‘neighbouring cells’ (Paton, 1957), and slightly or (usually) not differentiated at all from exothecial cells.

Two types of stomata, viz., superficial stomata (or phaneropore) and immersed stomata (or cryptopore), have been reported in the Orthotrichaceae (Lewinsky, 1977, 1984, 1992, 1993). In the present study, stomata in *Desmotheca*, *Schlotheimia*, *Ulota*, *Zygodon* and a few *Macromitria*, were found to be phaneroporic (Fig. 4.21A-E), while stomata of the remaining taxa studied were sunken (cryptopores) to various depths (Fig. 4.21F-H). Some stomata are deeply sunken and almost covered by the neighbouring cells, while others are hardly covered and these appear as little holes at the base of the urn. There

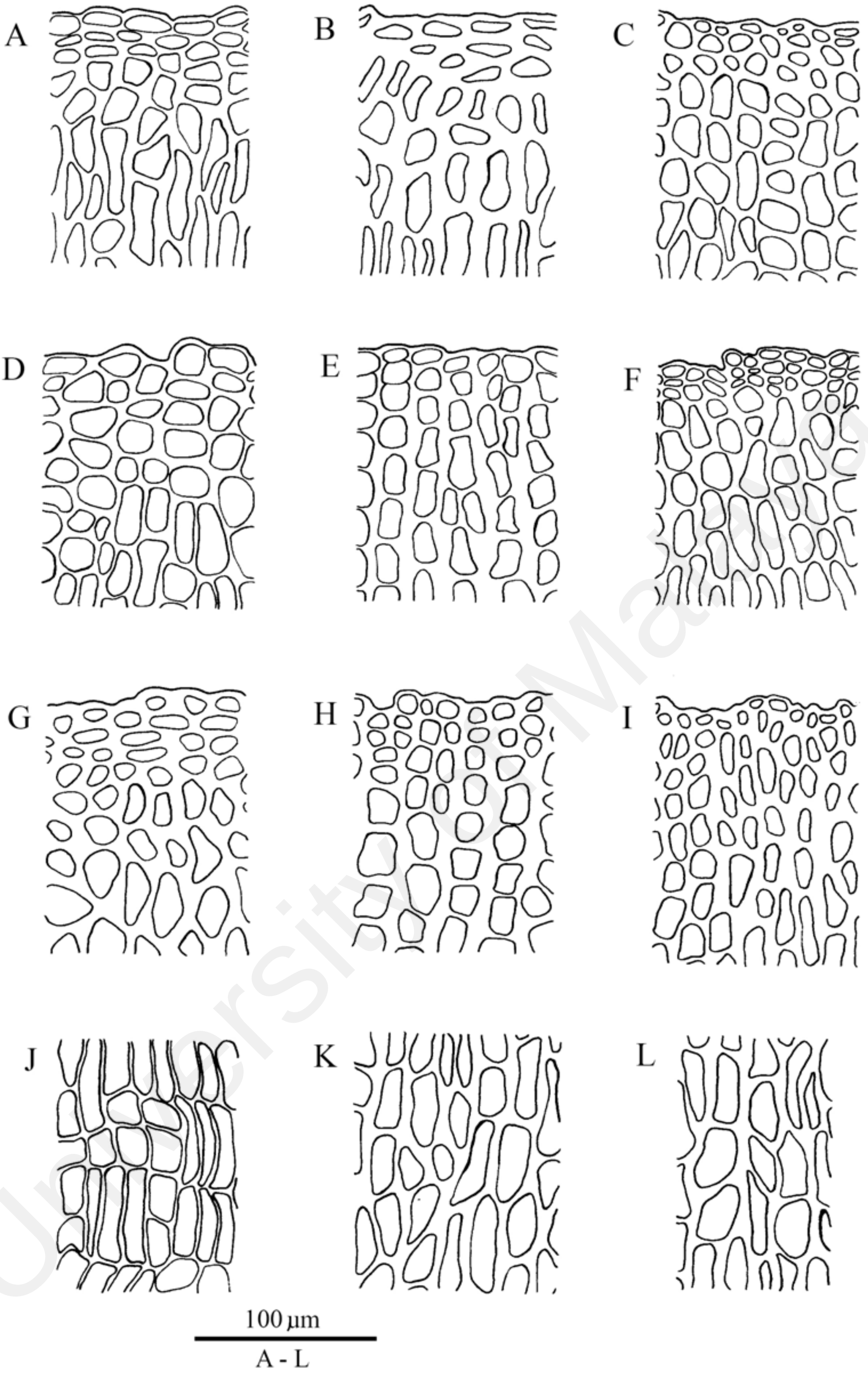

Figure 4.20. Exothecial cells near the mouth (A-I) and at the mid urn (J-L) in various Orthotrichaceae. — A, *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **B,** *Macromitrium blumei* Nees *ex* Schwägr.; **C,** *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr.; **D,** *Macromitrium papillisetum* Dixon; **E,** *Macromitrium parvifolium* Dixon; **F,** *Macromitrium salakanum* Müll. Hal.; **G,** *Schlotheimia rubiginosa* C.H. Wright; **H,** *Zygodon orientalis* (Dixon) Goffinet; **I,** *Zygodon reinwardtii* (Hornsch.) A. Braun; **J,** *Desmotheca apiculata* (Dozy & Molk.) Lindb.; **K,** *Macromitrium longipilum* A. Braun *ex* Müll. Hal.; **L,** *Macromitrium ochraceum* (Dozy & Molk.) Müll. Hal.

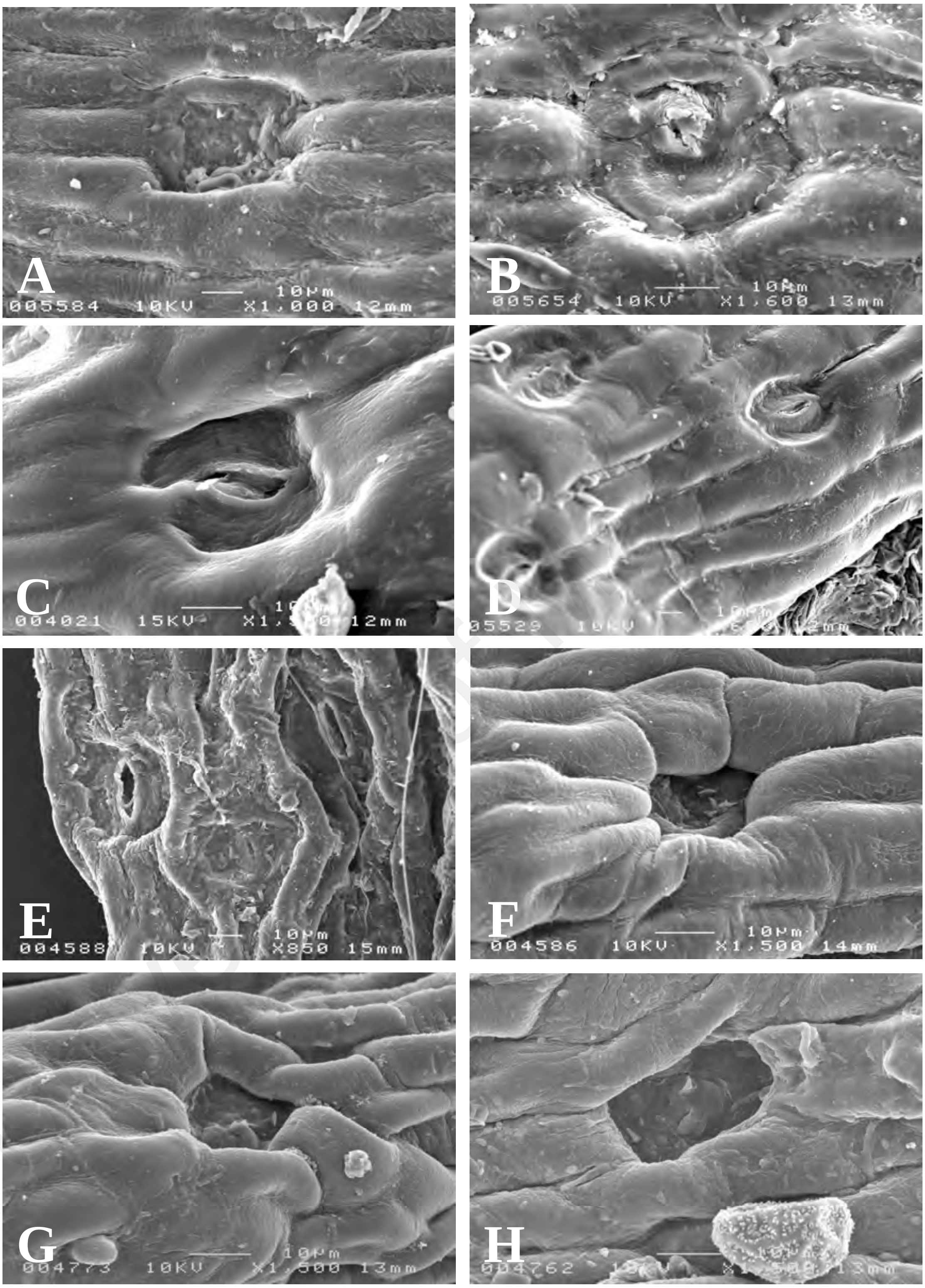

Figure 4.21. SEM images of superficial stomatae (A-E) and immersed stomatae (F-H) in the Orthotrichaceae. — A, *Macromitrium longipilum* A. Braun *ex* Müll. Hal.; **B,** *Macromitrium nepalense* (Hook. & Grev.) Schwägr.; **C,** *Schlotheimia wallisii* Müll. Hal.; **D,** *Zygodon intermedius* Bruch & Schimp.; **E,** *Zygodon orientalis* (Dixon) Goffinet; **F,** *Macromitrium cuspidatum* Hampe; **G,** *Macromitrium fuscescens* Schwägr.; **H,** *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr.

are also taxa with slightly immersed stomata that are not covered by the neighbouring cells. Lewinsky (1977) reported the latter type of stomata in her studies of *Orthotrichum* and regarded it as ‘semicryptopore’. She suggested that the semicryptopore condition might probably have evolved from cryptopores, caused by the development of neighbouring cells (Lewinsky, 1977). However, she reverted to the widely accepted concept of two fundamental stomatal types (either immersed or superficial stomata) and has avoided use of the term ‘semicryptopore’ in her later work on the same genus (Lewinsky, 1984, 1992, 1993). Thus, a similar ideal is followed in this treatment, where only two stomatal types are recognized.

4.3.4 The operculum

The operculum is the lid or cap of the capsule covering the peristome and closing the urn. The operculum shows little variation among the taxa studied. In general, the operculum is long-rostrate (with long-beak) in shape, with a straight, long, slender upper tubular beak that tapers abruptly from a broad base (Fig. 4.19A, 4.22A). Rostellate (or short-beaked) opercula are only found in both of the *Desmotheca* species (Fig. 4.22B). The surface of the operculum is smooth and glabrous and the opercula are mostly erect. Opercula with oblique beaks are only observed in the genera *Ulota* and *Zygodon* (Fig. 4.19B). One interesting observation in this genus is that the operculum often detaches together with, but remains inside, the calyptra (Fig. 4.22C). This condition warrants future study, especially its function in spore dispersal. It may be that the calyptra regulates removal of the operculum, facilitating spore dispersal.

4.3.5 The annulus

An annulus is absent in all Orthotrichaceae treated in this study. Operculum is just attached to the rim or capsule mouth without a distinct joint. Detachment of operculum

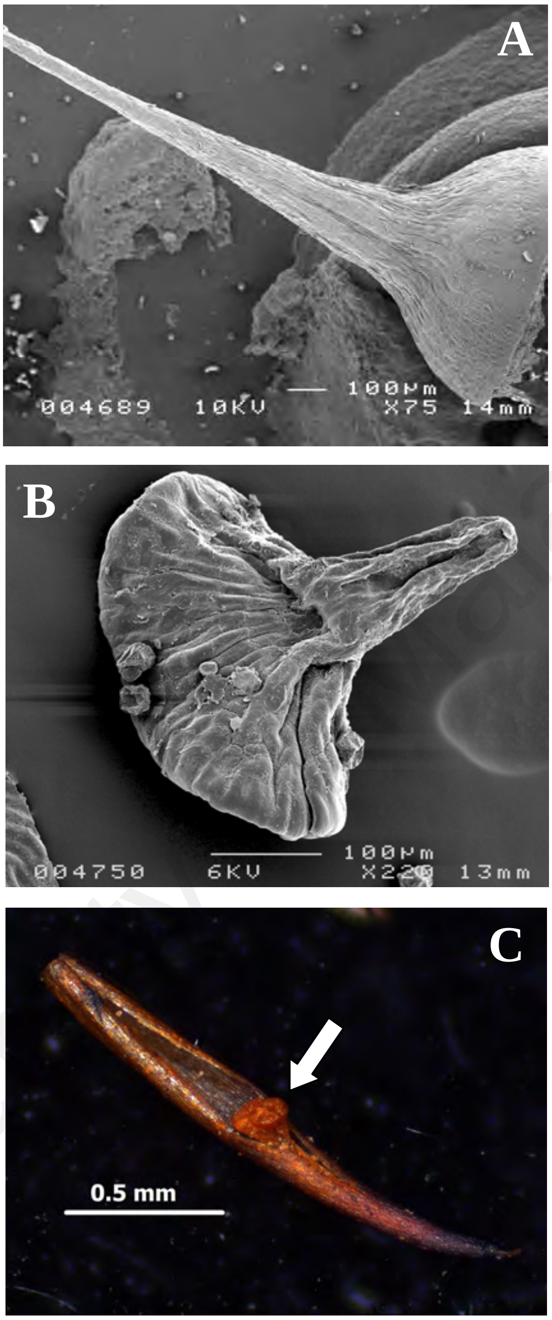

Figure 4.22. Opercula of some Orthotrichaceae. — A, rostrate operculum with a long beak in *Macromitrium macrosporum* Broth., typical also for *Groutiella*, *Macromitrium*, *Schlotheimia* and *Ulota* in this study; **B,** rostellate operculum with a consistently short beak in *Desmotheca apiculata* (Dozy & Molk.) Lindb., unique for this genus; **C,** front view of a calyptra with its operculum (arrow) in *Zygodon reinwardtii* (Hornsch.) A. Braun.

leaves a rough surface at its junction with the rim. The rim is always 3–6 cells thick in cross-section, and is made of quadrate cells that are usually much smaller than the other exothecial cells (Fig. 4.20A-I).

4.3.6 The peristome

The peristome in Malaysian Orthotrichaceae is of the arthrodontous type and is diplolepideous, with the endostome segment alternating with the exostome teeth (endostome segments opposite the teeth have been recorded in a few *Schlotheimia* species by Vitt, 1981a) (Fig. 4.23A). The exostome consists of a thickened and well ornamented outer plate (or outer peristomial layer, OPL), but a thinner and less ornamented inner plate (or primary peristomial layer, PPL). This unique feature in the diplolepideous members (Vitt, 1981a; Shaw & Rohrer, 1984) distinguishes them from the Bryaceae and Rhizogoniaceae, which exhibit similar endostome and exostome arrangements (Taylor, 1962).

In Malaysian Orthotrichaceae, the peristome is basically made of two rows of teeth, with the inner row (endostome) usually rudimentary or absent altogether, or in extreme cases both outer and inner rows are absent (a gymnostomous condition) as in the genus *Desmotheca* and *M. papillisetum* (Fig. 4.23B). However, there are also cases where the peristome is only equipped with an endostome but lacking an exostome, as in the three *Zygodon* species (Fig. 4.23C). Grout (1908) pointed out that a complete double peristome is not necessary for members of this family because they grow high above the ground where they can easily access air currents for effective spore dispersal. Similarly, Vitt (1981a) suggested that fusion and reduction in the peristome is common in Orthotrichaceae due to their epiphytic behaviour, and this is seen as an increased adaptation to xerophytism.

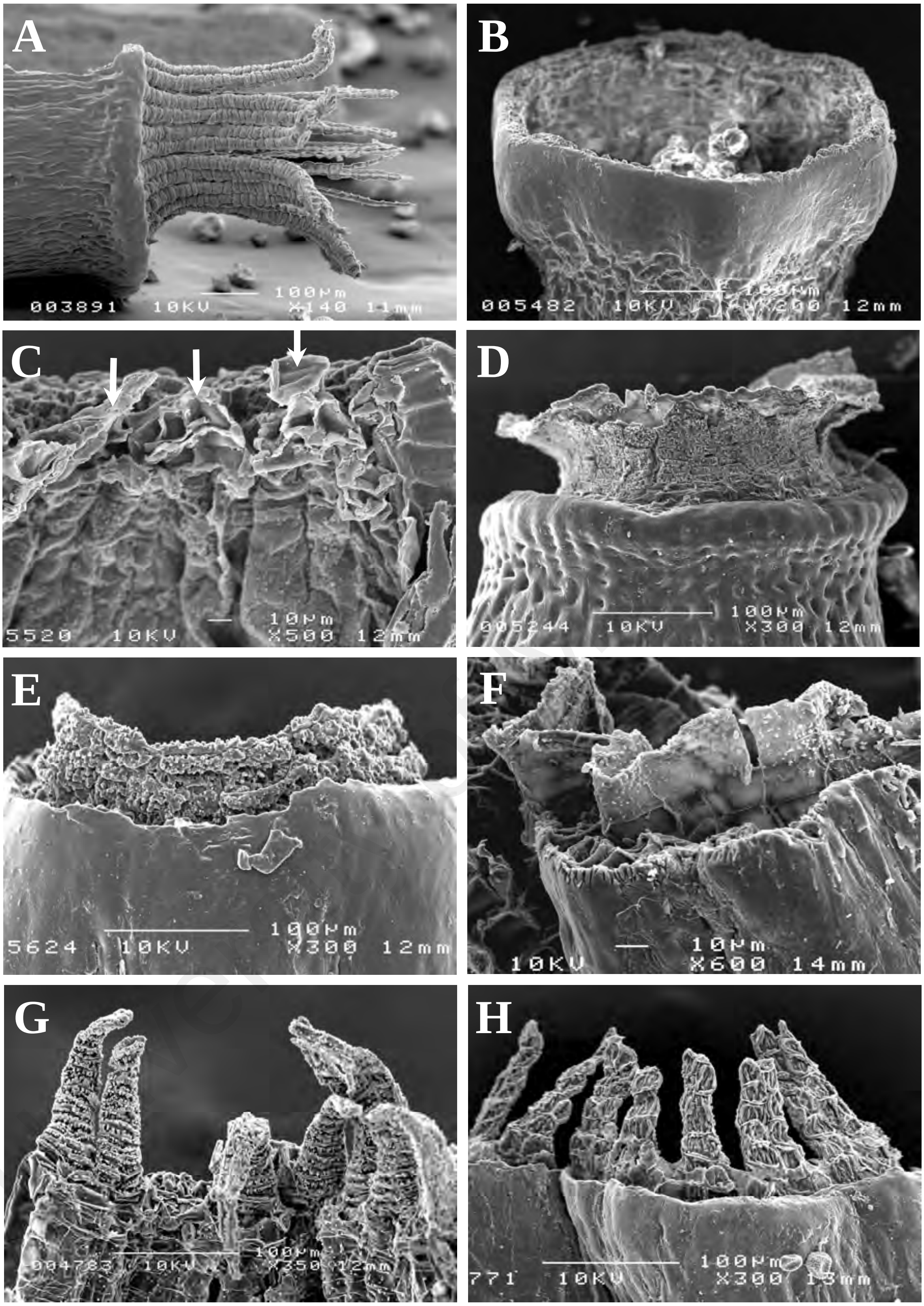

Figure 4.23. Peristome teeth I. — **A,** double peristome in *Schlotheimia wallisii* Müll. Hal.; **B,** capsule without peristome in *Macromitrium papillisetum* Dixon; **C,** reduced segments in *Zygodon reinwardtii* (Hornsch.) A. Braun (arrows); **D,** membranous peristome in *Macromitrium blumei* var. *zollingeri* (Mitt. *ex* Bosch & Sande Lac.) S.L. Guo, B.C. Tan & Virtanen; **E,** membranous peristome in *Macromitrium macrosporum* Broth.; **F,** membranous peristome in *Macromitrium parvifolium* Dixon; **G,** exostomes of *Macromitium longicaule* Müll. Hal. with acute tips; **H,** blunt end exostomes in *Macromitrium fuscescens* Schwägr.

The prostome, the rudimentary exostomial structure found outside of the main peristome teeth, has never been observed in any Malaysian taxa, although it has been reported in a few Orthotrichaceae (Goffinet & Shannon, 2002; Lewinsky, 1993; Vitt, 1973).

Exostome teeth are made of cell wall material derived from the inner wall of the OPL and the outer wall of the PPL (Edwards, 1979). Likewise, the endostome teeth are formed by cell wall material derived from the inner wall of the PPL and the outer wall of the inner peristomial layer (IPL). Each exostome tooth is made of two columns of OPL cells and a single column of PPL cells. Therefore, a clear middle divisural line separating the two cell columns, if present, is usually seen at the dorsal (outer) side but is absent at the ventral (inner) side of the tooth, except in *M. falcatulum* and *M. nepalense*. However, a middle divisural line is absent in most Malaysian Orthotrichaceae species, particularly in *Groutiella* and many *Macromitrium* species known to have disorganized peristomial layers (Shaw, 1986). In the later case, an undivided peristome or "undifferentiated peristomial membrane" (according to Shaw, 1986) is observed (Fig. 4.19D, 4.23D-F).

In Malaysian Orthotrichaceae, the exostomes usually consist of 16 teeth; the teeth are either solitary but connected by a basal membrane (e.g., *M. cuspidatum*, *M. longicaule* Müll. Hal., *M. salakanum*) (Fig. 4.23G-H, 4.24A), or fused together in pairs to form eight broad teeth (e.g., *U. splendida*), or fused into a continuous, "undifferentiated peristomial membrane" (e.g., *M. blumei*, *M. longipilum*, *M. orthostichum*) (Fig. 4.23D-F). When there are only eight teeth, they are usually placed in line with the eight rows of striae along the capsule; this has also been noted by Philibert (Taylor, 1962). For

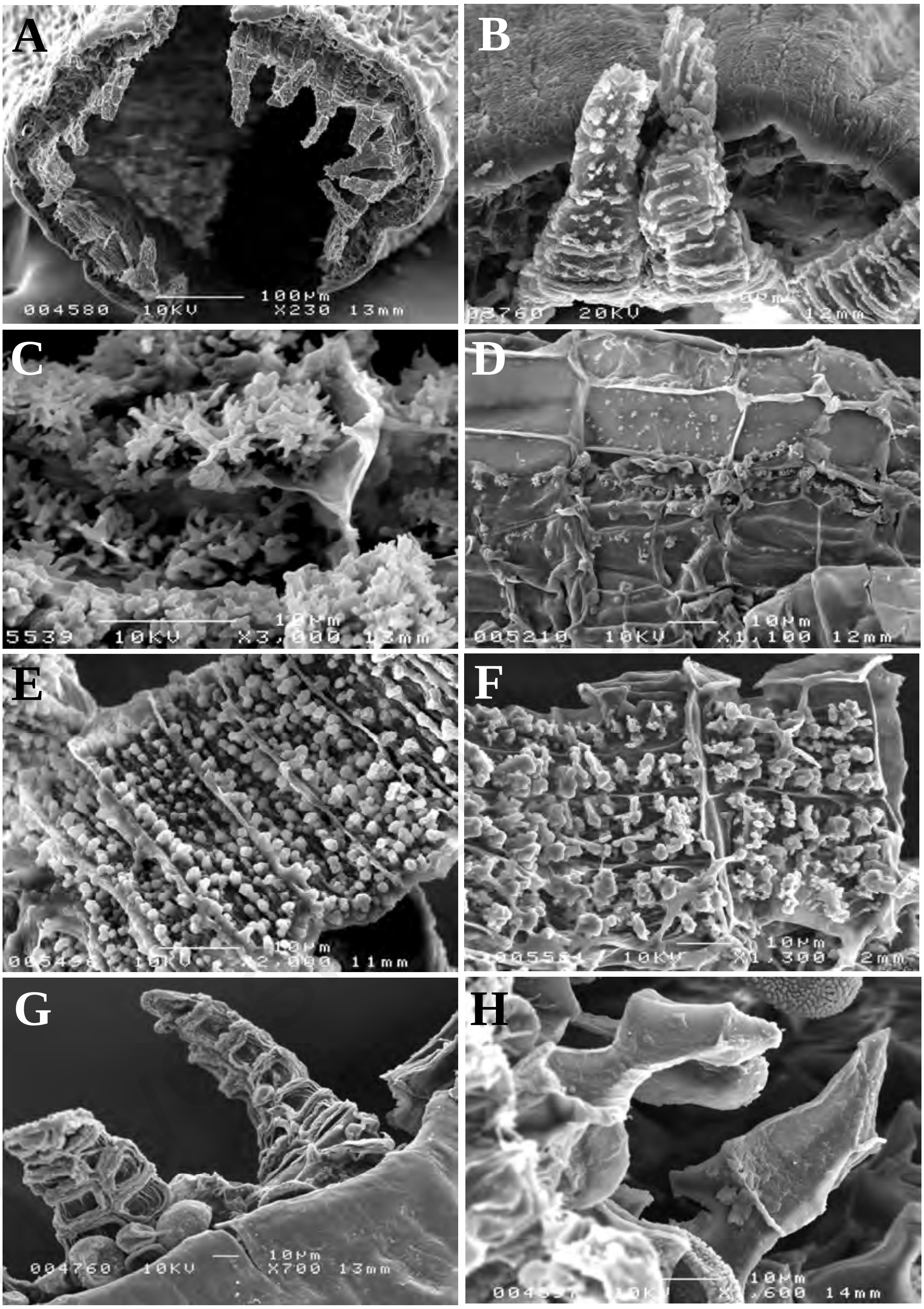

Figure 4.24. Peristome teeth II. — A, exostomes with a connecting basal membranous layer in *Macromitrium cuspidatum* Hampe; **B,** papillae that connected into short-vertical or horizontal ridges on exostomes of *Macromitrium salakanum* Müll. Hal.; **C,** highly branched papillae on exostomes of *Macromitrium ochraceoides* Dixon; **D,** upper half of the peristome showing a nearly smooth or minutely papillose surface in *Macromitrium orthostichum* Nees ex Schwägr.; **E,** papillae on horizontal rim in *Macromitrium salakanum* Müll. Hal.; **F,** papillae on reticulate networks in *Macromitrium longipilum* A. Braun ex Müll. Hal.; **G,** anticlinal and periclinal ridges fringing lower central regions in *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr.; **H,** reduced segments of *Zygodon orientalis* (Dixon) Goffinet.

species with distinct teeth, these are elongated with acute endings at the tips (Fig. 4.23G) only in *M. longicaule*, *S. rubiginosa* and *S. wallisii*, whereas in the rest, the teeth are commonly short with blunt ends (Fig. 4.23H, 4.24B). In species with membranous peristomes, teeth are usually low, some 3–6-cells tall.

Tooth surface ornamentation usually differs among species and presents useful taxonomic information. The surface of the exostome teeth varies from smooth to slightly ornamented, to (more commonly) papillose (Fig. 4.24B-F). The magnitudes and the shape of the papillae differ from one species to another. Papillae occur in various sizes, are wart-like to well developed, rarely simply rounded but more commonly compound to highly branched with finger-like branches. In addition, papillae are either distributed randomly on the teeth, (more typically) found on the upper half of teeth (Fig. 4.24D), or occurring either on horizontal or vertical ridges (connected raised structures on the surface of peristome teeth) (Fig. 4.24E). Sometimes the vertical and horizontal ridges are connected at their base to form an irregular network that is commonly referred to as reticulate (Fig. 4.24F). The reticulum is always low; it appears almost completely hidden by the papillae under low magnification. Among these, the most striking teeth surface ornamentation is found in *M. incurvifolium*, where the anticlinal side of the plate, or the original cell wall, is always thickened and papillose, emerging like a frame surrounding a lower central portion with a few low vertical striae, or ‘open box-like structure’ according to Lewinsky (1989) (Fig. 4.24G). This papillose, frame-like structure is clearly seen under the compound light microscope, and is a useful character in distinguishing this species from others. Although this type of peristome teeth was newly reported for the genus *Macromitrium*, a similar type of peristome structure has been reported in a number of *Orthotrichum* species by Lewinsky (1989), where the thickened anticlinal wall formation can either be on the dorsal or ventral faces of the teeth.

Very often, the teeth are ornamented differently on the outer and inner surfaces (dorsal and ventral views). In general, the papillae on inner surfaces are relatively stronger, denser and commonly developed on ridges. Likewise, the ridges are more pronounced on the inner surface relative to the outer surface; they are either in a dense transverse arrangement, on thin to thick horizontal ridges (Fig. 4.24E), or reticulate, but rarely vertical except at the apical part of the teeth (Fig. 4.24B). Lamellae that resemble the remnants of the anticlinal peristome cell walls are usually clearly seen on the inner surface as low and thin filmy structures

An endostome is absent in many Malaysian Orthotrichaceae. It is found only in *Schlotheimia*, *Ulota*, *Zygodon*, and *M. blumei* and its variety *zollingeri*. The endostome is always erect, imperforate, lacking cilia, with slender segments that are developed from a characteristically low basal membrane (Shaw & Rohrer, 1984). The basal membrane is generally 1–2-cells tall as exhibited by *U. splendida* and the three *Zygodon* species. Just like the exostome teeth, the segments are either 16 (in *Schlotheimia*) or 8 (in *Ulota* and *Zygodon*) in numbers, or fused as a membranous peristomial layer (e.g., *M. blumei* and its variety *zollingeri*) (Fig. 4.23A, C) that could not be distinguished from the basal membrane. The endostomial segments are normally fragile, easily deciduous when dry in most taxa, except *M. blumei* and its variety *zollingeri*, where the endostomial layer is relatively rigid and sometimes fused with the exostomial layer at their apical extent. Keeled segments occur only in the two *Schlotheimia* species, whereas segments are plane in the other species. The segments are rudimentary in the three *Zygodon* species, and are made up of 2–3 thin, hyaline cells with rather smooth or slightly ornamented surfaces (Fig. 4.24H). In the other taxa, the segments are better developed and are usually tall, made up of many cell plates, with surfaces that are either smooth (in *U. splendida*), distinctly ridged (in *S. rubiginosa* and *S. wallisii*), or papillose (in *M. blumei* & *M. blumei* var. *zollingeri*). Also, often the outer face ornamentation is different from the inner side.

4.3.7 Spores

The spores of Malaysian Orthotrichaceae are all unicellular; multicellular spores are rare among the Orthotrichaceae members and thus far only reported for genus *Muelleriella* (Sainsbury, 1955). Spores are apolar, almost globose to polygonial with many concave or flat faces. The spore shape is not a consistent character for particular taxa and most of the time, a capsule will contain spores of various shapes. In addition to this, Clarke (1979) pointed out that spore shape and size are mostly affected by environmental factors, and should only be taken into account when considered at the broadest level. Consequently, spore shape is not considered as a significant taxonomic character in this study.

Two spore sizes are found within the Orthotrichaceae. Spores of a single size class give the condition called isospory, and occur in the subfamily Orthotrichoideae (in *Ulota* and *Zygodon*), where spores are 15–38 µm across (Fig. 4.25A, B). On the other hand, almost all Macromitrioideae except *Groutiella*, produce spores of distinctly unequal size in the same sporangium, a condition described as anisospory (Fig. 4.25C, D). The term ‘anisospory’, was first used by Ernst-Schwarzenbach (1939) in reference to the very unequal spores in *Macromitria*. Anisospory is different from the heterosporous behaviour of the vascular plant. In mosses, both the micro- and

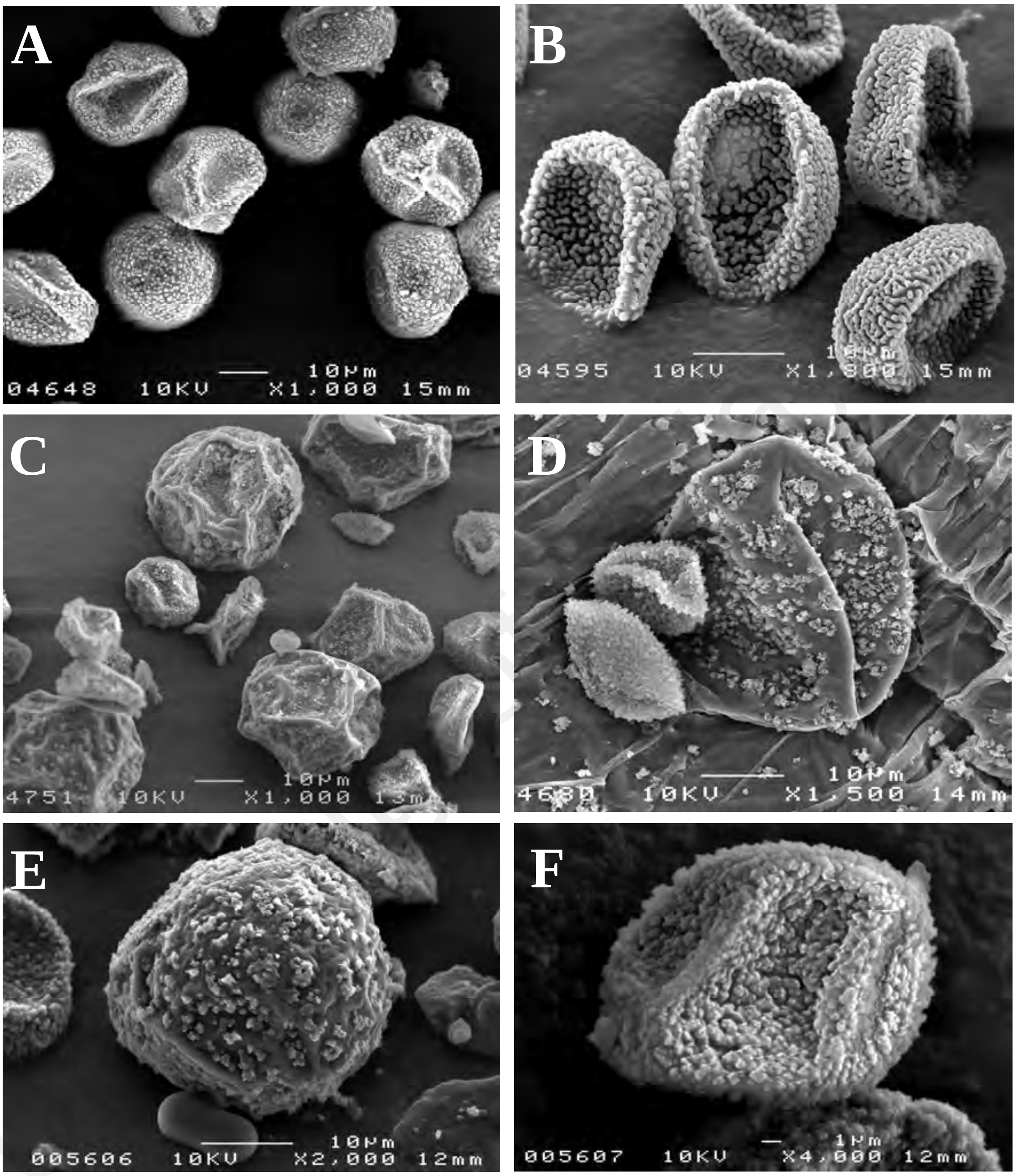

Figure 4.25. The isosporous and anisosporous conditions in Orthotrichaceae — A, isosporous condition in *Groutiella tomentosa* (Hornsch.) Wijk & Margad.; **B,** isosporous condition in *Zygodon orientalis* (Dixon) Goffinet; **C,** anisosporous condition in *Desmotheca apiculata* (Dozy & Molk.) Lindb.; **D,** anisosporous condition in *Macromitrium parvifolium* Dixon; **E,** macrospore in *Macromitrium falcatulum* Müll. Hal.; **F,** microspore in *Macromitrium falcatulum* Müll. Hal.

megaspores are borne in the same sporangium, as a direct result of meiosis, and not in different sporangia, as in vascular plants.

In general, the diameter of the larger spores are 30–50 µm, while the smaller spores are 15–28 µm, rarely exceeding 30µm (Fig. 4.25E-F). An interesting discovery in *G. tomentosa* was the occurrence of a few anisosporous populations, although most of the time the species is isosporous. In Orthotrichaceae, anisospory is usually associated with sexual dimorphism, where the smaller spore develops into a normal male plant or, more commonly, into an epiphytic dwarf male plant that survives for a season, while the larger spore develops into a perennial female plant (Ernst-Schwarzenbach, 1936, 1939, 1943; Ramsay, 1979). In discussing sex chromosomes in *Macromitrium*, Ramsay (1966) suggested that anisospory is correlated with chromosomal differences. The monoicous species always produce isosporous spores (Ramsay, 1966; Vitt, 1968), but dioicous species can either be isosporous or anisosporous (Ernst-Schwarzenbach, 1943; Noguchi, 1967).

Spores of Malaysian Orthotrichaceae lack apertures. The spore surface is covered by simple granulose papillae, even or unevenly distributed all over the outer wall (Fig. 4.25). The papillae are mostly minute and warty with many tiny projections in *Desmotheca* and *Macromitrium*, while the papillae are bigger in *Groutiella*, *Schlotheimia*, *Ulota* and *Zygodon*. The papillae are relatively smooth in *Ulota* and *Zygodon*, compared with those of the other genera. However, there are no distinctive differences in size, shape and density of papillae among the taxa within a genus in the Orthotrichaceae, as observed under the scanning electron microscope. This is congruent with the preliminary findings by Lewinksy (1977), based on a survey of over 14 *Orthotrichum* species of at least three different subgenera. A general feature relevant to anisosporous species (chiefly subfamily Macromitrioideae) is that the papillae are more densely distributed on smaller spores than larger ones (Fig. 4.25E-F).

4.4 Cytological information for Malaysian Orthotrichaceae

In the index of bryophyte chromosome counts complied by Fritsch (1991), chromosome information for 82 taxa in five genera of the Orthotrichaceae are listed, with the genus *Orthotrichum* the most well treated. Later, Ramsay (1993) and colleagues (1995) provided cytological information of another 19 Orthotrichaceae species and Maniselvan & Kumar (1999) published counts for another four *Macromitrium* species from India. However, most of the studies deal with taxa from temperate regions and the New World tropics. Some relevant information pertaining to taxa that also occur in Malaysia is listed here: *Desmotheca apiculata*, *n* = 6; *Macromitrium incurvifolium, n* = 9; *M. longicaule, n* = 6; *M. orthostichum, n* = 7; *M. salakanum, n* = 9; *Zygodon intermedius, n* = 11 (Ramsay & Vitt, 1984; Ramsay, 1993; Ramsay et al., 1995).

The chromosome numbers *n* = 6 and/or *n* = 11 (10+m; 'm' referring to 'micro-chromosome') are reported for some members of the subfamily Orthotrichoideae (*Ulota* and *Zygodon*) (Fritsch, 1991; Ramsay, 1993). Cases of chromosome number *n* = 11 are usually complemented with a micro-chromosome (Ramsay, 1993). Among subfamily Macromitrioideae, *Desmotheca* was reported to have *n* = 6, while *Macromitrium* has count of *n* = 7, 8, 9, 10, 11, 12 (Ramsay, 1966; Inoue, 1979; Kumar & Verma, 1983; Une, 1985b; Fritsch, 1991; Ramsay, 1979; Ramsay, 1993; Ramsay et al., 1995; Maniselvan & Kumar, 1999), and *Schlotheimia* has *n* = 8, 9, 10, 11 (10+m) (Inoue, 1979; Anderson, 1980; Ramsay, 1993; Ramsay et al., 1995). Unfortunately, there is no available chromosome information for *Groutiella*.

In general, $n = 6$ is suggested to be the basic chromosome number for Orthotrichaceae (Ramsay & Vitt, 1986; Ramsay, 1993), so that cytological evolution in the Orthotrichaceae may have actually involved chromosome doubling, followed by a few independent reduction events (Goffinet et al., 2004). A dimorphic bivalent at metaphase I of meiosis has been noted for many of the phyllodioecious and anisosporous species of *Macromitrium* and *Schlotheimia*, especially in species with $n = 6$, 7, or (sometimes) $n = 9$. A dimorphic bivalent is correlated with dioecism, especially for plants that produce dwarf males; this implied that sexual dimorphism may be chromosomally determined (Ramsay, 1966, 1979; Ramsay & Vitt, 1986; Ramsay et al., 1995). Nevertheless, a dimorphic bivalent does not occur in all the dioecious species; on the other hand, it was suggested that sex chromosomes in *Macromitrium* species can either be heteromorphic or similar in morphology (Ramsay, 1966, 1979; Ramsay & Vitt, 1984).

CHAPTER 5

TAXONOMIC TREATMENT

5.1 Family Orthotrichaceae Arn.

Disp. Méth. Mousses: 13 (1825). TYPE: *Orthotrichum* Hedwig.

Zygodontaceae Schimp., Coroll. Bryol. Eur. 39 (1856). TYPE: *Zygodon* Hook. & Tayl.

Macromitriaceae S.P. Churchill, Bibliot. José Jerónimo Triana 12: 588 (1995). TYPE: *Macromitrium* Brid.

Plants acrocarpous or cladocarpous. Stem or primary axis orthotropic (erect or ascending) or plagiotropic (creeping), branched sympodially or monopodially; epidermal cells distinctively thick-walled, orange to red in colour, cortical cells moderately thick-walled, hyaline to yellowish, central strand absent. Rhizoids thick-walled, verrucated-papillose, branched very often, dichotomously. Pseudoparaphyllia not seen. Axillary hairs solitary, occasionally present, of 3–4 long-rectangular cells, apical cell thick-walled and pointed. Plant densely foliated, leaves erect, or variously curled when dry, spreading when moist, lamina keeled, margin not differentiated. Costa single, composed of two ventral guide cells, substereid cells at dorsal row, ventral chlorophyllose cells lacking. Laminal cells parenchymatous or prosenchymatous, variable in size and shape, smooth to variously papillose, very often upper laminal cells are shorter than those found at lower lamina, and might different in surface feature. Dioicous, autoicous or phyllodioicous. Both perichaetia and perigonia terminal on stem or branches, or dwarf male bud-like if present. Seta single, outer and inner cortical cells thick-walled, central strand present. Capsule immersed or exerted; stomata with two guard cells, pore elongate, cryptoporous or phaneroporous. Operculum rostellate to rostrate. Peristome double, single or lacking. Teeth 16, well-developed or rudimentary, fugacious, free or fused into eight pairs, or forming continuous membrane, exostome with the dorsal layer thicker than the ventral layer. Anisospory or isospory, spores unicellular, granulose. Calyptra cucullate or mitrate, covering the capsule completely or only the operculum.

5.2 Key to Orthotrichaceae taxa in Malaysia

1. Plant acrocarpous, tufted or cushion-forming; stem (primary axis) erect or ascending, simple or sparsely branched, with 1–2 vertical (orthotropic) branches developed at a time on the stem………………………………………….………...2

1. Plant cladocarpous, mat-forming, or occasionally tufted in large plants; stem (primary axis) creeping on the substrate, freely branched, with numerous vertical (orthotropic) branches developed on the stem……………………………………5

2. Upper lamina slender and long, 5–8 times as long as the basal lamina; upper laminal cells unipapillate, or at the most with two papillae on each cell; calyptra mitrate, hairy, hairs erect and stiff; peristome well-developed, with 8 geminate teeth…………………………………………………...…………*Ulota splendida*

2. Upper lamina variable, usually much shorter, only 1–3 times as long as the basal lamina; upper laminal cells pluripapillose, of 4–8 simple papillae on each cell; calyptra cucullate, glabrous; peristome rudimentary or absent……………………3

3. Branch leaves slender and long, (2.2–)2.8–5.5(–5.9) mm in length; leaf length-width ratio 5:1 or more; upper lamina long and slender, gradually tapering to a slender acuminate apex; costa percurrent or reaching leaf tip; middle laminal margin irregular toothed to serrulate; basal laminal cells elongate, linear, length-width ratio from 5 and above…………………….………………. *Zygodon orientalis*

3. Branch leaves slender to broad, generally short, 0.9–2.3 mm in length; leaf length-width ratio 4:1 or less; upper lamina relatively short and broad, gradually tapering to an acute or broad-acuminate apex; costa failing, ending some distance below the

leaf tip; middle laminal margin linear, subentire or weakly crenulate from projecting papillae; basal laminal cells generally square, short to long rectangular, length-width ratio from 1 to 2…………………..…………………..……………….4

4. Plant autoicous or synoicous; stem and branch leaves elliptic-lanceolate to oblanceolate, with upper lamina wider than basal lamina; leaves large, 1.6–2.3 mm long; apical margin dentate.………………………………… *Zygodon reinwardtii*

4. Plant dioicous; stem and branch leaves elliptic-lanceolate to lingulate, upper lamina as wide as or narrower than the basal lamina; leaves small, 0.9–1.0 mm long; apical margin smooth to crenulate due to projecting papillae.…………..…… ……………..…………..…………………………………… *Zygodon intermedius*

5. Branch leaves dimorphic, proximal leaves on orthotropic branches slender and longer than those at more distal positions; seta extremely short, almost absent, capsule immersed…………………………………………...……………...6

5. Branch leaves monomorphic, proximal and distal leaves on orthotropic branches similar in size; seta short to long, capsule exserted…………………………..…7

6. Upper branch leaves ovate to elliptic, less than 1 mm long, length-width ratio <2:1; costa excurrent with short awn, awn less than 0.1 mm long; perichaetial leaves longer than the vegetative leaves, 1.25–1.5 mm long; perichaetial leaf apices variable from broadly acute, obtuse to retuse, not sharp pointed with percurrent costa…………………………………...………*Desmotheca apiculata*

6. Upper branch leaves elliptic-lanceolate, branch leaves length from 1.2–1.75 mm long, length-width ratio 2.5–3:1; costa excurrent with longer awn, awn 0.3–0.4 mm long; perichaetial leaves shorter than the vegetative leaves, 1.4–1.7 mm long; leaf apex acuminate with long excurrent costa….……..….*Desmotheca mohamedii*

7. Leaves bordered by slender rectangular to linear cells for the basal 1/4 to 1/5 of their length…..……………………………………………………………….8

7. Leaves not specially bordered, basal marginal cells similar to inner laminal cells..9

8. Branch funiform, with leaves tightly coiled on the branch when dry; leaf lamina plane; apex long-slender with an acute point, caducous (easily falling off); leaf apex of 2–3 cells thick in cross-section………………………*Groutiella tomentosa*

8. Branch not funiform, branch leaves variously flexuose, twisted-contorted when dry, occasionally with a few leaves coiled on the branch; leaf lamina rugose; apex short and broad, sharply acute, persistent; leaf apex unistratose in cross-section……………………..……………..…………..…………*Groutiella kelantanense*

9. Laminal cells prosenchymatous, prorate; calyptra broadly lobed, not plicate, glabrous; peristome double, well-developed.……………..…………….…………...10

9. Laminal cells parenchymatous, smooth, unipapillose to pluripapillose; calyptra deeply lobed or laciniate, plicate, glabrous or hairy; peristome absent, single or double, often reduced………….…………….…………….…………….………………..11

10. Vegetative leaf apices obtuse to broadly acute with piliferous costa; leaves smaller, 2.5–3.2 mm long; perichaetial leaf apices broadly acute to sharp acuminate; transverse rim on outer surface of exostome smooth; outer surface of endostome papillose……….…………….…………….………...*Schlotheimia wallisii*

10. Vegetative leaf apices usually retuse to emarginate, occasionally obtuse to broadly acute, costa percurrent or ending in a short mucro; leaves larger, 3–4.2 mm long; perichaetial leaf apices obtuse to mucronate; transverse rim on outer surface of exostome coronate-papillose; outer surface of endostome smooth…………………
……………….…………….…………….…………….………….*Schlotheimia rubiginosa*

11. Branch leaves arranged in five longitudinal ranks; rhizoids often growing from the marginal cells of leaf base, on the abaxial surface……*Macromitrium orthostichum*

11. Branch leaves spirally arranged on branch, unranked; rhizoids not developing from the leaf base……….…………….…………….…………….…………….…………...12

12. Upper laminal cells smooth to convex or conically papillose, in extreme cases with a single papilla on each cell (occasionally pluripapillose only in *M. longipilum* var. *longipilum*); teeth fused into a low membraneous structure…………………..…….13

12. Upper laminal cells pluripapillose, papillae either clearly seen or obscure (occasionally smooth cells only in *M. cuspidatum*); teeth solitary, of eight or sixteen exostome……….……….……….……….……….……….…………22

13. Branch leaves wide-spreading to squarrose-recurved when wet; upper laminal margin denticulate to sharply serrulate; calyptra hairy, hairs stiff and abundant; perichaetial leaves always longer than the vegetative leaves; perichaetia much shorter than the paraphyses; seta coarsely papillose throughout...……….………....14

13. Branch leaves erect, erect-spreading to wide-spreading, but not recurved when wet; upper laminal margin subentire to crenulate due to the bulging cell walls; calyptra glabrous; perichaetial leaves as long as or shorter than the vegetative leaves, but not longer; perichaetia and the paraphyses are almost similar in height; setae mostly smooth or sometimes prorate close to the neck……………………15

14. Costa long-excurrent in both vegetative and perichaetial leaves; basal laminal cells mostly smooth, occasionally unipapillose in some plants, papillae more commonly found near to the midleaf; perichaetial leaves long, 5.8–6.3 mm; paraphyses long, 1.2–1.8 mm, made of (28–)30–38(–41) cells………...*Macromitrium ochraceoides*

14. Costa filling the apex, percurrent or short excurrent, end in a cusp, in both vegetative and perichaetial leaves; basal laminal cells mostly unipapillose, papillae tall, occasionally smooth in some plants, smooth cells found at the juxtacostal region; perichaetial leaves short, 4.1–4.7 mm; paraphyses short, 0.7–1.0 mm, made up of 12–16 cells……….……….………………….*Macromitrium ochraceum*

15. Branch leaves cucullate; leaf apices obtuse to emarginated; costa shortly excurrent, ends in a mucro and recurved…………………...………..*Macromitrium densum*

15. Branch leaves not cucullate; leaf apices vary from obtuse, acute to acuminate; costa variable……….……………….……….……….…………………………..16

16. Plants small; branch leaves 1–2.5 mm long × 0.2–0.5 mm wide; branch leaves funiculate, at least some leaves loose or tightly coiled around the branch when dry; upper laminal cells oblate to quadrate, bulging, distinctly convex; vaginulae short, less than 1 mm height……….………….………….………….………………17

16. Plants robust; branch leaves 3.5–5.0 mm long × 0.5–1.5 mm wide; branch leaves erect-flexuose when dry, individually flexuose-twisted or irregularly twisted but not around the branch; upper laminal cells isodiametric, quadrate to rhombic, flat, convex to strongly bulging-conic or unipapillose; vaginulae tall, above 1.4 mm height……….………….………….………….………….………….…………19

17. Branch leaves slender, lingulate to lingulate-lanceolate, length-width ratio 5–7:1, with parallel margins along almost the whole leaf length; leaf apex sharply acute; costa percurrent; seta either sinistrorse- or dextrorse-twisted, short, length about 1 mm; calyptra deeply lacerated from the base, into 4–8 wide spreading strips…….. ……….………….………….………….…………………..*Macromitrium parvifolium*

17. Branch leaves broad, elliptic, elliptic-lanceolate to lingulate-lanceolate, length-width ratio 3–5:1, margins rarely parallel, at most only along a short length of the upper lamina; leaf apex obtuse to bluntly acute, or apiculate; costa excurrent in short or long awn; seta sinistrorse-twisted, long, length from 1.4 mm above; calyptra shallowly lacerated from the base, with straight strips close to each other ……….………….………….………….………….………….……………...18

18. Branch leaves elliptic to elliptic-lanceolate, short and broad, 1.1–1.4 mm long × 0.3–0.5 mm wide, length-width ratio 3–4:1; costa short-excurrent, aristae less than 0.15 mm long……….………….……………..*Macromitrium blumei* var. *blumei*

18. Branch leaves lingulate-lanceolate, slender and long, 1.4–1.8 mm long × 0.3–0.4

mm wide, length-width ratio 4–5:1; costa long excurrent, aristae 0.2–0.4 mm long ……….……….……….……………...*Macromitrium blumei* var. *zollingeri*

19. Branch leaves slender-lanceolate; costa percurrent or ending just below the apex; upper laminal cells isodiametric to elliptic; basal lamina cells mostly flat and smooth, occasionally unipapillose, papillae low and obscure, scattered in basal lamina; pitted cells only found at leaf base near juxtacostal region……………..… ……….……….……….……….………….*Macromitrium macrosporum*

19. Branch leaves variable, varying from slender-lanceolate, lingulate-lanceolate to broadly elliptic or ovate-lanceolate; costa excurrent; upper laminal cells elliptic to commonly rhombic or occasionally quadrate to rectangular; basal laminal cells flat to bulging, unipapillose, papillae tall, always distinct (although shorter papillae are occasionally found in var. *rugosum* and var. *ligulatum*); cells strongly pitted, most common at leaf base, with some extending far up to upper lamina……………...20

20. Branch leaves long-lanceolate, slender, less than 0.6 mm wide at the broadest region, length-width ratio 8–10:1; upper laminal cells flat and smooth; unipapillose cells occupying only a small region of the leaf base near its insertion.……........………….……..……..*Macromitrium longipilum* var. *ligulatum*

20. Branch leaves lingulate, elliptic-lanceolate to ovate-lanceolate, broad, 0.7–1.5 mm wide at the broadest region, length-width ratio 3–7:1; upper laminal cells either flat or convex to papillose-conic, or in some cases pluripapillose; unipapillose cells occupying the whole basal lamina region……....………….……………….…..21

21. Branch leaves lingulate; costa shortly excurrent, ending in a cusp, cusp 0.1–0.2 mm long; basal laminal cells equally thick-walled, with consistently straight lumina….……….……….……..……*Macromitrium longipilum* var. *rugosum*

21. Branch leaves elliptic-lanceolate to ovate-lanceolate; costa long-excurrent, often in a hyaline aristae, aristae 0.3–1.5 mm long; basal laminal cells variable, regular or

irregular thick-walled, cell lumina straight or curved and sigmoid (often both types of cell found in the basal lamina).………*Macromitrium longipilum* var. *longipilum*

22. Basal laminal cells smooth……….……….……….……….………..23

22. Basal laminal cells unipapillose to tuberculate……….………….…………….27

23. Costa excurrent as a long-filiform arista; upper laminal cells variable, from oblate, quadrate to short or long-rectangular, smooth or obscurely pluripapillose in some leaves…………..…….………….……….……….…...*Macromitrium cuspidatum*

23. Costa percurrent to shortly excurrent as a sharp awn; upper laminal cells oblate, quadrate to short or wide-rectangular, not elongated and always pluripapillose, either distinctly seen or obscurely……….……….……….…………....24

24. Leaf apex fragile, caducous; apex of perichaetial leaves gradually narrow into a long and acumen……….……………………...…..*Macromitrium angustifolium*

24. Leaf apex persistent; apex of perichaetial leaves abruptly narrow into a short and bluntly acute tip, or obtuse to retuse……………………………………...25

25. Branch leaves lingulate-lanceolate, slender and elongate, 2.4–2.8 mm long × 0.35–0.45 mm wide, leaf length-width ratio is 5–7:1; perichaetial leaves short-ovate to ovate-lanceolate, much smaller than the vegetative leaves (only 2/3 or half of the vegetative leaf length); cell remnants on exostome teeh with thickened anticlinal side that appears as a row of square cases in dorsal view…………..………………… ……….……….……….……………………*Macromitrium incurvifolium*

25. Branch leaves lanceolate from an oblong base or short-lingulate, 1.4–2.6 mm long × 0.4–0.8 mm wide, leaf length-width ratio is 3–4:1; perichaetial leaves long-elliptic, elliptic-lanceolate to lanceolate, about the same size or larger than the vegetative leaves; cell remnants on exostome teeth without thickened anticlinal side, surface irregularly roughened……….……….……….……………..26

26. Plant relatively small, erect branches 0.5–1 cm tall; branch leaves relatively small,

1.35–2.4 mm long × 0.4–0.6 mm wide, erect-spreading to incurved-spreading when moist; cells changing abruptly from pluripapillose and short to smooth and long at the midleaf, leaving a demarcated line (commonly found in lowland areas)…….………….……….……….…………*Macromitrium fuscescens*

26. Plant relatively larger, erect branches 1–3 cm tall; branch leaf relatively large, 1.8–2.6 mm long × 0.5–0.8 mm wide, wide-spreading to squarrose-recurved when moist; cells gradually losing their papillosity and becoming longer in shape from the midleaf toward the basal lamina (commonly found in montane areas)………… ……….……….……….……….…………………*Macromitrium salakanum*

27. Branch leaves slender-lanceolate from an oblong base, leaves longer than 3 mm; costa ending below the tips; apex bluntly acute and usually toothed near the tips; basal laminal cells unevenly thick-walled, lumina curved to sigmoid; calyptra with sparse hairs mostly developed near its base……………..*Macromitrium longicaule*

27. Branch leaves lingulate to lingulate-lanceolate, leaves 1.2–2.2 mm long; costa shortly excurrent as a short cusp; apex obtuse, rounded-acute to mucronate, entire to crenulated because of projecting papillae; basal laminal cells evenly thick-walled, lumens linear and straight; calyptra densely covered with hairs all over...28

28. Branch leaves small, short-elliptic, less than 1.4 mm long, length-width ratio 2–3:1; seta papillose, sinistrorse-twisted; capsule globose, length-width ratio 1:1…..... ……….……….……….……….…………*Macromitrium papillisetum*

28. Branch leaves large, slender-lingulate, longer than 1.4 mm, length-width ratio 4–7:1; seta smooth, either sinistrorse or dextrorse-twisted; capsule cylindric, usually long, length-width ratio 1.5–2.5:1……………………………………………...29

29. Plant small, erect branches below 1 mm tall; branch leaves small, length 1.4–1.75 mm; basal laminal margin denticulate to crenulated with projecting papillae; basal laminal cells mostly oblate to short-rectangular, length-width ratio 2:1 or less,

longer cells found only near the leaf insertion; cells bulging at basal lamina, moderate thick-walled, wall seldom thicker than lumen width except near leaf insertion, lumen 8–10 µm wide; perichaetial leaves erecto-patent, short (less than 1.1 mm long, shorter than the vegetative leaves and the vaginulae) and not hiding the vaginulae……….……………….…………….……………...*Macromitrium falcatulum*

29. Plant medium size, branches reaching 3 mm tall; branch leaves large, 1.6 mm or longer; basal laminal margin subentire to entire; basal laminal cells long-rectangular to linear, length-width ratio 3:1 or more; cells flat at basal lamina, distinctly thick-walled, wall thicker than lumen, lumen 3–5 µm wide; perichaetial leaves erect, long (2.2 mm or longer, exceeding the vegetative leaves and vaginulae) and ensheathing the vaginulae……………..…….*Macromitrium nepalense*

5.3 Taxonomic treatment of the Orthotrichaceae

5.3.1 *Desmotheca* Lindb.

J. Linn. Soc. Bot. 13: 184 (1873). *Cryptocarpon* Dozy & Molk., Ann. Sci. Nat. Bot. sér. 3, 2: 302 (1844), *nom. illeg*., non *Cryptocarpon* Dunal, Syn. Solan. 45 (1816). *Cryptocarpus* Dozy & Molk., Musci Fr. Ined. Archip. India 2: 37 (1846), *nom. illeg*., non *Cryptocarpus* Kunth, Nov. Gen. Sp. 2: 187 (1817). TYPE: *D. apiculata* (Dozy & Molk.) Lindb. *ex* Card.

Plants cladocarpous, generally small, mat-forming. Stem (primary axis) branched sympodially, plagiotropic, creeping with numerous, erect, short, simple, monopodial branches (secondary axis). Monopodial branches branched sympodially, branched regularly, with 1–2 subsequent branches formed almost immediate or short distance beneath perichaetium. Creeping stems tomentose, rhizoids never extended up to the erect branches. Stem leaves always smaller, resembling branch leaves in shape. Branch leaves dimorphic. Branch leaves found at the base of primary branch long, oblong-lanceolate to lingulate-lanceolate, leaf base not decurrent, and leaf lamina unistratose thick; but those leaves found along the primary, secondary and higher order branches short, ovate, oblong-lanceolate to lanceolate, spirally inserted on branch, in five distinctive ranks. Leaf cells parenchymatous, upper laminal cells short, oblate to rectangular, pluripapillose, but basal laminal cells long-rectangular and tuberculate; juxtacostal cells and marginal cells at basal lamina not distinctly differentiated. Plant phyllodioicous. Dwarf male bud-like. Perichaetial leaves either conspicuous or not. Vaginula not seen; paraphysis short, uniseriate, never branched. Seta reduced to a junction between urn and foot. Capsule immersed, exothecial cells thin-walled; stomata phaneroporous, infrequently found near urn base; operculum rostellate with a short beak that perpendicular to operculum base. Gymnostomous. Anisospory. Calyptra mitrate, covering only the operculum, plicate, pilose, base shallowly dissected into several lobes.

<u>Notes</u>:

1. *Desmotheca* is a small genus confined to the South East Asian and southwest Pacific regions. Wijk et al. (1962) listed six taxonomically valid names under *Desmotheca*, of which only two, *D. apiculata* (Dozy & Molk.) Cardot and *D. brachiata* (Hook. & Wils.) Vitt., were accepted as valid by Vitt (1990) in his revision of the genus. *Desmotheca apiculata* is widely distributed in the region, from Myanmar to its easternmost extent at New Caledonia, whereas *D. brachiata* was thought to be endemic in Luzon, the Philippines, is synonymised here under *D. apiculata*.

2. Members of this genus can be easily separated from other Orthotrichaceae by their strongly dimorphic leaves on both sterile and fertile branches, sessile capsules without peristome and delicate, mitrate and hairy calyptrae. Only young *Desmotheca* plants could possibly be confused with other Orthotrichaceae, especially *Macromitrium*. Without the elongated fertile branches, such young plants have a gross morphology

similar to that of *Macromitrium falcatulum*. Both plants form long-creeping stems with long, slender branch leaves tightly inrolled on short branches. One useful character for distinguishing such young *Desmotheca* plants is the consistently unipapillate, long and slender basal laminal cells (4–5:1 in length:width ratio) present in *Desmotheca*.

1. *Desmotheca apiculata* (Dozy & Molk.) Lindb. *ex* Card. (Figs. 5.1 & 5.2)

Ann. Jard. Bot. Buitenzorg Suppl. 1: 11 (1897). *Cryptocarpon apiculatum* Dozy & Molk., Ann. Sci. Nat. Bot. sér. 3 (2): 302 (1844). *Cryptocarpus apiculatus* Dozy & Molk., Musci Fr. Ined. Archip. Indici 2: 37, tab. 45 (1846). TYPE: Borneo, *s. coll*. (holotype L; isotype BM!).

Macromitrium brachiatum Hook. & Wilson, Icon. Pl. 8: 746b (1845). *D. brachiata* (Hook. & Wilson) Vitt. Trop. Bryol. 3: 84 (1990). LECTOTYPE (Vitt, 1990): Philippine Islands, *Cuming 2195* (BM-Hook.; isotypes BM-Hook., BM-Wils.).

Cryptocarpus cymosus Mitt. in Seem., Fl. Vit. 381 (1873). *D. cymosa* (Mitt.) Par., Ind. Bryol. Suppl. 114 (1900). LECTOTYPE (Vitt, 1990): Fiji, Island of Pines, *Milne s.n.* (NY-Mitt.; isolectotypes NY-Mitt., S).

Orthotrichum coralloides Duby, Flora 60: 74 (1877). *D. coralloides* (Duby) Broth., Nat. Pfl. 1 (3): 475 (1902). LECTOTYPE (Vitt, 1990): Aryat provinciae de Baluca Philippinaru, *Llanos* (G-Duby; isotype G-Duby).

Cryptocarpus cuspidatus Müll. Hal., Hedwigia 37: 141 (1898). *D. cuspidata* (Müll. Hal.) Par., Ind. Bryol. Suppl. 114 (1900). LECTOTYPE (Vitt, 1990): Birma, Pegu, Yomah, *Kurz 3408* (BM-Hampe; isolectotypes BM-Hampe, H-Broth.).

Cryptocarpon glaucon Müll. Hal., Hedwigia 37: 142 (1898). *D. glauca* (Müll. Hal.) Paris, Ind. Bryol. Suppl. 114 (1900). LECTOTYPE (Vitt, 1990): Philippines, prope oppilum Galumpit, *Llanos s.n.* (H-BR; isolectotypes BM! S).

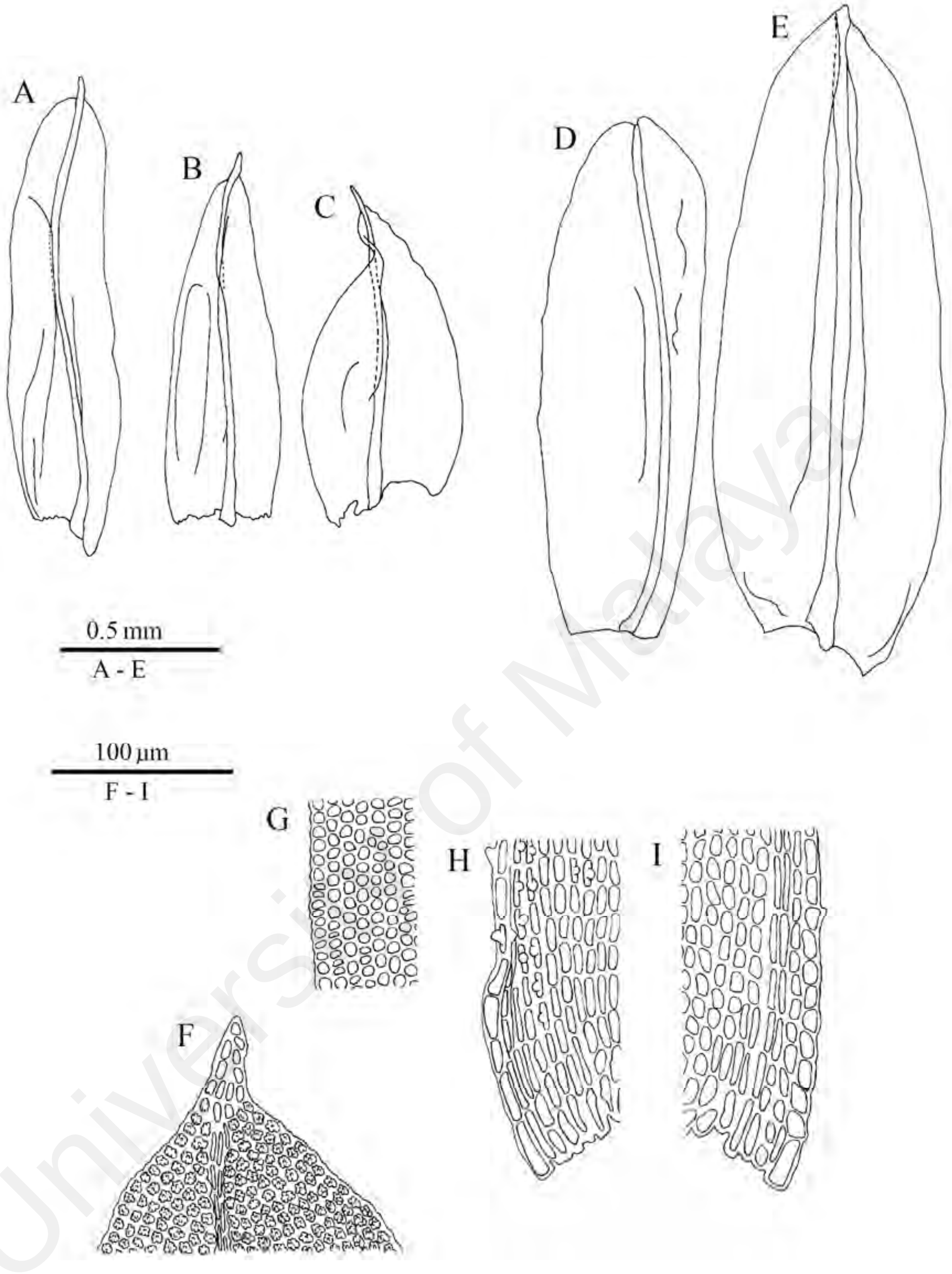

Figure 5.1. Illustrations of *Desmotheca apiculata* (Dozy & Molk.) Lindb. — A, leaf of sterile branch; **B-C,** leaves of fertile branch; **D-E,** perichaetial leaves; **F,** leaf apex; **G,** mid-leaf cells; **H-I,** basal laminal cells. (All from *Yong 829*, KLU).

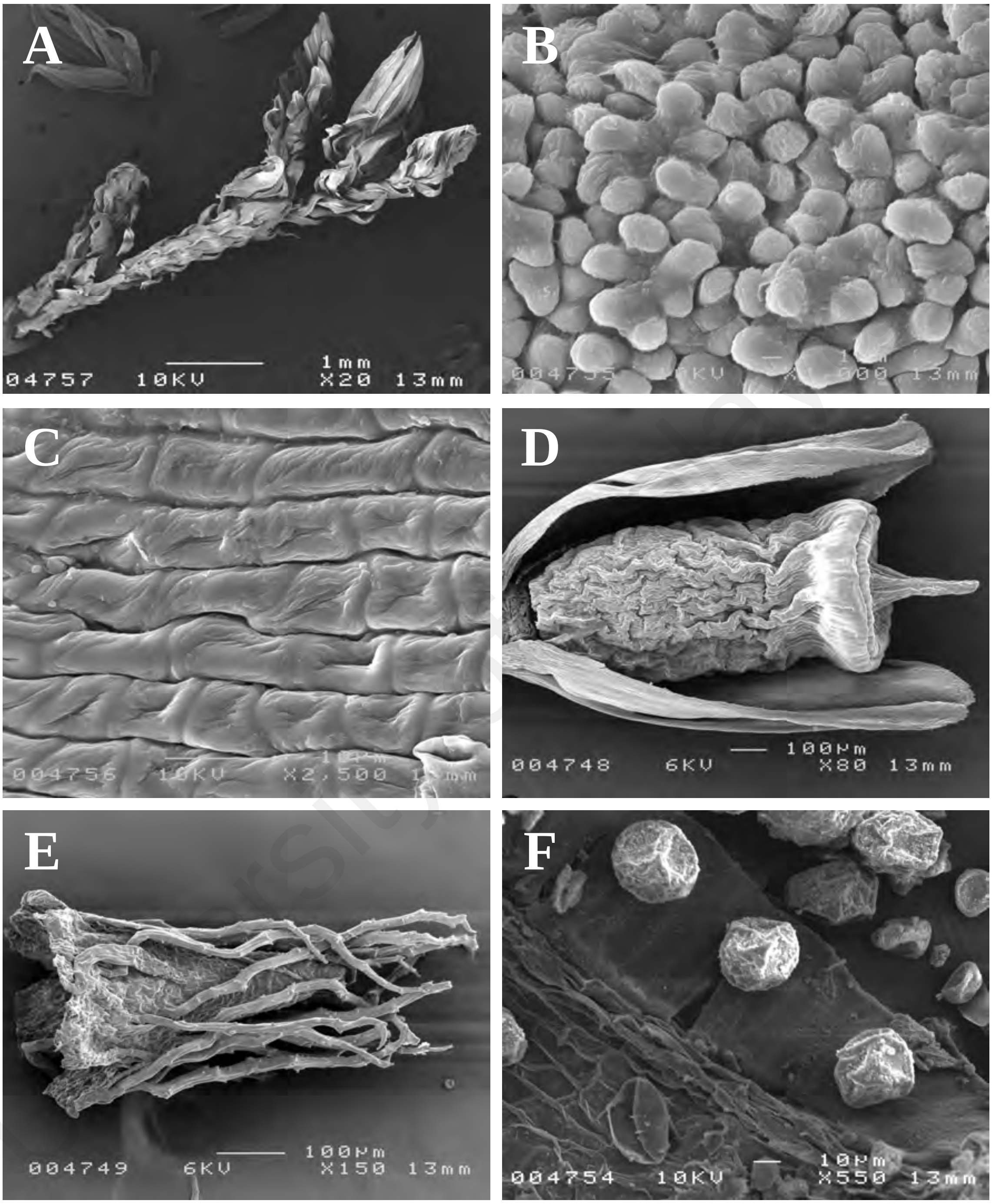

Figure 5.2. SEM images of *Desmotheca apiculata* (Dozy & Molk.) Lindb. — A, detailed view of a branch; **B,** upper laminal cells; **C,** basal laminal cells; **D,** capsule and perichaetial leaves; **E,** calyptra; **F,** mouth of capsule (inner view) with anisosporous spores. (All from *Yong 5766*, KLU).

Cryptocarpus manii Müll. Hal., Hedwigia 37: 141 (1898). *D. manii* (Müll. Hal.) Paris, Ind. Bryol. Suppl. 114 (1900). LECTOTYPE (Vitt, 1990): India orientalis, Andaman, Port Blair, *Man 1892 et 1895* (H-BR; isolectotypes BM, G, H-Broth., S).

Cryptocarpus marginatulus Müll. Hal. in Jaeger, Ber. S. Gall. Naturw. Ges. 1874–75: 177 (1876), *nom. nud.*

Plant small, mat-forming; young shoots dark-green, gradually turning to olive-green and brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Primary branches erect, short, 1.5–2 cm tall, loosely arranged, frequently branched, into many short secondary and tertiary branches, like a crown on top of the erect primary branch. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate to triangular-lanceolate on young shoots, becoming more lanceolate at older portions, apex acuminate with excurrent costa.

Branch leaves dimorphic. Branch leaves found at the base of primary branch loosely and irregularly twisted, flexuose or flexuose-contorted with incurved to involute apices (when dry), erecto-patent to erect-spreading (when moist); leaves 1.5–2.0 mm × 0.3–0.5 mm, length:width ratio 4–5:1, oblong-lanceolate to lingulate-lanceolate, apex blunt to broadly acute, apiculate; margin subentire to crenulate, plane above but reflexed at basal lamina; costa short-excurrent, extending beyond leaf tip with an apiculus achieved 0.10 mm long. Branch leaves found along the primary, secondary and higher order branches spirally inserted on branch, in five distinctive ranks, leaves erect to erect-flexuose, loosely appressed on branches with leaf apices variously curved (when dry), wide-spreading to recurved-spreading (when moist); branch leaves 0.7–1.0 × 0.3–0.5 mm, length:width ratio 1.5–2:1, ovate to oblong-lanceolate, often without a conspicuous oblong base, lamina straight to lightly recurved, smooth; apex firm, short, acute to acuminate, apiculate; margin subentire to crenulate, plane at distal part but reflexed at leaf base; costa short-excurrent, extending beyond leaf tip as an apiculus that achieved 0.1 mm long. Upper and middle laminal cells 6–8 × 6–8 µm, length:width ratio 1:1, oblate to short-rectangular, moderately thick-walled, walls not pitted, cells bulging, pluri-papillose, cells sometime obscure due to the dense papillae; basal laminal cells 12–16 × 6–8 µm, length:width ratio 2:1, cells grading from oblong or short-rectangular to gradually elongate only near extreme leaf base, evenly incrassate, lumina broad, short- to long-rectangular, pitted only near juxtacostal region and insertion, cells bulging or flat, unipapillose above but smooth toward marginal lamina and extreme base.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.2–0.3 mm long, ovate to ovate-lanceolate. Perichaetial leaves conspicuously erect, sheathing the seta, much larger than branch leaves, 1.3–1.5 × 0.5–0.6 mm, oblong to oblong-lanceolate, upper lamina broad, with margins almost parallel to leaf base; apex slender retuse to obtuse, occasionally broadly acute; margin sparsely denticulate to serrulate up to mid-leaf, entire below, plane; costa percurrent; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pluripapillose at leaf apex but smooth below, rarely pitted. Paraphyses scarce, 0.3 mm long, made of 5–7 short- or long-rectangular cells. Capsule urns 1.2–1.4 × 0.6–0.9 mm, oblong, broad-cylindric, smooth, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length:width ratio 2–3:1, thin-walled; stomata 2–4, phaneroporous; operculum rostellate, beak 0.1–0.2 mm. Larger spore 34–38 µm in diameter while smaller spore 16–20 µm in diameter. Calyptra mitrate, plicate, pilose, hairs many, erect and long, mostly originated near calyptra base, base shallowly lobed.

Other descriptions and illustrations: Dozy & Molkenboer (1861) p. 110, as *Cryptocarpus apiculatus*; Fleischer (1904) p. 463–466, fig. 86; Brotherus (1925) p. 49, figs. 433E–K; Bartram (1939) p. 186, pl. 14, fig. 232; Gangulee (1976) p. 1195–1197, fig. 581; Vitt (1990) p. 83–84, figs. 1, 3; Vitt et al. (1995) p. 87–91, figs. 3f, 38; Eddy (1996) p. 94, fig. 394.

Distribution: As.3: India (Andaman Islands), Myanmar (South), Thailand (Peninsula Thailand), Vietnam; As.4: Indonesia (Ambon, Borneo, Flores, Java, Sulawesi, Sumatra), Malaysia (Borneo, Malay Peninsula), Papua New Guinea, Philippines (Luzon, Mindanao), Singapore; Oc.: New Caledonia.

Habitat and ecology: Canopy epiphyte, often collected on branches fallen from big tree or rotten logs. In Malaysia, the species occurs at elevation near to sea level in primary forest. However, elsewhere the species is also found on roadside trees and those trees planted in the garden (Vitt, 1990). In the region with monsoon climate, the plant has only reported from the wetter parts of the monsoon county (Touw, 1992).

Notes:

1. *Macromitrium brachiatum* was collected from the Philippines and described by Hooker & Wilson in 1845. It was placed in the synonymy under *D. apiculata* since Dozy & Molkenboer (1861) until 1990, when Vitt (1990) distinguished it as a different species, by its lanceolate-lingulate to narrowly oblong vegetative branch leaves, where the upper lamina cells grade quickly from densely pluri-papillose to unipapillose over the lower half of the leaf lamina, and the generally shorter lower laminal cells. However, these characters are found to be variable and inconsistent in *D. apiculata* (based on a wide range of specimens examined); even some New Guinean specimens determined by Vitt as *D. apiculata* have the features he described for *D. brachiata*. On the other hand, two specimens annotated by Vitt as *D. brachiatum* (*Williams 3140* and *Ramos 7972*, NY) show no difference from the widespread *D. apiculata* in terms of vegetative branch

length as well as leaf cell characters. In fact, these two specimens were first identified as *D*. *apiculata* by Bartram (1939), and a duplicate of *Ramos 7972* in the BM was likewise determined by Brotherus.

2. Similarly, Eddy (1996) noted some Peninsular Malaysia and New Guinea specimens that appeared to fit the description of *D. brachiata* but which could not be separated from *D*. *apiculata* with confidence. Meanwhile, Vitt (1990) admitted that some Malaysian populations of *D. apiculata* have densely papillose and obscure upper laminal cells that might confused with *D*. *brachiata*. On the other hand, Bartram (1939) doubted the identity of *D*. *glauca* and *D*. *coralloides* (both listed as synonyms of *D*. *brachiata* by Vitt (1990)) and suggested that these two names were possibly synonymous with *D*. *apiculata*. This suggestion is borne out by the current findings.

<u>Specimens examined</u>:

BORNEO: *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe ex Hb*. *Dozy & Molk*. (isotype of *Cryptocarpus apiculatus*: BM!); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe ex Hb*. *Lugd*. *Batav*. [*c.fr*.] (BM!). **INDONESIA. Java:** Batavia, Buitenzorg Garden, 260 m, 1893, *Schiffner 10737* [*c.fr*.] (NY!); *ibidem*, 27.III.1984, *Schiffner 10734* [*c.fr*.] (BM!); *ibidem*, *s.date*, *Schiffner 3682*, [*c.fr*.] (NY!); *ibidem*, *s.date*, *Schiffner 213892* (NICH!); Salak, 1897, *Nyman 169* [*c.fr*.] (NY!). **Kalimantan:** East Kalimantan, Nunukan, Krayan, Pa’ Raye Village, along Pa’ Raye River, 870 m, 10.IV.2003, *Suleiman 1162* (BORH); West Kalimantan, Montrado bei Singkawang, 1904, *Fleischer 306* (BM-Dixon 3 sheets! NY 2 sheets!). **Sumatra:** *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Besch*. [*c.fr*.] (BM!); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe ex Lacoste* (BM); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Lacoste* [*c.fr*.] (BM!); *s.loc*., *s.date*, *Teysmann s.n*. *ex Hb*. *Lindberg* (BM!); West Sumatra, Payakumbuh, Air Putih, 560 m, 30.X.1999, *Zakaria 122* (KLU!). **MALAYSIA, Kelantan**: Taman Negara, Kuala Koh, 100 m, 23.V.1999, *Yong & Damanhuri 829* (UKMB!); *ibidem*, 70–120 m, 8.IX.1999, *Yong 1497*, *1498* (UKMB!). **Negeri Sembilan**: Jelebu, Kuala Kelawang, Kenaboi Forest Reserve, 255 m, 8.V.2006, *Rahmat et al. 51* [*c.fr*.] (KLU!). **Pahang**: Gua Kechil limestone outcrop, 1000 ft [=305 m], 21.VI.1971, *Chin 1186* [*c.fr*.] (KLU!); Janda Baik, 400 m, 29.II.1989, *Mohamed 9113* [*c.fr*.] (KLU!); Taman Negara, Gua Luas, on limestone hill, *Damanhuri 1860* (UKMB!); Taman Negara, Merapoh, Kuala Juram, Mt. Harimau, 220 m, 21.VI.1995, *Mohamed & Ibrahim 370b* [*c.fr*.] (KLU!). **Perak**: Ulu Perak, Belum Royal Park, Sg. Kenarong area, 200–300 m, 29.VII.2003, *Yong 4430*, *4431*, *4440* (KLU!). **Sabah:** Kota Marudu, Taman Kinabalu Substesen Serinsim, 200 m, 17.VI.2002, *David DM1* (BORH! SNP); Lower Kinabatangan River, Lummun River, 15 m, 6.V.2002, *Suleiman 823* (BORH! SAN); Lower Kinabatangan River, Panggi Forest Reserve, 45 m, 5.V.2002, *Suleiman 822* (BORH! SAN); Tenom, 5.V.1913, *Binstead 154* (BM-Dixon!); *ibidem*, 6.V.1913, *Binstead 162* [*c.fr*.] (BM-Dixon!). **Sarawak**: *s.loc*., II–VI.1914, *native collector 2730*, [*c.fr*.] (NY!); First Division, Landih, 50–100 m, I.1990, *Bakar s.n*. [*c.fr*.] (KLU!); Limbang, Nanga Mendamit, Kampung Long Napir, 80–100 m, 10.X.2004, *Mohamed & Yong 5274* (KLU!). **Selangor**: Hulu Langat Forest Reserve, Sg. Congkak, 15.III.1997, *Damanhuri & Ahmad 97-141*, *97-181* (UKMB!). **Terengganu**: Dungun, Kampung Pasir Raja, Pasir Raja Forest Reserve, 150 m, 6.VI.2004, *Yong 5766* (KLU!); Ulu Terengganu, Sg. Berua, 60 m, 24.V.1989, *Mohamed 9569a* (KLU!). **MYANMAR:** Kyanktalan, Mergui, III.1911, *Meebold 16618* [*c.fr*.] (BM-Dixon!). **PAPUA NEW GUINEA, Central:** Koitaki, 1500 ft [=457 m], V.1935, *Carr 120* (SING) *& 12273* [*c.fr*.] (BM! NY! SING 3 sheets! BM!). **East Sepik:** Wewak, Wewak to Yangoru Road, 600 ft [=183 m], 15.VI.1971, *Tan & Streimann 10271* [*c.fr*.] (KLU! SING!). **Morobe:** Forestry College, Bulolo, 730 m, 31.I.1981, *Streimann 14059* [*c.fr*.], *14121* [*c.fr*.] (NY! H, LAE, NICH), *24829* (NY! NICH, B); *ibidem*, 5.III.1989, *Streimann 41924* [*c.fr*.] (NY! B); *ibidem*, 750 m, 27.I.1996, *Vinas 96-4*, [*c.fr*.] (TNS!); Lae, Oomsis Forest Station, 12.I.1981, *Streimann & Umba 10820*, *10825* (GRO, H, LAE, NY!). **PHILIPPINES, Luzon:** *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe* (BM!); Bataan, Lamao river, 90 m, I.1904, *Williams 3140* (NY!); Bataan, Olongpo Nawal Recreation Park, 25.V.1935, *Barlett 14096* [*c.fr*.] (KLU! SING); Cagayan, IV.1909, *Ramos 7972* [*c.fr*.] (NY!); prope oppilum Galumpit, *s.date, Llanos s.n. ex Hb. Besch. ex Hb. Müll. Hal.* (isolectotype of *Cryptocarpon glaucon*: BM!). **SINGAPORE:** Bukit Timah, 1894, *Ridley 801* (SING!).

2. *Desmotheca mohamedii* sp. nov. ined. prop. (Figs. 5.3, 5.4 & 5.5)

PROPOSED TYPE: Peninsular Malaysia, Terengganu, Ulu Terengganu, Sg. Berua, off Jalan Tapah Road, 60 m, 24.V.1989, *Mohamed 9568* (holotype KLU!).

Plant small, mat-forming; young shoots dark-green, gradually turning to olive-green and brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Primary branches erect, short, 2 cm tall and 1–2 mm wide, loosely arranged, frequently branched, into many short secondary and tertiary branches, like a crown on top of the erect primary branch. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate to triangular-lanceolate on young shoots, becoming more lanceolate at older portions, apex acuminate with excurrent costa.

Branch leaves dimorphic. Branch leaves found at the base of primary branch loosely and irregularly twisted, flexuose or flexuose-contorted with incurved to involute apices (when dry), erecto-patent to erect-spreading (when moist); leaves 1.7–2.2 mm × 0.3–0.4 mm, length:width ratio 5–6:1, long, slender-lanceolate to ligulate-lanceolate, apex blunt to broadly acute, cuspidate; margin subentire to crenulate, plane above but reflexed at basal lamina; costa short-excurrent, extending beyond leaf tip with a cusp achieved 0.40 mm long. Branch leaves found along the primary, secondary and higher order branches spirally inserted on branch, in five distinctive ranks, leaves erect to

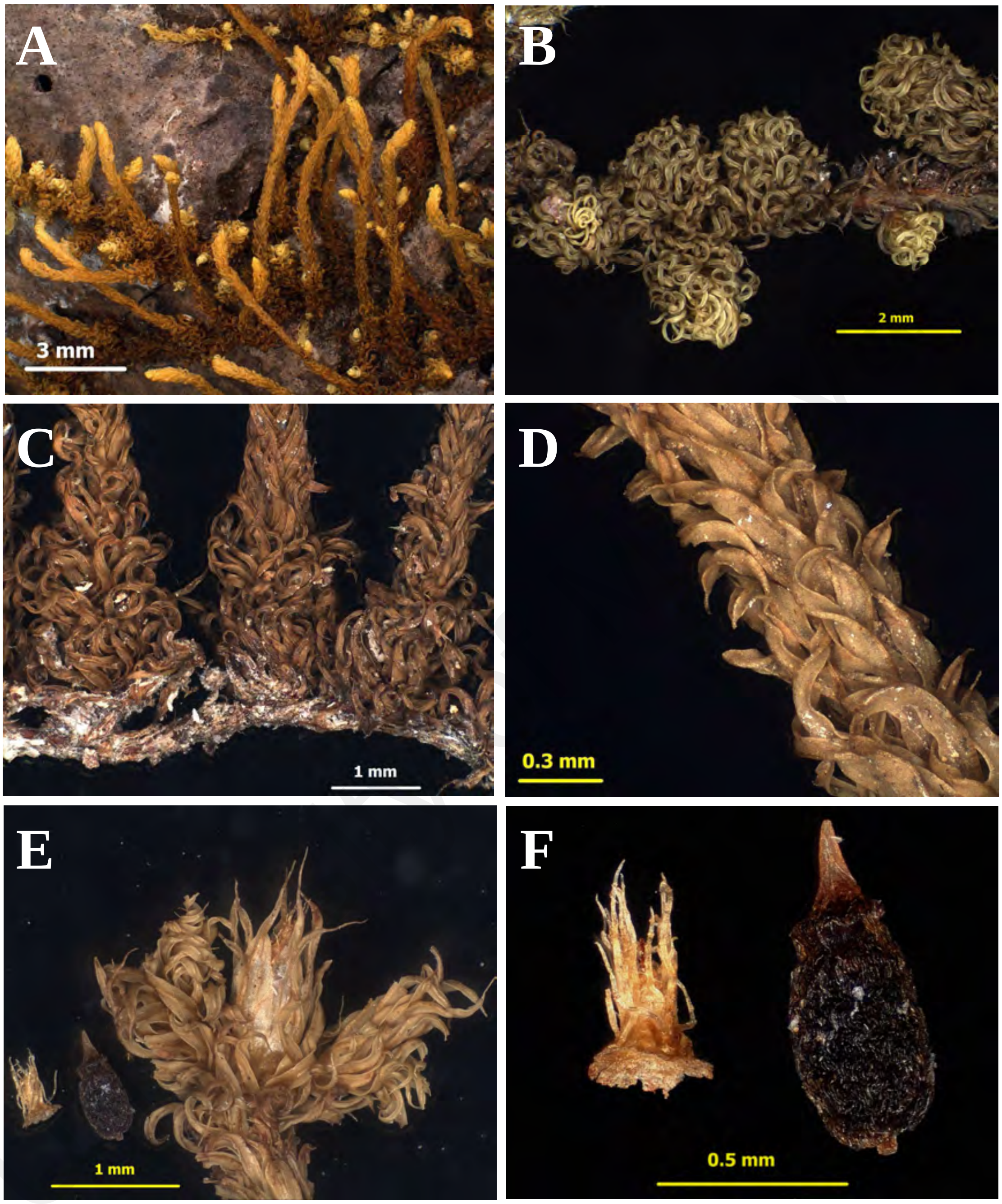

Figure 5.3. View of *Desmotheca mohamedii* sp. nov. ined. prop. — **A,** habitual view; **B,** newly developed branches on creeping stem; **C,** sterile branch; **D,** middle portion of fertile branch; **E,** terminal of fertile branch with sporophytic structures; **F,** detail view of calyptra and fully developed capsule (All from *Mohamed 9568*, KLU).

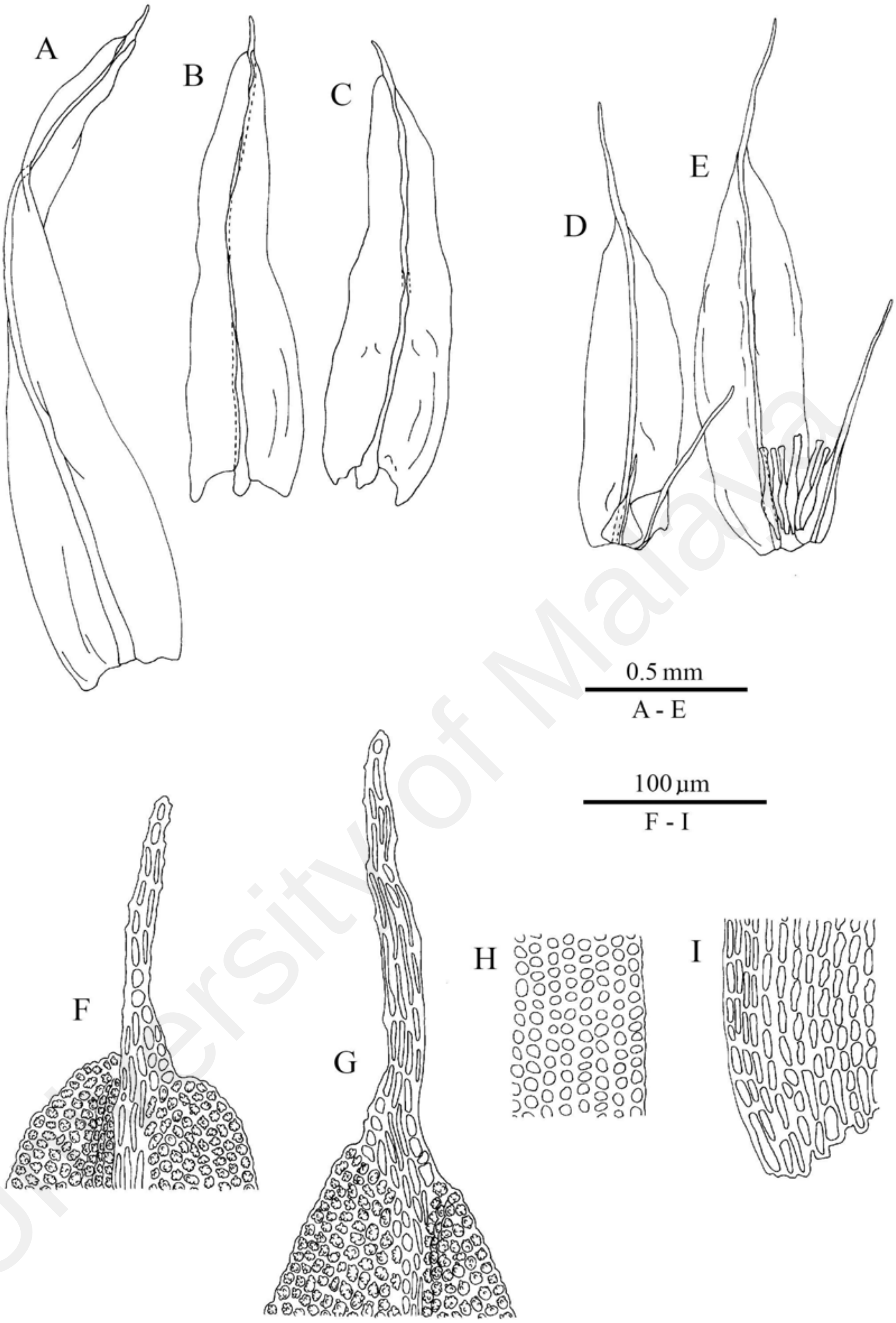

Figure 5.4. Illustrations of *Desmotheca mohamedii* sp. nov. ined. prop. — A, leaf of sterile branch or basal of fertile branch; **B-C,** leaves of fertile branch; **D-E,** perichaetial leaves; **F,** leaf apex of sterile branch leaf; **G,** leaf apex of fertile branch leaf; **H,** mid-leaf cells; **I,** basal laminal cells (All from *Mohamed 9568*, KLU).

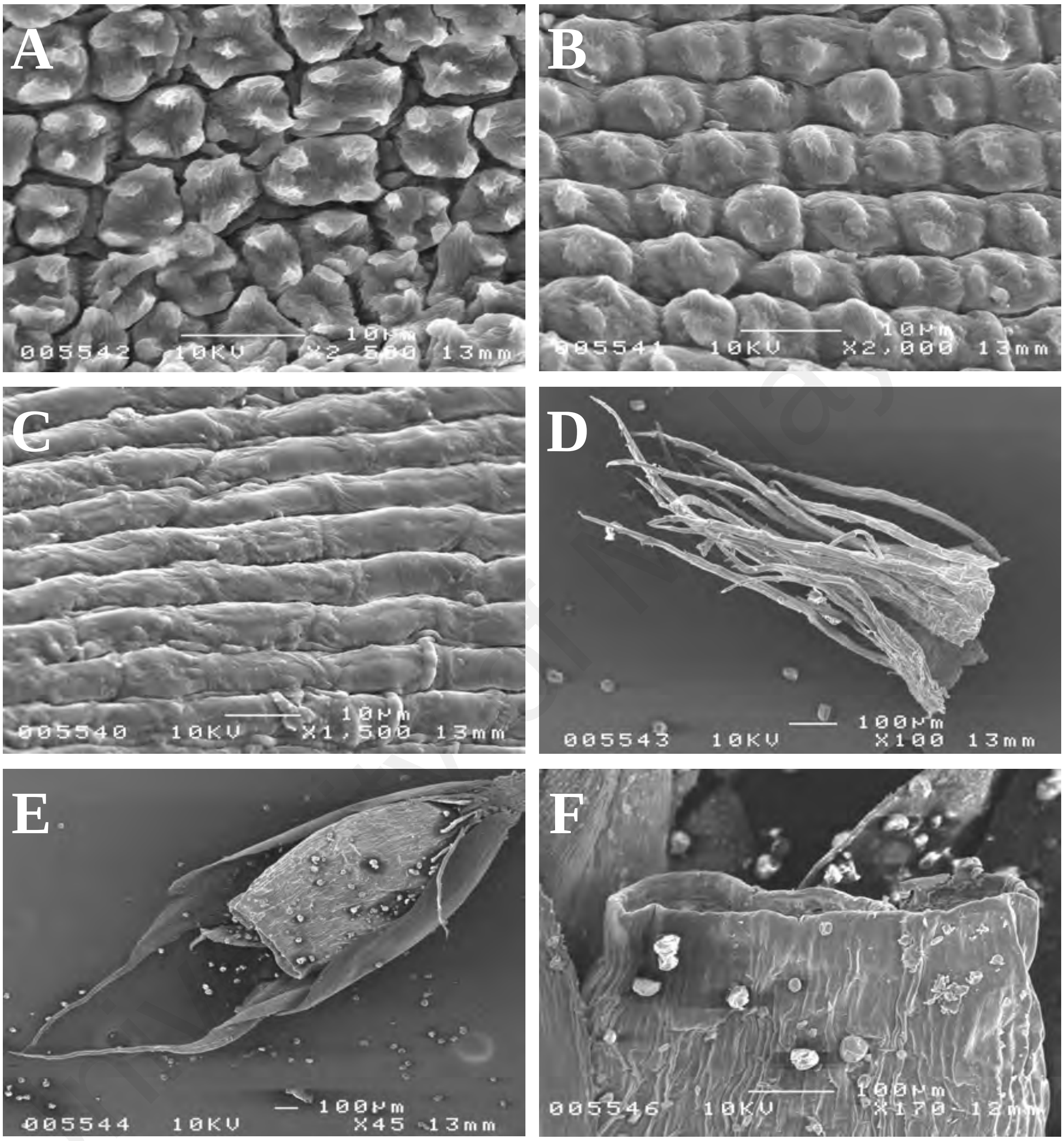

Figure 5.5. SEM images of *Desmotheca mohamedii* sp. nov. ined. prop. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** calyptra; **E,** urn and perichaetial leaves; **F,** urn, mouth part. (All from *Mohamed 9568*, KLU).

erect-flexuose, loosely appressed on branches with leaf apices variously curved (when dry), wide-spreading to recurved-spreading (when moist); branch leaves 1.2–1.8 × 0.4–0.6 mm, length:width ratio 3–4:1, lanceolate, upper lamina narrow, gradually expanding at mid-leaf forming an oblong base, lamina straight to lightly recurved, smooth; apex firm, short, acute to acuminate, cuspidate; margin subentire to crenulate, plane at distal part but reflexed at leaf base; costa short-excurrent, extending beyond leaf tip as an cusp that achieved 0.4 mm long. Upper and middle laminal cells 6–8 × 6–8 µm, length:width ratio 1:1, oblate to short-rectangular, moderately thick-walled, walls not pitted, cells bulging, pluri-papillose, cells sometime obscure due to the dense papillae; cells grading from oblong or short-rectangular to gradually elongate only near mid-leaf; basal laminal cells 20–25 × 6–8 µm, length:width ratio 3–4:1, long-rectangular, evenly incrassate, lumina broad, long-rectangular, pitted only near juxtacostal region and insertion, cells bulging or flat, unipapillose above but smooth toward marginal lamina and leaf insertion.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.2–0.3 mm long, ovate to ovate-lanceolate. Perichaetial leaves conspicuously erect, sheathing the seta, shorter or achieve the size of branch leaves, 1.4–1.7 × 0.5–0.6 mm, oblong to oblong-lanceolate, upper lamina broad, with margins almost parallel to leaf base; apex acuminate, cuspidate to piliferous; margin sparsely denticulate to serrulate up to mid-leaf, entire below, plane; costa long-excurrent, awn up to 0.6 mm long; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pluripapillose at leaf apex but smooth below, rarely pitted. Paraphyses scarce, 0.3 mm long, made of 5–7 short- or long-rectangular cells. Capsule urns 1.2–1.5 × 0.6–0.8 mm, oblong, broad-cylindric, smooth, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length:width ratio 2–3:1, thin-walled; stomata 2–4, phaneroporous; operculum rostellate, beak 0.1–0.2 mm.

Larger spore 34–38 µm in diameter while smaller spore 16–20 µm in diameter. Calyptra mitrate, plicate, pilose, hair many, erect and long, mostly originated near calyptra base, base shallowly lacerated.

Distribution: Endemic to Malaysia. As.4: Borneo, Malay Peninsula.

Habitat and ecology: Canopy epiphyte, usually found on branches fallen from big tree. The species is only known from area below 120 m, mostly collected from primary forest, except a single collection (*Ridley 11622*, SING) from coffee plantation.

Notes:

1. Perichaetial leaves with piliferous apices are here reported for the first time for *Desmotheca* and appear to be unique to *D. mohamedii*. This new species can also be differentiated from *D. apiculata* by a larger plant size, lanceolate fertile branch leaves with cuspidate apices and stiff excurrent costae. *Desmotheca apiculatum* is smaller, has typically oblong to oblong-lanceolate leaves with blunt to apiculate apices and short-excurrent costae.

2. The specimen *Ridley 11622* (SING!) was mistaken for an indeterminate *Macromitrium* species by Dixon (1926). In the publication, Dixon noted its “somewhat doubtful habit" in which "many branches are globose while others are several centimetres in length”, which in fact was due to a mixture of well developed and undeveloped fertile branches found on the stem, common for any *Desmotheca* species.

Specimens examined:

MALAYSIA. Johor: Castlewood, IV.1903, *Ridley 11622* (SING!). **Kelantan:** Taman Negara, Kuala Koh, 70–120 m, 8.IX.1999, *Yong 1499*. **Sabah:** Lower Kinabatangan River, Keruak Forest Reserve, 15 m, 7.V.2002, *Suleiman 840* [*c.fr*.] (BORH!). **Terengganu:** Ulu Terengganu, Sg. Berua, off Jalan Tapah Road, 60 m, 24.V.1989, *Mohamed 9568* [*c.fr*.] (holotype of *D. mohamedii*: KLU!).

5.3.2 *Groutiella* Steere

Bryologist 53: 145 (1950). *Macromitrium* sect. *Micromitrium* Mitt., J. Linn. Soc. Bot. 12: 197 (1869). *Micromitrium* Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 190 (1872), *nom. illeg.*, non *Micromitrium* Aust. (1870). *Craspedophyllum* Grout, N. Amer. Fl. 15A: 38 (1946), *nom. illeg.*, non *Craspedophyllum* Copeland (1938). TYPE: *G. tomentosa* (Hornsch.) Wijk & Margad.

Plants cladocarpous, medium-sized, mat- or cushion-forming. Stem (primary axis) branched sympodially, plagiotropic, creeping with numerous, erect, short, simple, monopodial branches (secondary axis). Monopodial branches branched sympodially, branched irregularly, with 1–2 subsequent branches formed almost immediate or short distance beneath perichaetium. Creeping stems tomentose, with some rhizoids extended up to the erect branches. Stem leaves always smaller, resembling branch leaves in shape. Branch leaves more or less uniform in shape, slender-lanceolate, subulate-lanceolate to lingulate-lanceolate, leaf base not decurrent, and leaf lamina unistratose, or 2-3 cell layers thick at leaf apex. Leaf cells parenchymatous, upper laminal cells oblate to oval, smooth to bulging, but basal laminal cells conic-papillose to tuberculate; juxtacostal cells before leaf insertion and basal marginal cells well-differentiated. Plant dioicous. Perigonial leaves small. Perichaetial leaves inconspicuous. Vaginula long, densely covered by short and filamentous paraphysis; paraphysis uniseriate, never branched. Seta moderately long, extended. Capsule exerted, urn narrowed to seta in short distance, exothecial cells incrassate; stomata phaneroporous, infrequently found near urn base; operculum rostrate with a long beak that perpendicular to operculum base. Peristome double. Both exostome and endostome fused into a continuous membrane.

Anisosporous or isosporous. Calyptra mitrate, covering the operculum leaving urn exposed, plicate, naked, base shallowly dissected into several lobes.

Notes:

1. *Groutiella* is a small genus of tropical or subtropical areas, mostly in continental America but with a small representation in Africa and Asia. Thus far, only two species are known in South East Asia, viz., *G. tomentosa* (Hornsch.) Wijk & Margad., pantropical and common in the region, and *G. macrorrhyncha* (Mitt. *ex* Bosch & Sande Lac.) Wijk. & Margad., a rare species probably only known from its type gathering from Java (*s.coll*., NY-Mitt.).

2. The genus is traditionally separated from the closely related *Macromitrium* by the presence of a limbidium at the lamina base and the distinctively incrassate but short basal laminal cells. The often short calyptrae, which only covers the operculum or slightly more, also distinguishes *Groutiella* from *Macromitrium* (at least in this part of the world). All Malaysian *Macromitrium* have large calyptra enveloping the whole capsule.

1. *Groutiella kelantanense* sp. nov. ined. prop. (Figs. 5.6, 5.7 & 5.8)

PROPOSED TYPE: Peninsular Malaysia, Kelantan, Gua Teja, Betis, 500 ft [=152 m], 15.VII.1935, *s.coll*. *SFN29699* (holotype SING!).

Plant medium-sized, forming short-cushion or mats; shoots rusty-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 1.0–2.0 cm tall and 2–4 mm wide, tightly arranged, rarely branched. Stem leaves inconspicuous, small, covered by rhizoids, slender, ovate-lanceolate to triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with percurrent costa.

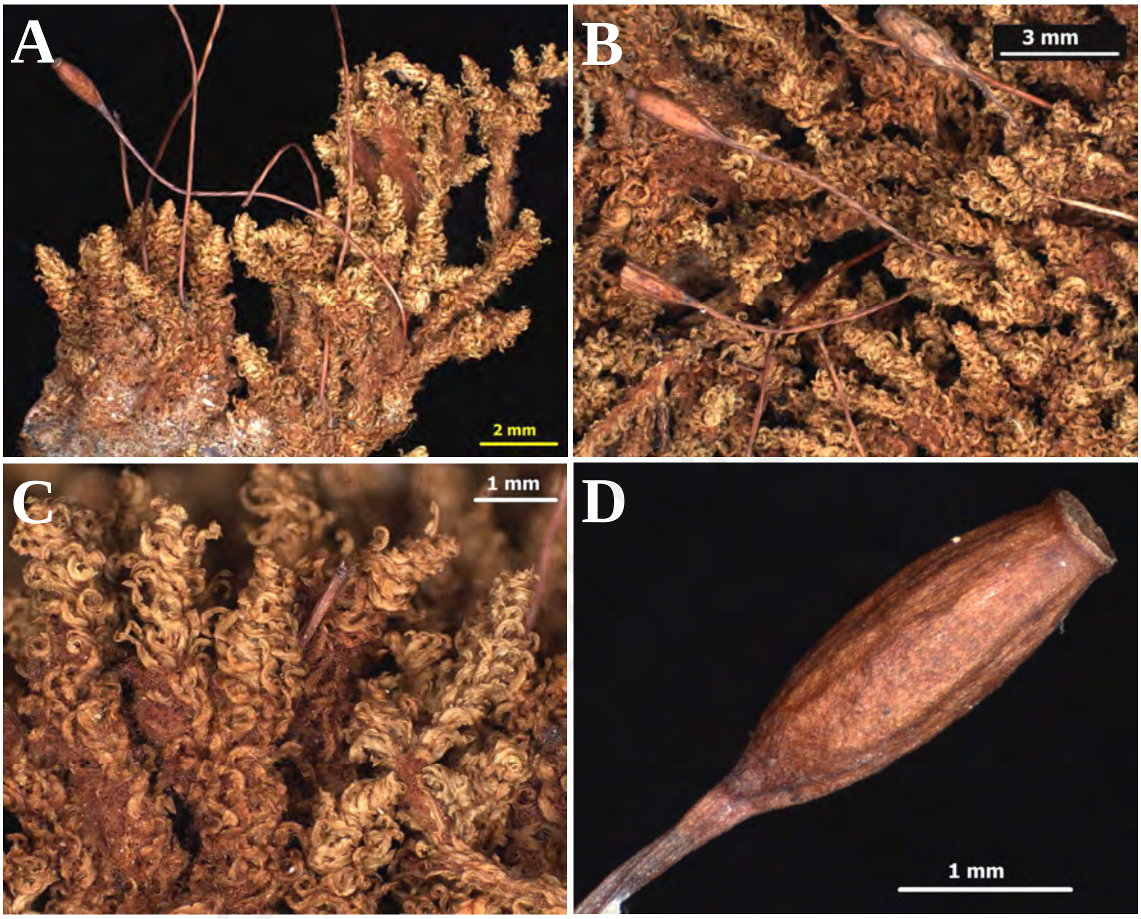

Figure 5.6. View of *Groutiella kelantanense* sp. nov. ined. prop. — A-B, habitual view; **C,** detail view of branches; **D,** urn. (All from *s.coll*. *SFN29699*, SING).

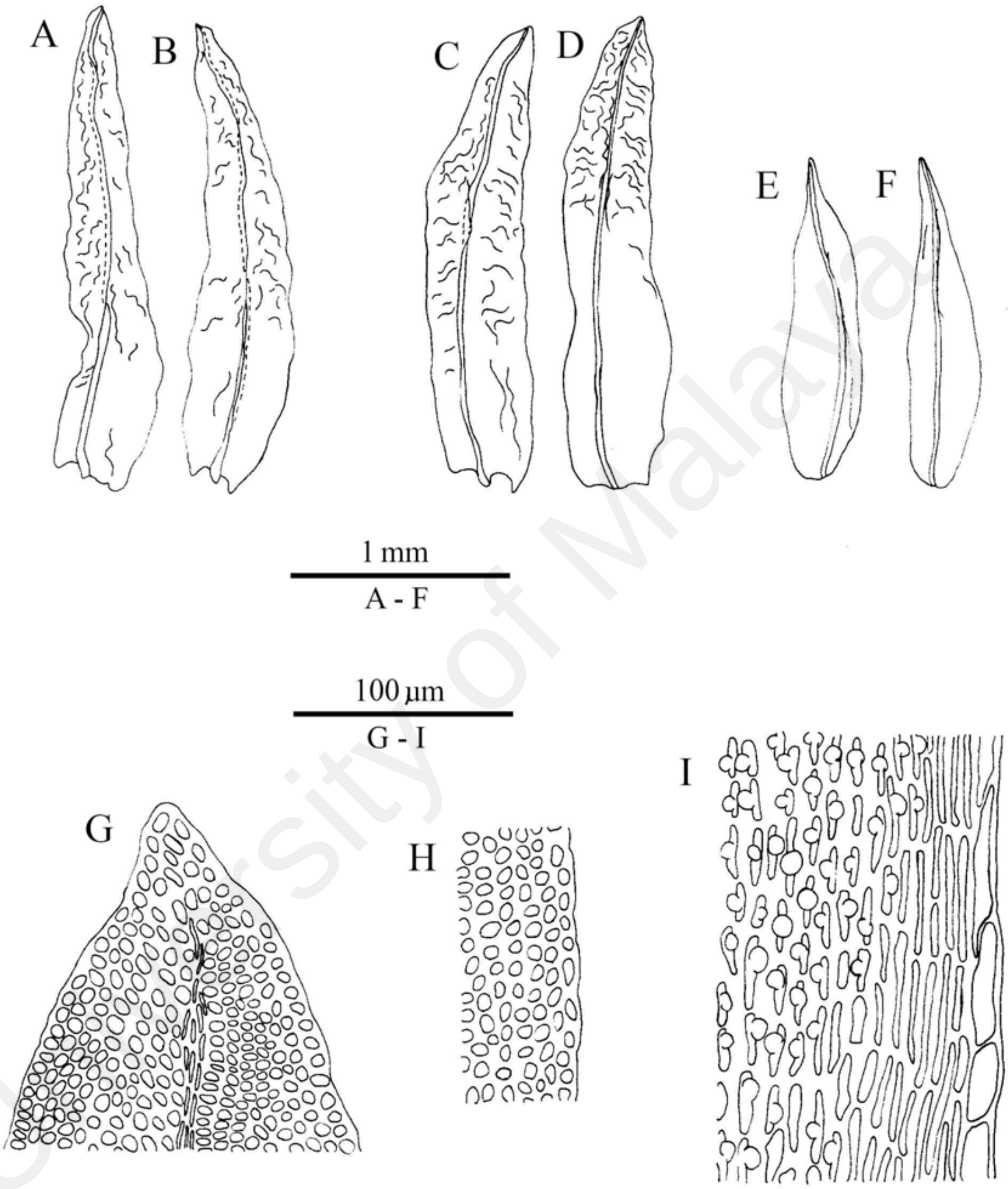

Figure 5.7. Illustrations of *Groutiella kelantanense* sp. nov. ined. prop. — A-D, branch leaves; **E-F,** perichaetial leaves; **G,** leaf apex; **H,** mid-leaf cells; **I,** basal laminal cells. [**A-B, G-I** from *s.coll. SFN29699* (SING); **C-D** from *Singh 956* (SING)]

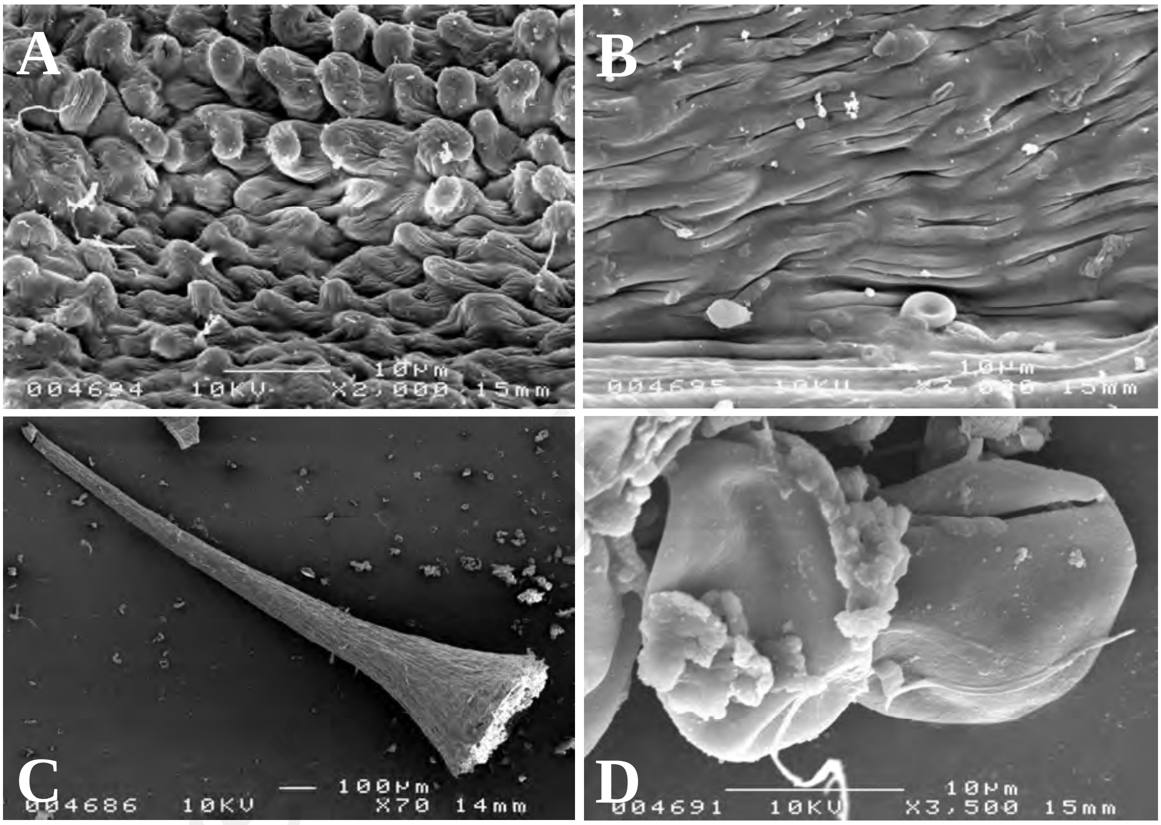

Figure 5.8. SEM images of *Groutiella kelantanense* sp. nov. ined. prop. — A, upper laminal cells; **B,** basal laminal cells; **C,** operculum; **D,** spores. [All from *s.coll. SFN29699* (SING)]

Branch leaves spirally inserted on branch, densely arranged, distinctly funiculate with leaves more or less spirally wound around branch, each leaf flexuose-twisted to occasionally irregular twisted (when dry), erect-spreading to wide-spreading (when moist); branch leaves 1.3–2.1 × 0.3–0.5 mm, length:width ratio 4–5:1, lingulate to lingulate-lanceolate, lamina slender, gently bent, unistratose, rugose especially at upper lamina; apex firm, broad, acute; margin entire, plane at distal part but deflexed at leaf base; costa failing, ends at short distance before leaf tip. Upper laminal and middle laminal cells 6–8 × 6–8 µm, length:width ratio 1:1, oblate to wide-rectangular, moderately thick-walled, not pitted, flat to strongly bulging, smooth, lumina rounded to oval; marginal cells found below mid-leaf sharply differentiated from inner laminal cells, cells being long-rectangular with thicker cell-wall, flat, smooth, in 2–5 rows and forming a distinctive border at leaf base; basal laminal cells 8–20 × 6–8 µm, length:width ratio 1–2.5:1, oblate, oval to long-rectangular, longer cells found toward leaf margin, incrassate, walls evenly thickened, not pitted, cells strongly bulging, unipapillose to tuberculate, lumina 4–6 µm wide.

Dioicous. Perigonial leaves 1.0–1.5 mm × 0.4–0.5 mm, ovate-lanceolate with a long, narrow apex. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, smaller than the branch leaves, 1.5–1.6 × 0.3–0.4 mm, oblong-lanceolate, upper lamina narrow, expanding gradually toward mid-leaf to form a long-oblong base, leaf base without long-plications; apex slender, acuminate; costa failing or percurrent; margin subentire, entire; laminal cells distinctively incrassate with oval, short- to long-rectangular lumen, cells gradually elongate toward leaf base, not pitted. Vaginula 1.6–1.8 mm long; paraphyses scarce, scattered on vaginula, 0.5–0.6 mm long, made of 8–12 short- or long-rectangular cells. Seta 12–14 mm long, smooth, dextrorse-twisted. Capsule urns 2.8–3.0 × 0.9–1.0 mm, broad-cylindric, smooth, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length:width ratio 2–

4:1; stomata 2–4, cryptoporous; operculum rostrate, beak 0.9–1.2 mm. Exostome teeth not seen. Endostome segments fused into a continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal and ventral side of teeth densely reticulate-papillose, papillae simple to compound; remains of original cell-wall visible on both side of teeth, marked by low and filmy trabeculae. Spores isomorphic, spores 20–24 µm in diameter. Calyptra mitrate, plicate, naked, calyptra base shallowly dissected into several lobes.

Distribution: Known only to Peninsular Malaysia (As. 4) and thus far only collected from southern Kelantan.

Habitat and ecology: Epiphytic on trees growing in limestone area, only known from lowland area.

Notes:

1. This new species is characterized by its strongly rugose leaf lamina, with an acute apex that does not easily break off. By this, it is easily separated from the common *G. tomentosa*, which has a long subulate apex that easily breaks and a smooth leaf lamina. *Groutiella kelantanense* is related to the endemic Javanese *G. macrorrhyncha* (Mitt. *ex* Bosch & Sande Lac.) Wijk & Margad., where their branch leaves are oblong-lanceolate to lingulate in shape with persistent or usually intact apices. However, the leaf lamina of latter species is always plane, never rugose, and the leaf costa is short-excurrent, ending in a mucro (in *G. kelantanense,* the costa is percurrent, i.e., ending at the leaf tip, never extending beyond).

2. The other *Groutiella* species with strongly rugose leaf laminae are *G. obtusa* (Mitt.) Florsch. and *G. wagneriana* (Müll. Hal.) Crum & Steere from America (Caribbean, Central America and South America). Both, however, have obtuse to mucronate-apiculate apices (Allen, 2002) that are not gradually tapered as in *G. kelantanense*.

3. This species has only been collected from inland limestone sites in the Malay Peninsula. On the other hand, *G. tomentosa* has a wide altitudinal range from sea level up to 2000 m, occurring in a wide range of habitats, including primary and disturbed forests, gardens, and limestone or other substrates.

Specimens examined:

MALAYSIA. Kelantan: Gua Teja, Betis, 500 ft [=152 m], 15.VII.1935, *s.coll. SFN29699* [*c.fr.*] (holotype of *G. kelantanense*: SING!); Gua Musang, VIII 1962, *Singh 956* (SING!).

2. *Groutiella tomentosa* (Hornsch.) Wijk & Margad. (Figs. 5.9 & 5.10)

Taxon 9: 51 (1960). *Macromitrium tomentosum* Hornsch. in Mart., Fl. Bras. 1 (2): 21 (1840). TYPE: Uruguay, in campis montevidensibus, *Sellow s.n.* (B, destroyed). *Schlotheimia goniorrhyncha* Dozy & Molk., Plantae Junghuhnianae 3: 338 (1854). *Macromitrium goniorrhynchum* (Dozy & Molk.) Mitt., J. Proc. Linn. Soc. Bot. Suppl 1: 53 (1859). *Micromitrium goniorrhynchum* (Dozy & Molk.) Jaeger, Ber. S. Gall. Naturw. Ges. 1872–73: 157 (1874). *Groutiella goniorrhyncha* (Dozy & Molk.) Wijk & Marg., Taxon 9: 50 (1960). LECTOTYPE (Touw, 2007): Java, in monte Ungarang provinciae Medini, 3000–4000 ft [=914–1220 m], Mense Apr. Junio., *Junghuhn s.n.* (L).

Macromitrium diffractum Card., Rev. Bryol. 28: 113 (1901). TYPE: Sulawesi, G. Bonthain, *Fruhstorfer s.n.* (E?) — fide Fleischer (1904).

Macromitrium andamaniae Müll. Hal. in Paris, Ind. Bryol. Suppl. 236 (1900), *Macromitrium andamanum* Müll. Hal. in Cardot, Rev. Bryol. 28: 113 (1901), *nom. nud.* — fide Fleischer (1904).

Macromitrium subretusum Broth. in Fleisch., Musci Fl. Buitenzorg 2: 456, 459 (1904), *nom. nud.*

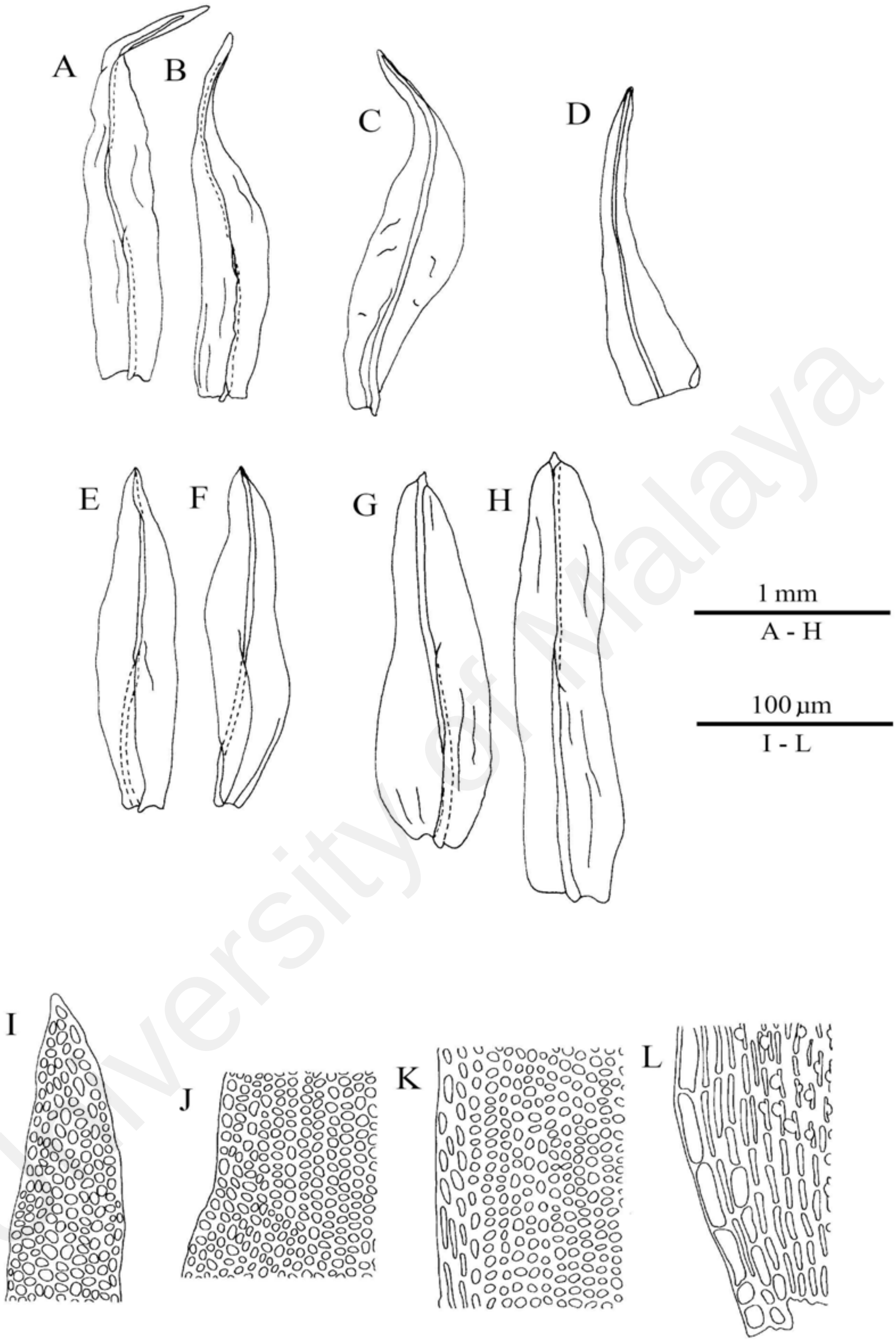

Figure 5.9. Illustrations of *Groutiella tomentosa* (Hornsch.) Wijk & Margad. — A-C, branch leaves (normal form); **D,** perichaetial leaf; **E-H,** branch leaves (abnormal form); **I,** leaf apex; **J,** upper mid-leaf cells; **K,** lower mid-leaf cells including border; **L,** basal laminal cells including border. [**A-B** from *Mansor 9* (KLU); **C, D, I-L** from *Yong 3413* (KLU); **E-F** from *Damanhuri 98-962* (UKMB); **G-H** from *Damanhuri s.n.* (UKMB)]

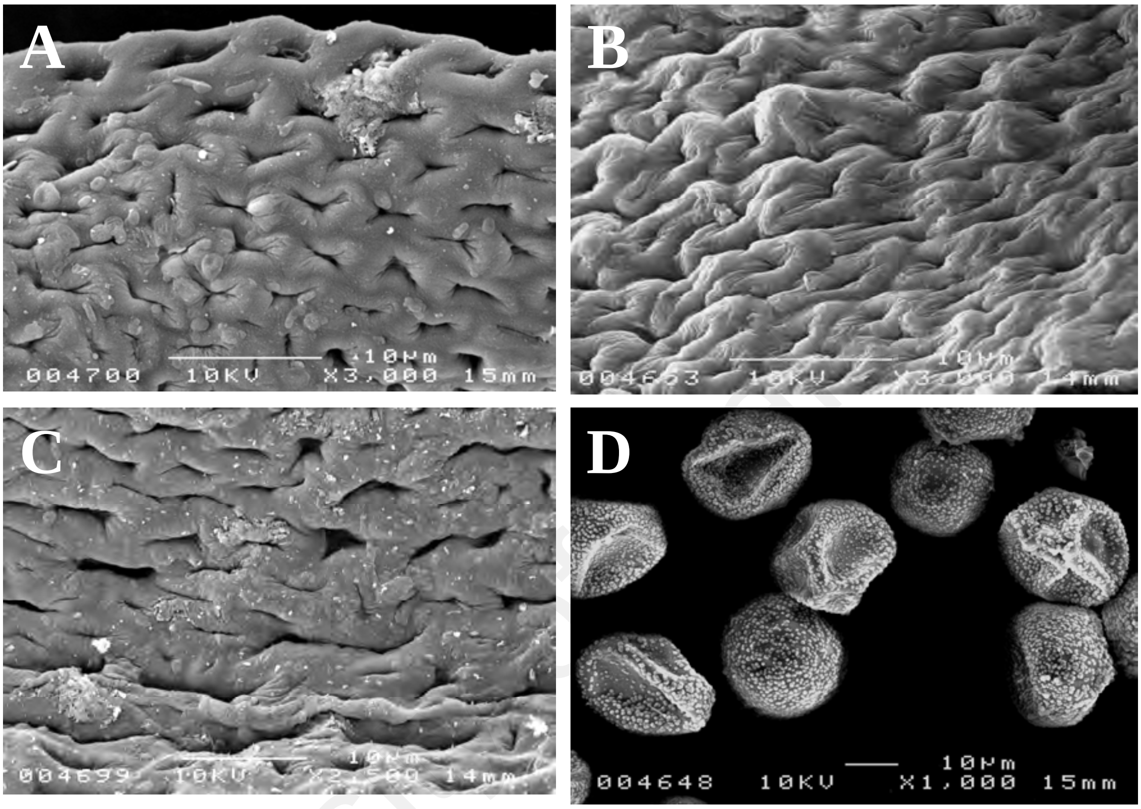

Figure 5.10. SEM images of *Groutiella tomentosa* (Hornsch.) Wijk & Margad. — A-B, upper laminal cells; **C,** basal laminal cells; **D,** spores. [**A, C-D** from *Touw 18316b* (NY); **B** from *Yong 3413* (KLU)]

Plant medium-sized, forming short-cushion or mats; young shoots dark-green, gradually turning olive-green to rusty-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5–1.5 cm tall and 3–4 mm wide, tightly arranged, rarely branched. Stem leaves inconspicuous, small, covered by rhizoids, slender, ovate-lanceolate to triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, densely arranged, distinctly funiculate with leaves spirally wound around branch, each leaf flexuose-twisted (when dry), erect-spreading to wide-spreading (when moist); branch leaves 1.7–2.3(–2.5) × 0.4–0.6 mm, length:width ratio 4–5:1, slender lanceolate to subulate-lanceolate, lamina slender, apex freely bent and in 2–3 cell layers thick, but straight and unistratose at lower half of leaf, lamina smooth throughout; apex fragile, often broken off in older leaves, long, narrow and end in a blunt-acute point; margin entire, plane at distal part but deflexed at leaf base; costa failing, terminates at short distance before leaf tip. Upper laminal and middle laminal cells 6–8 × 6–8 µm, length:width ratio 1:1, rounded to oblate, moderately thick-walled, not pitted, flat to strongly bulging, smooth, lumina rounded to oval; marginal cells found below mid-leaf sharply differentiated from inner laminal cells, cells being long-rectangular with thicker cell-wall, flat, smooth, in 2–5 rows and forming a distinctive border at leaf base; basal laminal cells 8–20 × 6–8 µm, length:width ratio 1–2.5:1, oblate, oval to long-rectangular, longer cells found toward leaf margin, incrassate, walls evenly thickened, not pitted, cells strongly bulging, unipapillose to tuberculate, lumina 4–6 µm wide.

Dioicous. Perigonial leaves 1.0–1.5 mm × 0.4–0.5 mm, ovate-lanceolate with a long, narrow apex. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, smaller or achieving the size of branch leaves, 1.7–1.8 × 0.4–0.5 mm, triangular-lanceolate to oblong-lanceolate, upper lamina narrow, expanding gradually toward mid-leaf to form a long-triangular or oblong base, leaf base without long-plications; apex slender, acuminate; costa failing or percurrent; margin subentire, entire; laminal cells distinctively incrassate with oval, short- to long-rectangular lumen, cells gradually elongate toward leaf base, not pitted. Vaginula 1.5–1.8 mm long; paraphyses scarce, scattered on vaginula, 0.4–0.6 mm long, made of 10–14 short- or long-rectangular cells. Seta 7–8 mm long, smooth, dextrorse-twisted. Capsule urns 2.5–3.0 × 0.7–1.0 mm, broad-cylindric, smooth, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length:width ratio 2–4:1; stomata 2–4, cryptoporous; operculum rostrate, beak 0.9–1.2 mm. Exostome teeth not seen. Endostome segments fused into a tall continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal and ventral side of teeth densely reticulate-papillose, papillae simple to compound; remains of original cell-wall visible on both side of teeth, marked by low and filmy trabeculae. Spores anisomorphic or isomorphic, larger spores 38–50 µm in diameter, smaller spores 24–32 µm in diameter, but spores only attained 18–22 µm in diameter, for those in isosporous condition. Calyptra mitrate, plicate, naked, calyptra base shallowly dissected into several lobes.

Other descriptions and illustrations: Dozy & Molkenboer (1861) p. 111, tab. 88, as *Macromitrium goniorhynchum*; Fleischer (1904) p. 456–459, fig. 84 as *Micromitrium goniorhynchum*; Brotherus (1925) p. 45, fig. 463 as *Micromitrium goniorhynchum*; Bartram (1939) p. 183–184, pl. 14, fig. 229, as *Macromitrium goniorhynchum*; Gangulee (1976) p. 1192–1194, fig. 580 as *Groutiella goniorrhyncha*; Vitt & Ramsay (1985) p. 431–434, figs. 328–329, 331, 333–340; Vitt et al. (1995) p. 85–86, fig. 37; Eddy (1996) p. 82–84, figs. 386, 387.

Distribution: Pantropical, tropic to subtropical region. Am. 1: U.S.A. (Florida); Am. 2: Belize, Costa Rica, Guatemala, Honduras, Mexico, Nicaragua, Panama; Am. 3:

Dominican Republic, Jamaica, Lesser Antilles, Puerto Rico; Am. 4: Bolivia, Colombia, Ecuador, Galápagos Islands, Trinidad, Venezuela; Am. 5: Brazil, French Guiana, Guyana, Suriname; As. 2: China; As. 3: Bangladesh (Khasia), Cambodia, India (Andaman Islands), Myanmar, Sri Lanka, Thailand (Eastern, Northern, Southeastern, Peninsula), Vietnam; As. 4: Indonesia (Bali, Flores, Java, Lombok, Sulawesi, Sumatra, Sumbawa), Malaysia (Borneo, Malay Peninsula), Papua New Guinea, Philippines (Luzon, Panay); OC.: New Caledonia; Austr. 1: North Australia.

Habitat and ecology: Epiphytic or epilithic, the species is well-known to tolerance on wide sort of substrates, from granitic rocks, sandstones, rotten log or tree trunks and branches. The plant is more commonly found in open area, rather than in deep shaded forest; it has been collected from disturbed forest, maintained garden and cultivated areas, especially in the highland. However, the plant actually occupied a wide elevation range, from 200 m in the lowlands, up to 2000 m on a mountain.

Notes:

1. The species is easily recognized by its fragile apex, easily broken off even by a gentle touch. The leaves also often tightly coil around the branch when dry and appear rope-like, allowing rapid recognition of this plant.

2. This species sometimes produces a different leaf form along the lower portion of erect branches, as noted by Allen (2002). These leaves resemble younger leaves at branch tips in that they are shorter than fully expanded leaves and sometimes have persistent, acute to acuminate apices. *Groutiella tomentosa* may be mistaken for a smaller form of *G. macrorrhyncha* if the upper branch leaves are not checked.

3. Fleischer recognized *G. tomentosa* forma *exorrhizon* for material that lacks tomentose rhizoids (Fleischer, 1904). After checking a wide range of specimens, including Fleischer's material (*Fleischer 305*, BM), it is now clear that tomentose

rhizoids are sometimes scanty to absent on younger branches, and do not provide a consistent character.

4. *G. tomentosa* was thought to be isosporous (with spores of a single size-class) (Vitt & Crum, 1970; Allen, 2002) but, interestingly, several anisosporous populations have been discovered in the present study. This is the only Orthotrichaceae taxon known to have occasional anisospory. Anisospory is usually associated with sexual dimorphism (see section 4.3.7, this chapter), however it has been noted that dioicous species can be either isosporous or anisosporous (Ernst-Schwarzenbach, 1943; Noguchi, 1967), consistent with the present species.

5. Most Malaysian collections are not fertile, although fruiting material is common in the neighbouring region. Both Vitt & Crum (1970) and Eddy (1996) have pointed out that the peristome teeth of this species have 2–3 layers ("double peristome"). However, the peristome teeth are fragile and easily lost, rarely leaving behind the endostomial layer even.

6. The holotype material of this species was kept in Hornschuch's herbarium in Berlin, but destroyed during World War II (Vitt & Crum, 1970). A search for extant duplicate material needs to be carried out (Sayre, 1977) before considering neotypification.

Specimens examined:

AUSTRALIA. Queensland: Tinnaroo Perimeter Road, Danbulla State Forest, 23 km SE of Mareeba, 700 m, 25.X.1995, *Streimann 57730* (TNS! SING!). **INDONESIA. Java**: *s.loc.*, *s.date, Motley s.n.* (NY!); *s.loc.*, *s.date, Reinwardt s.n.* (2 materials in NY!); *s.loc.*, 7.II.1897, *Moller s.n.* (NY!); Batavia, Buitenzorg, Botanischen Garten, 2.III.1894, *Schiffner 3971* (NY 2 sheets!); Batavia, horto botanico Buitenzorgensi, 260 m, 1894, *Schiffner 10706* (BM!); Batavia, in agro Buitenzorgensi and arborum, 250 m, 1894, *Schiffner 10701* (NY!); Batavia, in agro Buitenzorgensi, Dessa Kotta Batu, 270 m, 7.II.1894, *Schiffner 10704* (NY!); Bogor, Bogor Botanical Garden, 300 m, 6.IX.2005, *Yong 6609* (KLU!); Buitenzorg, 280 m, V.1898, *Fleischer 305* (BM! NY 2 sheets!); Bogor, Mt. Tuas, summit area, VII.1977, *Wee W92* [*c.fr*.] (KLU! SING!); Gedeh apund Lebak-Antja ad arbores, 1000 m, 21.II.1894, *Schiffner 10718* (BM! NY!); Kandang Badak, Gedeh, IV.1908, *Fleischer s.n.* (NY!); Mt. Halimun National Park, park headquater, 700 m, 9.IX.2005, *Yong 6611*, *6612*, 6617; Mt. Pangerango, 780–960 m, IV.1894, *Schiffner 10730* (NY!); *ibidem*, 1300–1400 m, 17.VII.1894, *Schiffner 10731* [*c.fr*.] (BM!); Mt. Megamendong, Tugu, 1300–1400 m, 5.I.1894, *Schiffner 10715* (NY!); Mt. Megamendong, 4000–7000 ft [=1219–2134 m], *s.date*, *Motley s.n.* (NY!); Papaudajan, 3.V.1897, *Moller s.n.* (NY!); Salak, 1897, *Nyman 168* (NY!); West Java, VII & X.1854, *Motley s.n.* (NY!); Tjibodas, V.1900, *Fleischer 133* [*c.fr*.] (BM! NY 2 sheets!). **Sulawesi:** Süd Celebes [=South Sulawesi], Grenzgebirge zur Tjamba und Goa, sine date, *Warburg s.n.* (NY!). **Sumatra:** *s.loc*., *s.date, s.coll*. *ex Hb. Hampe ex Lacoste* [*c.fr*.] (BM!). **Sumbawa:** West Sumbawa, Mt. Batulanteh, trail from Batudulang tu Pukis, 700–800 m, 18.IV.1961, *Kostermans 18316B* [*c.fr*.] (KLU! NY!). **MALAYSIA. Peninsular Malaysia:** Ridge trail, 31.VIII.1993, *s.coll*. *4164* (KLU!). **Kedah**: Langkawi Island, KEDA housing area, 40 m, 15.IV.2003, *Mohamed & Yong 3410*, *3413* (KLU!). **Pahang**: Cameron Highlands, IV.1988, *Damanhuri s.n.* (UKMB!); Cameron Highlands, Gag Course, 7.VII.1964, *Clear 1283* (KLU!); Cameron Highlands, Habu, 1400m, 11.VII.2004, *Yong 6055a*, *Yong 6055b* (KLU!); Cameron Highlands, Mt. Brinchang, 1950–1980 m, 3.VIII.1988, *Mohamed & Damanhuri 1030e* (KLU!); Cameron Highlands, Ringlet, Boh Tea Plantation, 1460 m, 28.X.1987, *Mohamed & Zamzuri 1121b* (KLU!); *ibidem*, 22.XI.1990, *Damanhuri s.n.* (UKMB!); *ibidem*, 1235 m, 6.V.1992, *Mohamed 6002* (KLU!); Cameron Highlands, Tanah Rata Town, 1450 m, 24–25.IV.1999, *Gunaseelan & Mohamed 124,150a* (KLU!); Cameron Highlands, Tanah Rata, Pelangi Apartment, 1375 m, 5.XII.2004, *Yong & Goh 6124* (KLU!); Cameron Highlands, Ulu Bertam Forest Reserve, 1440 m, 7.X.2003, *Yong et al*. *4674*

(KLU!); Fraser's Hill, 1120 m, 10.III.2000, *Damanhuri et al*. *2000-84*, *2000-92* (UKMB!); *ibidem*, 1180 m, 10.III.2000, *Damanhuri et al*. *2000-16* (UKMB!); Fraser's Hill, Alan's Water, 1180 m, 3.I.2008, *Yong 7466*, *7470*, *7475* (KLU!); Fraser's Hill, Bishop Trail, 1200 m, 26.V.2006, *Yong 7463* (KLU!). **Penang**: Penang Hill, XII.1958, *Johnson 502* [*c.fr*.] (SING 3 sheets!); *ibidem*, I.1993, *Mansor 9* (KLU!); *ibidem*, 9.XII.2002, *Mohamed 2003-1* (KLU!); *ibidem*, 600 m, 29.XI.1979, *Mohamed 9506* (KLU!); *ibidem*, 700 m, 14.IV.1971, *Tixier 5668*. (SING!); *ibidem*, 2500 ft [=762 m], XII.1958, *Johnson 319*, [*c.fr*.] (SING!)Penang Hill, Bellevue Hotel, 715 m, 21.VIII.2005, *Mohamed & Yong 6485*, *6487* (KLU!); Penang Hill, Convalescent Bungalow, 730 m, 21.VIII.2005, *Mohamed & Yong 6502*, *6510*, *6518* (KLU!); Penang Hill, Crag Hotel, 665 m, *Mohamed & Yong 6594* (KLU!); Penang Hill, Erythrope Bungalow, 670 m, 18.XII.1983, *Mohamed 8434* (KLU!). **Perak**: Ulu Perak, Belum Forest Reserve, Sg. Semeliang Trail, 235–290 m, 21.V.1998, *Damanhuri 98-310* (UKMB!); Ulu Perak, Belum Royal Park, Sg. Kenarong, 200–300 m, 29.VII.2003, *Yong 4433*, *4435*, *4439* (KLU!); *ibidem*, 30.VII.2003, *Yong 4487* (KLU!); Taiping, Maxwell Hill, Mt. Hijau, 6–12.VI.1983, *Mohamed et al*. *s.n*., *8002a*, *8148* [*c.fr*.] (KLU!); Taiping Lake Garden, *s.date*, *Mohamed 8250* (KLU!). **Sabah**: Ranau, Kinabalu Park, park headquater, 1500 m, 8.V.2005, *Yong 6224*, *6226* (KLU!). **Selangor**: Genting Highland, Awana cable car station, 955 m, 22.V.2006, *Yong 6679* (KLU!); *ibidem*, 1000 m, 4.X.2003, *Yong 4532* (KLU!); Genting Highland, Gohtong Jaya, road to Batang Kali, 935 m, 11.X.2003, *Yong et al*. *4712* (KLU!); Langat Basin, Mt. Nuang, 24.IV.1997, *Damanhuri & Ahmad 97-319* (UKMB!); *ibidem*, 450 m, 10.VIII.1997, *Abdullah 7, 8* (UKMB!). **MYANMAR:** Crag east of Taunggyi, 4500 ft [=1372 m], 24.I.1957, Lois & Egerod *B-13* (NICH!). **PAPUA NEW GUINEA:** Kaiser Wilhelms Land [=Northeast New Guinea], Sattelberg, 18.VI.1899, *Nyman 27* (NY!); [Northeast New Guinea], an einem Baumstam auf der Grasflach Yabim, 5.IX.1903, *Zahn 27* (NY!); [Northeast New

Guinea], Yabim bei Limbang, XI.1904, *Zahn s.n*. [*c.fr*.] (NY!). **PHILIPPINES, Luzon:** Bataan, Upper Lamas, I.1904, *Williams 3148* (NY!); Benguet, Baguio, 24.IX.1904, *Williams 1754* [*c.fr*.] (NY!); *ibidem*, III.1907, *Elmer 8345* [*c.fr*.] (NY!); *ibidem*, Benguet, IV.1907, *Mearns 2852* (NY!); *ibidem*, Benguet, V.1911, *Merill 7850* [*c.fr*.] (NY!); *ibidem*, V.1911, *Robinson 14106* (NY!); *ibidem*, 1570 m, 24.XI.1904, *Williams 1753* [*c.fr*.] (NY 2 sheets!); Benguet, Sablang, XI–XII.1910, *Fenix 12806* [*c.fr*.] (BM! NY!); Bontoc, Sagada, 30.V.1983, *Ponciano 522* (KLU! NICH! TNS!); Mountain Province, Baguio, 25.III.1935, *Bartlett 13368* (NY!); Mountain Province, Bontoc, Cordillera, 10.X.2000, *Bawingan & Rosuman s.n*. (SINU *ex* SING!); Pangasinan, Umingan, IV–VI.1914, *Otanes 18358* [*c.fr*.] (NY!); Rizal, XI–XII.1910, *Ramos 12550* [*c.fr*.] (NY!); *ibidem*, XII.1912, *Reillo 19321* (NY!); Rizal, Bosoboso, VI.1906, *Ramos 988* [*c.fr*.] (BM! NY 2 sheets!); **Mindanao:** Nord Cotabato, road from Ilomavis to Kidapawan, 740 m, 7.VIII.1999, *Schumm & Schwarz 4456* (SINU *ex* SING!); **Panay:** Antique, Muncipality Culasi, Mt. Madja-as, Wald am Trail vom Barangay Flores zum Batang-Batang-Einschnitt, 1050 m, 27.I.2001, *Schwarz 7749* (SINU *ex* SING!). **SINGAPORE**: Singapore Botanical Gardens, III.1958, *Johnson 267* (KLU!). **THAILAND**: Doi Pha Dam between Hang Dong & Bo Luang, 5.VII.1968, *Larsen et al. 2194* (KLU!); Nakhon Sawan, Ban Mussoe, between Tak and Mae Sot, 400 m, 24.VIII.1959, *Floto 7683* [*c.fr*.] (NY!); Nakhon Sawan, Doi Musae Agricultural Experiment Station, 20.XI.1965, *Touw 8215* (L, NY!); Pattani, waterfall of Yala, 21.X.1970, *Charoenphol et. al 4140* (MO, NY!); Payap, between the Karen villages of Pha Mon and Sop Aep, Mae Hoi River, 21.XII.1965, *Touw 10300* (L, NY!); Payap, limestone massive Mt. Chiengdoa, 4.XII.1965, *Touw 8901* (L, NY!); Udawn, sandstone massive Mt. Luang, 9.I.1966, *Touw 10583* (L, NY!).

5.3.3 *Macromitrium* Brid.

Muscol. Recent. Suppl. 4: 132 (1819). TYPE: *M. aciculare* Brid.

Dasymitrium Lindb., J. Bot. 2: 385 (1864). TYPE: *D. incurvum* Lindb.

Teichodontium Müll. Hal., Nuovo Giorn. Bot. Ital., new ser. 4: 119 (1897). TYPE: *T. rusbyanum* (E.G. Britton) Müll. Hal.

Plants cladocarpous, variable in size, mat- or cushion-forming. Stem (primary axis) branched sympodially, plagiotropic, creeping with numerous, erect, short or long, simple, monopodial branches (secondary axis). Monopodial branches branched sympodially, with 1–2 subsequent branches formed almost immediate or short distance beneath perichaetium. Creeping stems tomentose, occasionally with some rhizoids extended up to the erect branches. Stem leaves always smaller, resembling branch leaves in shape. Branch leaves more or less uniform in shape, differ in sizes and shape of different taxa, oblong-lanceolate to ligulate-lanceolate, leaf base not decurrent, and leaf lamina unistratose thick. Leaf cells parenchymatous, cells variable in shapes and their surface ornamentations, grade from oblate, polygonal to rectangular, with usually longer cells at basal lamina, smooth, conic-papillose to pluripapillose; cells at juxtacostal and insertion region sometime differentiated but not distinctive, basal marginal cells not differentiated. Plant phyllodioicous (occasionally autoicous for *M. blumei*). Dwarf male bud-like. Perichaetial leaves either conspicuous or not. Vaginula short or long, densely covered by short or long paraphysis, all filamentous; paraphysis uniseriate, never branched. Seta short or long, extended. Capsule exerted, urn narrowed to seta in short distance, exothecial cells incrassate; stomata cryptoporous or phaneroporous, few, present in the base of urn; operculum rostrate with a long beak that perpendicular to operculum base. Peristome mostly single (double peristome only found in *M. blumei* and its variety). Exostome 16, either free or fused into a continuous membrane. Anisospory. Calyptra mitrate, completely covering the urn, plicate, naked or pilose, base fringed or lacerated, rarely lobed.

Note:

1. *Macromitrium* is a pantropical genus, with its highest diversity in the southern hemisphere, which might be taken to suggest a Gondwanan origin (Ramsay & Vitt, 1986; Rooy & Wyk, 1992). The genus is well represented in South East Asia and is the largest genus of the family there, occupying a wide range of habitats from lowlands to the subalpine zone of high mountains. Although the species are mostly epiphytic, at times they can be epilithic and may also occur in open environments, especially at higher elevations.

2. In addition to there being a range of plant sizes represented by the species, the genus is also morphologically complex. There are various combinations of oblong to slender-lanceolate leaves; often short upper laminal cells that are either smooth or pluripapillose, but usually elongated basal laminal cells that are either smooth or tuberculate; and short- to long-exerted seta with mitrate calyptra that are either hairy or naked.

3. Taxonomically, the genus is characterized by the long-creeping stem that gives rise to many monopodial branches of more-or-less even length, and the cladocarpic habit. In Malaysia, various *Macromitrium* species have some morphological resemblance to species of *Desmotheca* and *Groutiella*, but these are possible to distinguish (see under those genera).

1. *Macromitrium angustifolium* Dozy & Molk. (Figs. 5.11, 5.12 & 5.13)

Ann. Sci. Nat. Bot. sér. 3 (2): 311 (1844). LECTOTYPE (Vitt et al., 1995): Sumatra, Java et Borneo, Gédé, Mt. Simpai, Mt. Sakoenbang, *Korthals s.n.* (L; isolectotype BM!).

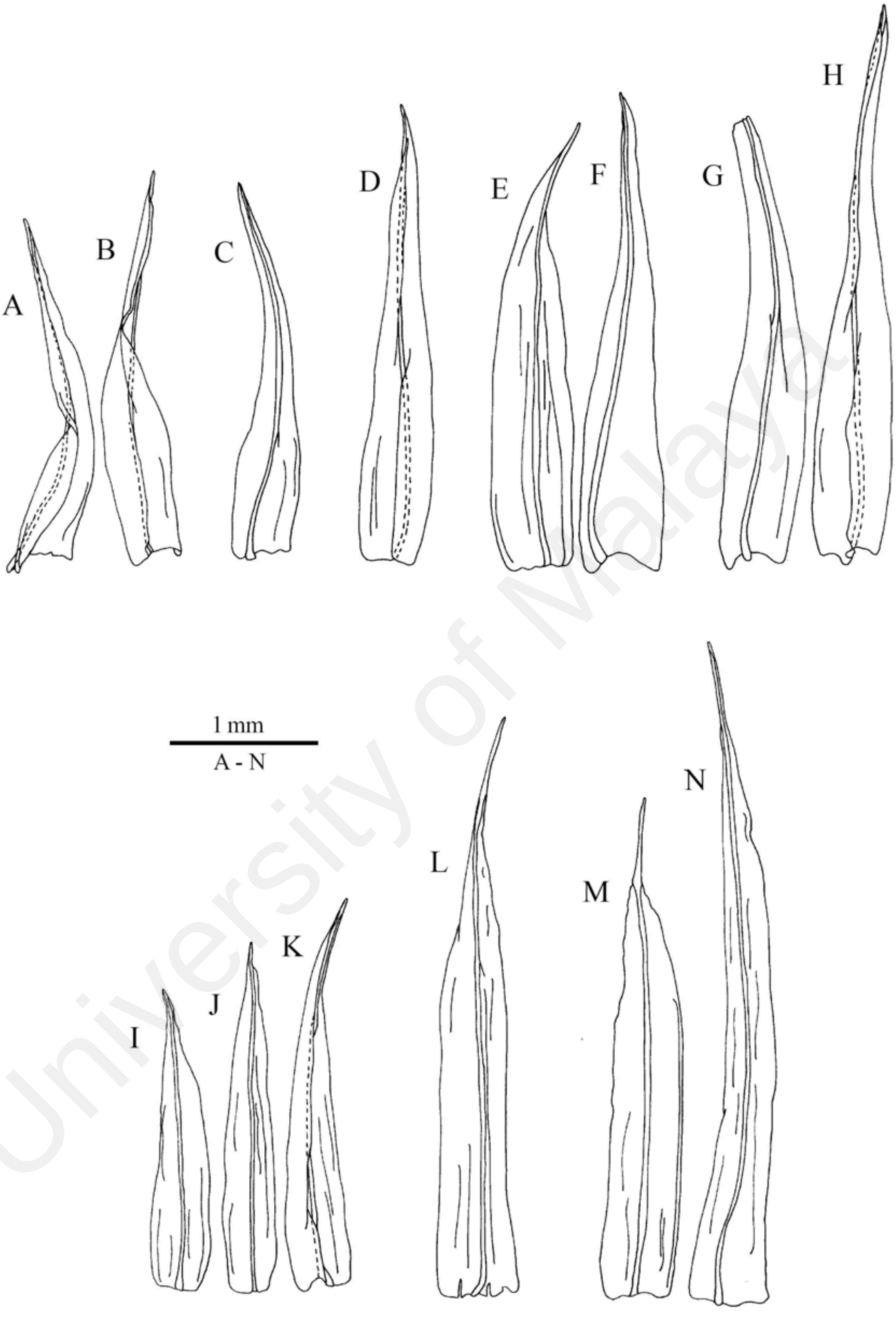

Figure 5.11. Illustrations of *Macromitrium angustifolium* Dozy & Molk.— A-H, branch leaves; **I-N,** perichaetial leaves. [**A-B, I-K** from *Yong 6236* (KLU); **C** from *Yong 6208* (KLU); **D** from *Yong 6277* (KLU), **E-F, L** from *Yong 6337* (KLU); **G-H, M-N** from *Yong 6409* (KLU)]

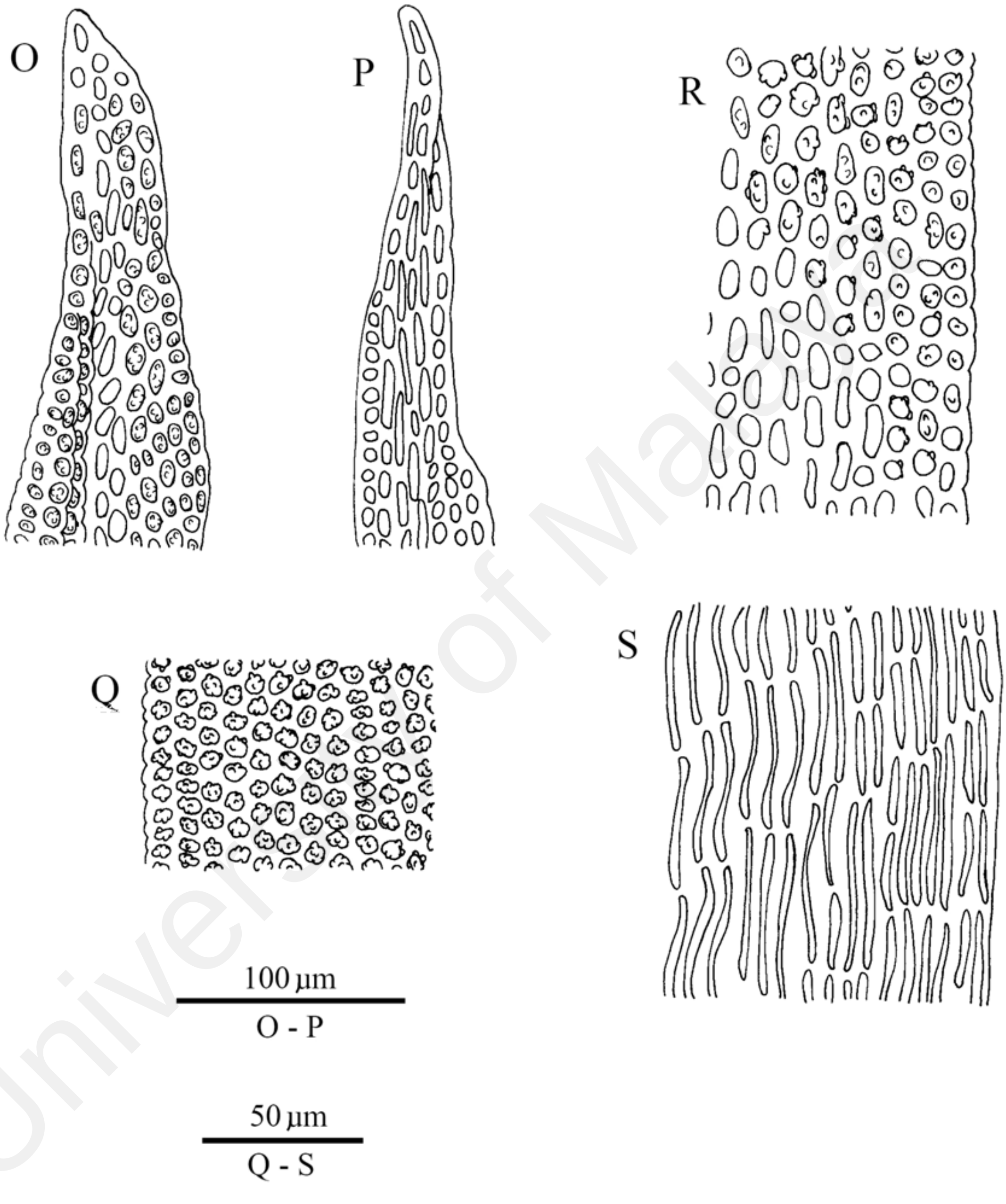

Figure 5.12. Illustrations of *Macromitrium angustifolium* Dozy & Molk.— O-P, leaf apex; **Q,** upper laminal cells; **R,** mid-leaf cells; **S,** basal laminal cells. [**O** from *Yong 6409* (KLU); **P-S** from *Yong 6337* (KLU)]

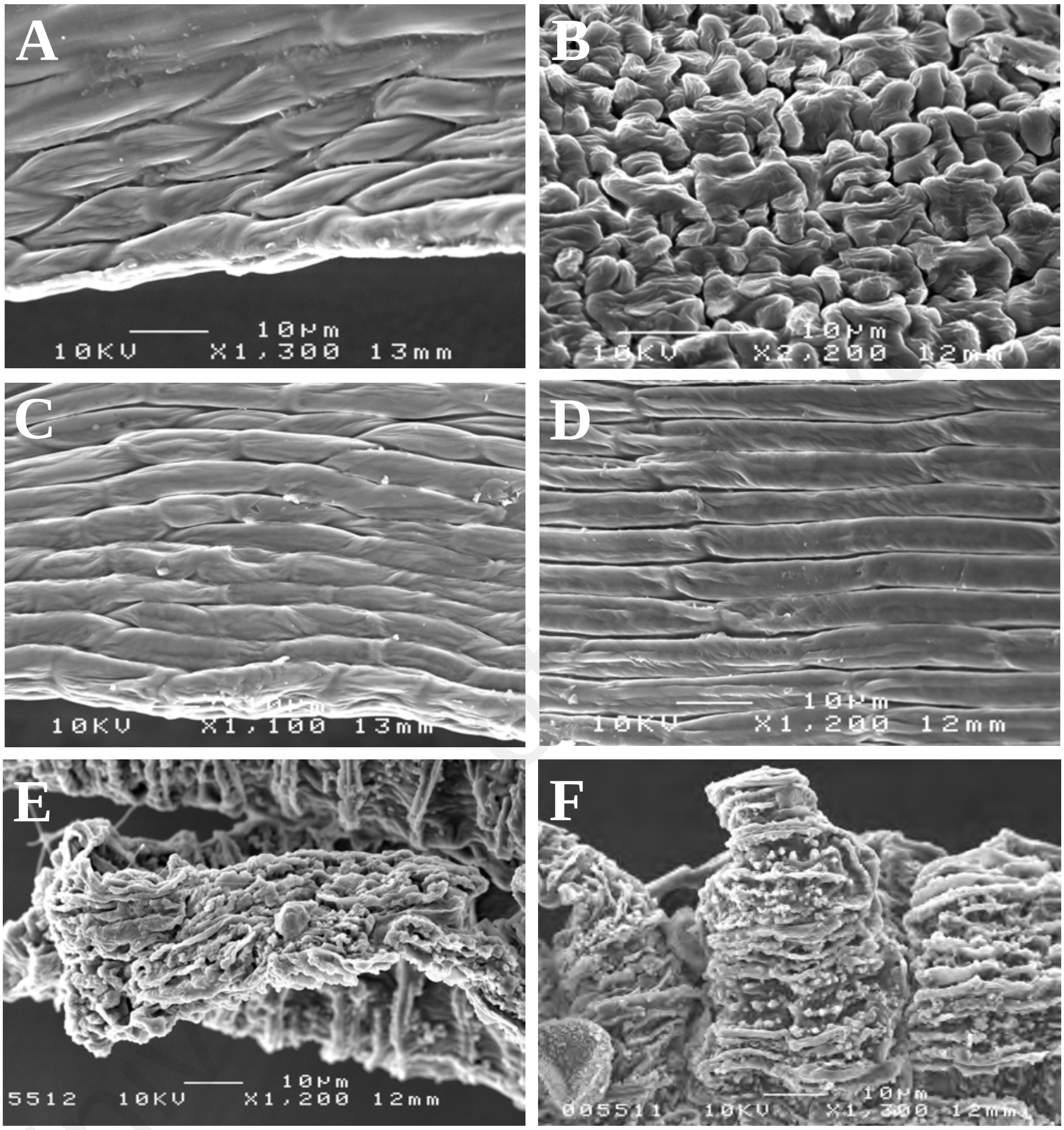

Figure 5.13. SEM images of *Macromitrium angustifolium* Dozy & Molk.— A-B, upper laminal cells; **C,** mid-leaf cells; **D,** basal laminal cells; **E,** dorsal view of peristome teeth; **F,** ventral view of peristome teeth. [All from *Yong 6408* (KLU)]

M. semperi Müll. Hal., Linnaea 38: 559 (1874). LECTOTYPE (Vitt et al., 1995): Insulae Philippine, Luzon, Marivelas, *C. Semper s.n.* (BM) — fide Bartram (1939).

M. stephanodictyon J. Froehl., Rev. Bryol. Lichénol. 31: 93 (1962), ***syn. nov.*** HOLOTYPE: North Borneo, summit area of Kinabalu, 10000–13000 ft [=3048–3962 m], 9.III.1961, *W. Meijer s.n.* (S!).

Plant medium-sized to fairly large, forming short-cushions or mats; young shoots yellowish-green, gradually turning to olive-green and brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches generally short, 1–2(–3) cm tall and 4–6 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate on young shoots, becoming more lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, lax to densely arranged, indistinctly funiculate with leaves erect-twisted to flexuose-twisted, with most apices strongly incurved-twisted (when dry), erect-inflexed, wide-spreading to sometime recurved-spreading (when moist); branch leaves 2.6–3.7(–4.0) × 0.45–0.55 mm, length-width ratio 5–8:1, slender-lanceolate to ligulate-lanceolate with an oblong base, lamina mostly straight, plane; apex fragile, often broken off in older leaves, weakly incurved, slender to rather broad, long, generally acuminate, but sometimes with acute tip; margin entire, plane at distal part but reflexed at base; costa ending in the apex or percurrent, occasionally short-excurrent with 1–2 cells extending beyond the tip. Upper laminal cells 8–11 × 8–11 µm, length-width ratio 1:1, rounded, oblate to short- or wide-rectangular, evenly incrassate, walls not pitted, cells flat or low-bulging, densely pluri-papillose or nearly smooth, cells mostly obscure due to the papillae but clear in latter case; middle laminal cells 8–16 × 8–12 µm, grading from oblate or short-rectangular to gradually elongate toward the basal lamina, cells not uniform in length, incrassate, with curved to more-or-less straight lumina, cells flat, weakly papillose to smooth, clear; basal laminal cells 38–64(–70) × 8–12 µm, length width / ratio 4–6:1, long-rectangular, incrassate, walls either even or unevenly thickened, lumina 2–3 µm wide, appearing linear with even thickened walls but strongly curved to sigmoid with uneven walls, pitted only near juxtacostal region and insertion, cells flat, smooth.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves conspicuously erect, sheathing the seta, usually much larger than branch leaves, 3.4–4.8 × 0.45–0.6 mm, broad-lanceolate to oblong-laceolate, upper lamina narrow, expanding gradually toward the mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender acuminate to sometimes cuspidate; margin subentire to entire, plane; costa percurrent or ending in a cusp, occasionally short-excurrent; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 1.2–1.8 mm long; paraphyses many, 1.0–1.4 mm long, made of 6–10 short- or long-rectangular cells. Seta 5–8 mm long, smooth, sinistrorse-twisted. Capsule urns 1.4–1.6 × 0.9–1.4 mm, short-ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 4–5, cryptoporous; operculum rostrate, beak 0.8–1.0 mm. Peristome single. Exostome of 16 teeth that are separated above but connected at their base as a low membrane, erect to incurved at top in both dry and wet conditions; dorsal side of teeth vertically striolate-papillose with simple wart-like to compound papillae, irregularly distributed on coarse vertical or diagonal ridges; ventral side of teeth horizontally striolate-papillose with simple relatively large papillae, sometimes on irregular reticula but mostly found on distinctly raised thick horizontal ridges; remains of original cell-wall obscure on dorsal teeth, hidden by dense papillae and ridges, but marked by thickened trabeculae on ventral side. Endostome absent. Spores anisomorphic, larger spores 30–42 µm in diameter, smaller spores 20–24 µm in diameter. Calyptra mitrate, plicate, naked or more commonly with a few stiff erect hairs mostly on ridges near to the calyptra base, base fringed or lacerated.

Other descriptions and illustrations: Müller (1849): p. 743; Dozy & Molkenboer (1861): pp. 119–120, tab. 97; Fleischer (1904): pp. 447–448; Bartram (1939): pp. 178–179, pl. 13, fig. 222; Vitt et al. (1995): pp. 17–19, figs. 1c, 7, as *M. angustifolium*; Vitt et al. (1995): pp. 68–70, figs. 2a, 30, 40, as *M. semperi*; Eddy (1996): p. 46, fig. 358.

Distribution: As. 2: China, Japan; As. 4: Indonesia (Ambon, Flores, Irian Jaya, Java, Kalimantan, Lombok, Sulawesi, Sumatra), Malaysia (Sabah), Papua New Guinea, Philippines (Luzon, Mindanao); Oc.: New Caledonia, Solomon Islands.

Habitat and ecology: Canopy and subcanopy epiphyte, also collected from lower branches and trunks of medium to large trees, and occasionally growing on boulders, in mossy forest or exposed sites at higher elevation. Altitudinal range 1450–3360 m, most commonly found in lower to upper montane forest zone with a single collection from a subalpine sites. The plant was known to occupy a wider altitudinal range in New Guinea, from sea level to highland, and has been collected from pristine forest, as well as from disturbed secondary forest and scrub (Vitt et al., 1995; Eddy 1996).

Notes:

1. The plant can be recognized by: a) more-or-less funiculate inserted branch leaves with strongly decurved-twisted apices when dry; b) long, slender lanceolate branch leaves with percurrent costae; c) fragile leaf apices that often break off, leaving apically blunt laminae; d) pluripapillose upper laminal cells that gradually change into smooth cells at the basal lamina, with either even or uneven thickened-walls, or both; e) erect,

conspicuously sheathing perichaetial leaves that are often larger than the branch leaves; f) sparsely hairy calyptrae.

2. The species is closely related to *M. fuscescens*, *M. incurvifolium* and *M. salakanum*. The plant can be confused with the atypical form of *M. fuscescens*, where the laminal cells change gradually from pluripapillose to smooth and do not have a distinctive demarcation line between upper and lower laminae, and the plant has large perichaetial leaves. However, *M. angustifolium* is consistently larger in size with longer plant leaves; this, together with the peculiar broken leaf apices, serve as good characters to separate the species from *M. fuscescens*. In addition to this, *M. angustifolium* is only found above 1400 m in montane forest in Malaysia, whereas *M. fuscescens* and *M. incurvifolium* are mostly confined to lowland areas and rarely found around 1500 m. *Macromitrium angustifolium* can be differentiated from *M. incurvifolium* by its wide-spreading to recurved-spreading branch leaves (when moist), and large perichaetial leaves, whereas *M. incurvifolium* is characterized by its erect-incurved branch leaves (when moist) and small ovate perichaetial leaves. Although *M. salakanum* shares a similar elevation range and leaf orientation with this species, they have very different perichaetial leaves. The leaf apex is blunt or obtuse in *M. salakanum*, but consistently sharp, acute to acuminate in *M. angustifolium*. On the other hand, the branch leaf apices are persistent in *M. salakanum*, whereas they are easily broken in *M. angustifolium*.

3. The plant size is variable in this species. In general, those found in Borneo are more robust in size relative to most from New Guinea. A similar robust form is common among collections from Ambon, Java and the Philippines. A collection by Blume from Java was named *M. braunii* Müll. Hal., established in 1851 (Dozy & Molkenboer, 1861; Fleischer, 1904), but a study of the material annotated by Fleischer and the illustration in 'Bryologia Javanica' suggests that this taxon could be merely a larger form of *M. angustifolium*. Eddy (1996) has noted this as well. Both Fleischer (1904) and Eddy

(1996) described *M*. *braunii* as with ‘leaves up to 4 mm long and inner perichaetial bracts finely acuminate’, which fit well with more robust *M*. *angustifolium*. However, the presence of inner peristome teeth in *M*. *braunii*, as illustrated by Dozy & Molkenboer (1861), cannot be assessed; because the only material of *M*. *braunii* available for the present study is incomplete (there are just a few old capsules without peristome teeth). It would not be surprising if *M*. *braunii* later turns out to be a synonym of *M*. *angustifolium*, when more material can be studied.

4. Bartram (1939) first suggested including *M*. *semperi* under this species based on published description, although he did not examine the type of that species. Present examination of New Guinean specimens identified as *M*. *semperi* by Vitt et al. (1995) [*Koponen 34359*, *Streimann 18094*, *Streimann 26572*; all deposited in NY] did not differentiate them from typical *M*. *angustifolium* recognized in this region. This strengthens our argument for considering *M*. *semperi* as a synonym.

5. Fleischer’s no. 130, published under ‘Musci Archipelagi Indici, Series III (No. 101–150)’ (1900), is actually a mixture of two plants; the set received by Dixon in BM is wholly *M*. *salakanum*, while the set kept by NY is entirely *M*. *angustifolium*.

6. I have examined the type materials of *M. stephanodictyon* and could not detect any morphological differences from *M. angustifolium*, so that name is reduced to synonymy.

Specimens examined:

MALAYSIA. Borneo, Sabah: Ranau, Kinabalu Park, Bukit Tupai Trail, 1450–1455 m, 13.V.2005, *Yong 6438*, *6439*, *6445*, *6446* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, 10000–13000 ft [=3048–3962 m], 9.III.1961, *Meijer s.n*. (holotype of *M. stephanodictyon*: S!); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Timpohon Gate to Panar Laban, 2900–3090 m, 9.V.2005, *Yong 6277*, *6286*, *6296* (KLU!); *ibidem,* 12.V.2005, *Yong 6403, 6408* [*c.fr*.], *6409* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, Columbon river, 5000–6000 ft [=1524–1829 m], VIII.1933, *Clemens 34491* [*c.fr*.]

(NY!); Ranau, Kinabalu Park, Mt. Kinabalu, Paka Cave, 3000–3100 m, 10.V.2005, *Yong 6311* [*c.fr*.], *6312* [*c.fr*.], *6314* [*c.fr*.], *6316*, *6317* [*c.fr*.], *6318*, *6332*, *6337* [*c.fr*.], *6339* (KLU!); *ibidem*, 17.I.1997, *Akiyama et al*. *684* (BORH! Yamaguchi); Ranau, Kinabalu Park, Mt. Kinabalu, Pondok Villosa, 2900 m, 30.VIII.1986, *Menzel et al*. *4035* (NY!); Ranau, Kinabalu Park, Mt. Kinabalu, Sayat-Sayat, 3360 m, 11.V.2005, *Yong 6372* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, road from Park Headquater to multipurpose hall, 1500 m, 8.V.2005, *Yong 6229*, *6230*, *6232* [*c.fr*.], *6235*, *6236*, *6242* [*c.fr*.], *6245*, *6247*, *6248* [*c.fr*.], *6251*(KLU!); Ranau, Kinabalu Park, road from Park Headquater to Timpohon Gate, 1490–1500 m, 8.V.2005, *Yong 6203*, *6208*, *6209*, *6215*, *6216*; Ranau, Kinabalu Park, Mt. Tambuyukon, Musang Camp (km 10) to the summit, 1480 m, 14.VIII.2008, *Suleiman 3664* [*c.fr*.], *3668* (BORH, KLU! SNP); *ibidem*, 1520 m, 14.VIII.2008, *Suleiman 3677* [*c.fr*.] (BORH, KLU! SNP); *ibidem*, 1720 m, 14.VIII.2008, *Suleiman 3709* (BORH, KLU! SNP); *ibidem*, 2200 m, 14.VIII.2008, *Suleiman 3733*, *3740* (BORH, KLU! SNP); Tambunan, Mt. Alab, 1544 m, 13.IV.2002, *Juri 53* (BORH! SAN). **INDONESIA. Ambon:** *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Lugd*. *Batav*. (BM!); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Dozy & Molkenboer* (BM!); *s.loc*., VII–XI.1913, *Robinson 2296* [*c.fr*.] (NY!). **Java:** *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Fleischer* [*c.fr*.] (FH!); *s.loc*., *s.date*, *Gesker s.n*. *ex Hb*. *Vriese* (NY!); *s.loc*., *s.date*, *Horsfield 26* [*c.fr*.] (BM! NY!); *s.loc*., *s.date*, *Teijsmann s.n*. *ex Hb*. *Bosch* (NY!); Am Urwald u. Berggarten in Tjibodas an Baumrinde, 1450 m, II.1900, *Fleischer 130* [*c.fr*.] (NY! non BM); Tjibodas am Gedeh, 1500 m, III.1900, *Fleischer s.n*. [*c.fr*.] (NY!); Tjibodas, Tjibereum, 1931, *Renner 108* (BM!); West-Java, Gedehgebirge oberhalb Tjibodas an Baumasten im Urwald, 1500 m, IV.1900, *Fleischer 360* (NY!). **Java & Sumatra:** *s.loc*., *s.date*, *Korthals s.n*., *spec*. *of Bryol*. *Jav*. [*c.fr*.] (isolectotype of *M*. *angustifolium*: BM! — N.H.M. London no.: BM000858452). **Sulawesi:** South Sulawesi, Latimojong Mountains, slope of Gunung Rantemario, 2000 m, 22.XI.1969, *Eddy 5517* [*c.fr*.] (BM!). **Sumatra:** *s.loc*., *s.date*, *Teijsmann s.n. ex Hb. Dozy & Molk.* (NY!). **PAPUA NEW GUINEA. Central:** Boridi, 4500 ft [=1372 m], 10.X.1935, *Carr 14513* (NY!). **Eastern Highlands:** Daulo Pass, 18 km WNW of Goroka, 7.IV.1982, *Streimann 18094* [*c.fr*.] (ALTA, H, LAE, NICH, NY!); Goroka District, Mt. Gahavisuka Provincial Park, 6700 ft [=2042 m], 3.VIII.1994, *Tan 94-4130* [*c.fr*.] (SING!); Keglsugl, 2350 m, 21.II.1965, *Eddy 2297* [*c.fr*.] (BM!). **Milne Bay:** Woodlark Island, between Kropan Village and Gidaloga (old wharf), 3.5 km SW of Kulumadau, 12.X.1984, *Kumei 96* (ALTA, NY!); Woodlark Island, Kaurai logging area, 9 km N of Kulumadau, 8.X.1984, *Kumei 32* [*c.fr*.] (ALTA, LAE, NICH, NY!). **Morobe:** Lake Wamba 5 km S of Teptep airstrip, 2400–2500 m, 26.VII.1981, *Koponen 34359* [*c.fr*.] (NY!). **Southern Highlands:** Andawe River, Lama Sawmill Logging Area (Rongo), 6 km SE of Ialibu, 11.XII.1982, *Streimann 26572* [*c.fr*.] (ALTA, H, NY!); Tari Subdistrict, Ibiwara, 2700 m, 18.VI.1966, *Vink 16924B* (NY!). **West Sepik:** Kilifax, S of Vanimo, 250 m, 1.IV.1970, *Eddy 6710* [*c.fr*.] (BM!); Star Mts., 2300 m. Folongonom, 11.V.1975, *Touw 17635* [*c.fr*.] (NY!); Star Mts., Folongonom, upper montane forest above Papuan hunting camp, 2300–2350 m, 12.V.1975, *Touw 17790* [*c.fr*.] (TNS!). **PHILIPPINES. Luzon:** Benguet Prov., Panuai, 2100 m, VI.1909, *McGregor 8705* [*c.fr*.] (NY!); Mt. Maquiling, 3000 ft [=914 m], 16.VIII.1931, *Herklots P.13a* (BM!); Mt. Tabayoc, 19.II.1968, *Jacobs B596* [*c.fr*.] (TNS! L); Mt. Tabayoc, Southern Spur, 2500–2850 m, 16.II.1968, *Jacobs B499* [*c.fr*.] (L, NY! TNS!); Zambales, Palauig, high peak, 1800 m, *s.date, Linis 563-03* (SING!). **Mindanao:** Bukidonon Province, westlich Malabalay, Mt. Kitanlad, 1870 m, 2730 m, 19.VIII.1999, *Schumm & Schwarz 4243* (SING!); Misamis Occidental, Mt. Malindang, 1565 m, XI.2003, *Azuelo 180* (SING!); Nord Cotabato Province, Lake Agko camping site, 1240 m, 7.VIII.1999, *Schumm & Schwarz 4642* (SING!); Nord Cotabato Province, Mt. Apo, Lake Venado, 10.VIII.1999, *Schumm & Schwarz 4574* (SING!).

2. ***Macromitrium blumei*** **Nees** ***ex*** **Schwägr. var.** ***blumei*** (Figs. 5.14 & 5.15)

Sp. Musc. Frond., Suppl. 4: 316b (1842). *Leiotheca blumei* (Nees *ex* Schwägr.) Duby *ex* M. Fleisch., Musci Buitenzorg 2: 424 (1904). TYPE: Java, *Blume s.n. ex Hb. Nees* (holotype BM! isotypes BM! H-BR).

Schlotheimia teres Dozy & Molk., Ann. Sci. Nat. Bot., sér. 3 (2): 314 (1844). TYPE: Java [and Sumatra, Borneo], Patoeha, Papandajang, Singalang, Limbangan, G. Sakoenbang, *Korthals s.n.* (syntype L) — fide Dozy & Molkenboer (1861).

M. concinnum Mitt. *ex* Bosch & Sande Lac., Bryol. Jav. 1: 132, tab. CX (1860), ***syn. nov***. — TYPE: Java, *Zollinger itia. Jav. secundi 3716?* (holotype FH!).

M. copelandii Broth., Philipp. J. Sci. 3 (1): 16. (1908). TYPE: Philippines, Province of Bataan, Luzon, Mt. Mariveles, V.1904, *Copeland s.n.* (isotype NY!) — fide Bartram (1939).

M. magnirete Dixon, Bull. Torrey Bot. Club 51: 234 (1924), ***syn. nov***. TYPE: G. Tahan, Pahang, 7000 ft [=2134 m], 1922, *Haniff & Nur 7907* (holotype BM! isotype SING!).

M. horridum Dixon, Ann. Bryol. 5: 30 (1932). TYPE: Sumatra, on branches of tree, mossy jungle on the upper slopes of Dolok Soeroengan, Habinsaran, Tapanoeli, 18.V.1927, *Bartlett 7988* (holotype BM) — fide Eddy (1996).

M. miquelianum Mont., Syn. Musc. Frond. 1: 730 (1849), *nom. nudum*. — fide Dozy & Molkenboer (1861).

Plant small to medium-sized, forming short-cushion or mats; young shoots dark-green, gradually turning olive-green to rusty-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5–1.0 cm tall and 2–3 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids,

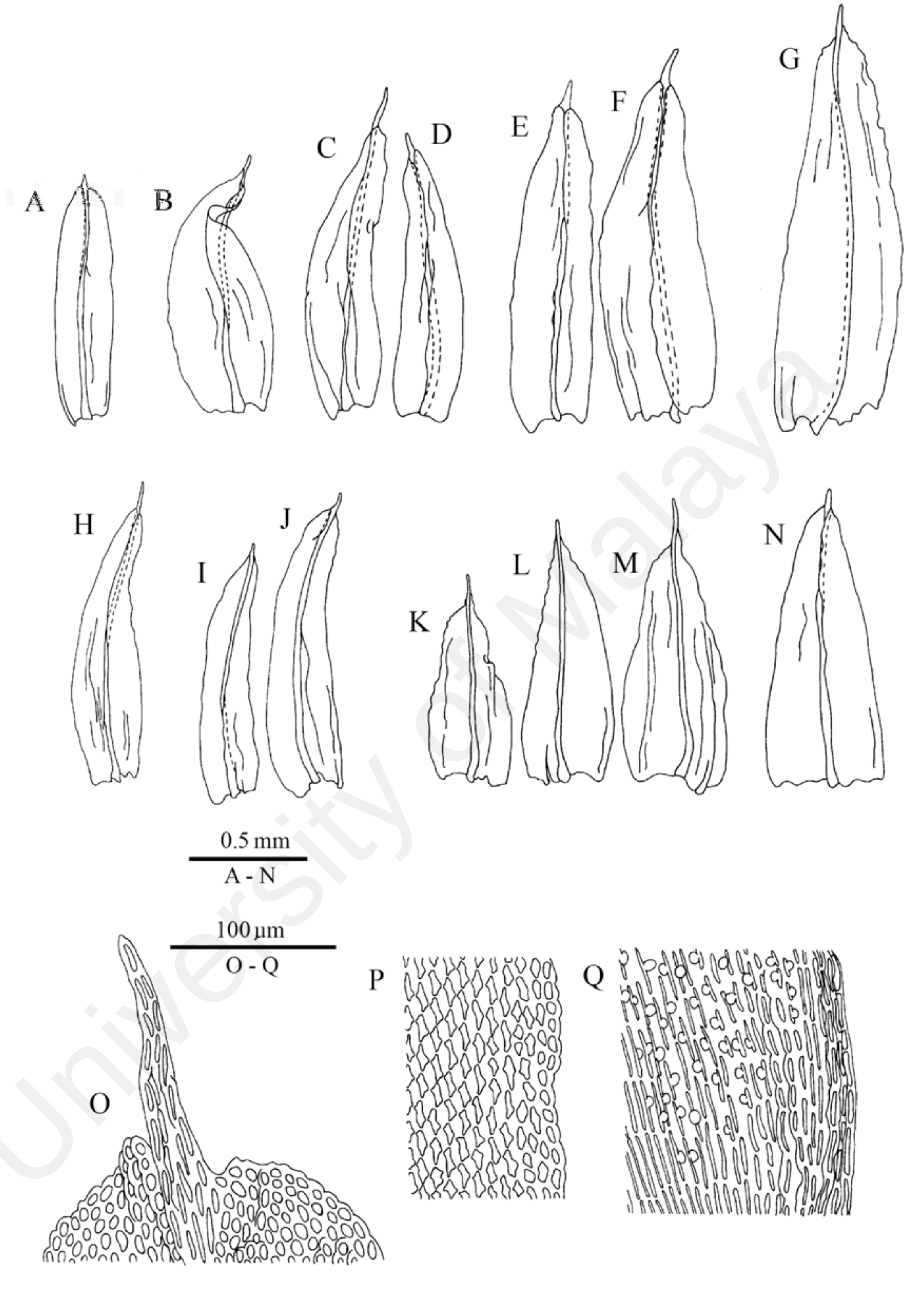

Figure 5.14. Illustrations of *Macromitrium blumei* Nees *ex* Schwägr. var. *blumei* — A-J, branch leaves; **K-N,** perichaetial leaves; **O,** leaf apex; **P,** mid-leaf cells; **Q,** basal laminal cells. [**A** from *Yong 4694* (KLU); **B** from *Guna 92* (KLU); **C-D** from *Holttum 20869* (SING); **E-F** from *Halimatul et al. 150b* (KLU), **G** from *Manuel 2468* (KLU); **H, K-M, O-Q** from *Holttum 20866* (BM); **I-J, N** from *Elbert 1546* (SING)]

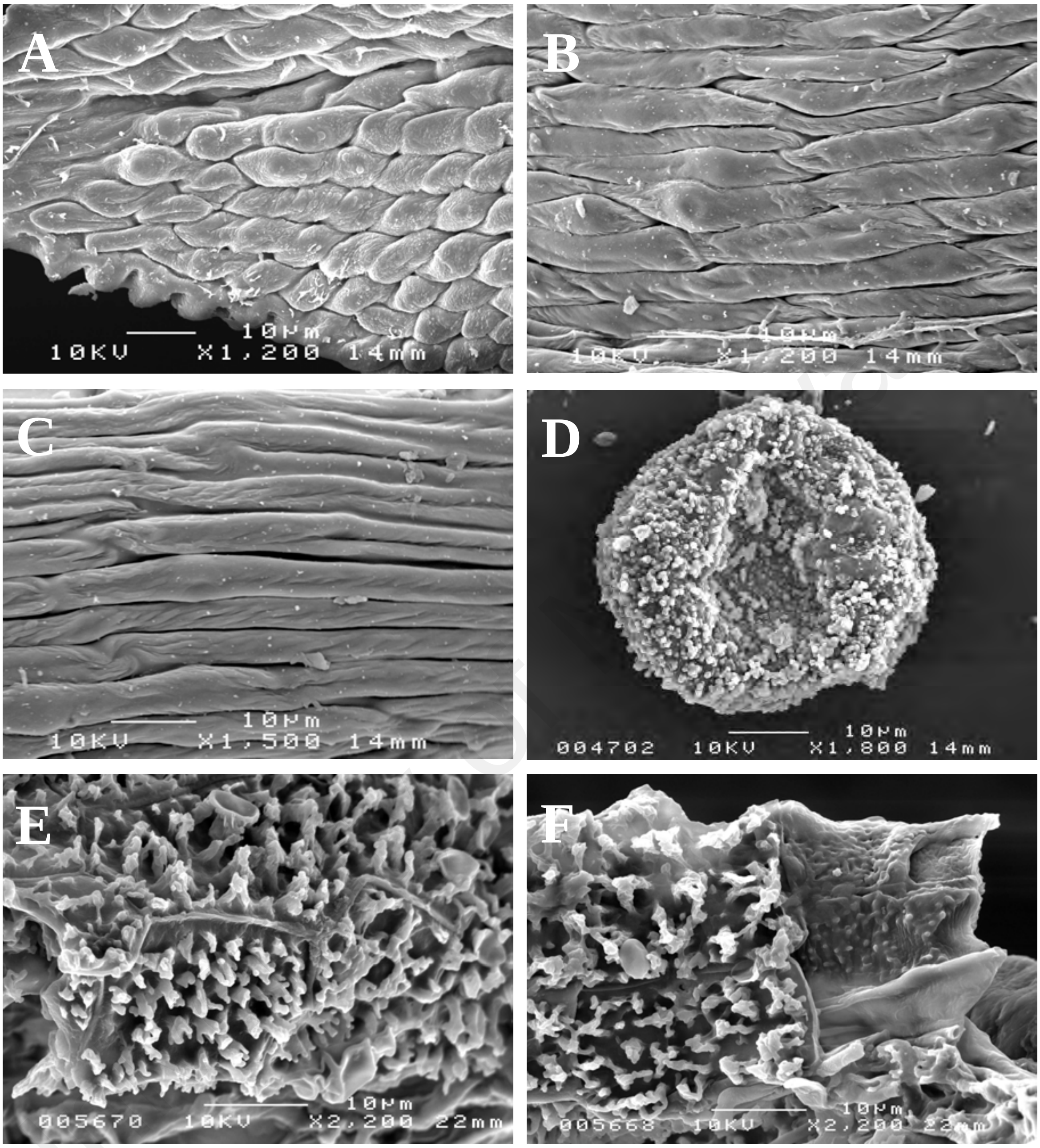

Figure 5.15. SEM images of *Macromitrium blumei* Nees *ex* Schwägr. var. *blumei* — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** macrospore; **E,** dorsal view of unsplit peristome teeth; **F,** ventral view of unsplit peristome teeth. [All from *Ibrahim 351* (KLU)]

slender, triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, densely arranged, distinctly funiculate with leaves spirally wound around branch, each leaf flexuose-twisted (when dry), erect-spreading to wide-spreading (when moist); branch leaves 1.1–1.4(–1.6) × 0.3–0.5 mm, length-width ratio 3–4:1, oblong-lanceolate to lingulate, lamina straight to gently bent, plane; apex firm, obtuse to broadly acute, mucronate to apiculate; margin subentire to crenulate, plane at distal part but deflexed at base; costa short-excurrent, ending in a mucro or apiculus, apiculus up to 0.1 mm long. Upper laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, oblate to quadrate, evenly incrassate, not pitted, flat or strongly bulging, smooth, lumina oval; middle laminal cells 10–16 × 8–12 µm, grading from short-rectangular to gradually long-rectangular toward the basal lamina, incrassate, not pitted, with narrow-rhombic lumina, cells flat or strongly bulging, smooth, clear; basal laminal cells 25–50(–60) × 8–12 µm, length-width ratio 3–5:1, long-rectangular, incrassate, walls more or less evenly thickened, lumina 2–3 µm wide, linear, pitted only near juxtacostal region and insertion, cells flat, strongly unipapillose to tuberculate.

Autoicous or pseudoautoicous, if dwarf male plants present, bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, smaller or achieving the size of branch leaves, 1.2–1.6 × 0.4–0.5 mm, broad-lanceolate to oblong-lanceolate, upper lamina broad, expanding gradually toward mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender, acute to acuminate, apiculate to cuspidate; margin subentire, plane; costa short-excurrent, ending in an apiculus; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 0.7–1.0 mm long; paraphyses abundant, densely covering the vaginula, 0.5–0.6 mm long, made of 7–12 short- or long-rectangular cells. Seta 14–18 mm long, smooth, sinistrorse-twisted. Capsule urns 1.2–1.5 × 0.7–0.8 mm, short-ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.8–1.0 mm. Peristome double. Exostome teeth fused into a tall, continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal side of teeth densely reticulate-papillose, papillae simple to compound, while ventral side of teeth weakly ornamented; vertical and horizontal cell-wall visible on both side of teeth, marked by low and thin lamellae. Endostome teeth fused into a continuous membrane, fused with exostome at their apical extent; dorsal side of teeth weakly ornamented, while ventral side of teeth densely reticulate-papillose, papillae simple to compound; vertical and horizontal cell-wall visible on both side of teeth, marked by low and thin lamellae. Spores anisomorphic, larger spores 38–42 µm in diameter, smaller spores 20–28 µm in diameter. Calyptra mitrate, plicate, naked, calyptra base fringed or lacerated.

Other descriptions and illustrations: Müller (1849) p. 730; Dozy & Molkenboer (1861) p. 112, tab. 89; Fleischer (1904) p. 421–422 as *M. concinnum*, p. 424–428, fig. 78 as *M. blumei*; Bartram (1939) p. 175–176, pl. 13, fig. 217; Eddy (1996) p. 74–76, fig. 382 as *M. blumei*, p. 76, fig. 383 as *M. concinnum*.

Distribution: As. 3: Thailand (Northern), Vietnam; As. 4: Indonesia (Borneo, Flores, Java, Lombok, Sulawesi, Sumatra); Malaysia (Malay Peninsula, Borneo); Philippines (Luzon, Mindanao, Mindoro, Negros, Palawan).

Habitat and ecology: Epiphytic on tree trunks and lower branches or occasionally on rocks and boulders. The species has been collected from both primary forest and rather open sites, and is especially common on trees growing in gardens on mountains. The plant has a wide elevational range (200–2000 m), but is more common above 900 m.

Notes:

1. The very variable leaf form and size of this common and handsome species has caused much confusion. Generally, it can be recognized by following characters: a) small to medium plant size; b) strongly whorled branch leaves giving a rope-like appearance; c) flat to strongly bulging, rounded and smooth upper laminal cells; d) long seta; and e) naked calyptra.

2. The setae of *M. blumei* var. *blumei* are generally smooth, rarely weakly roughened near the junction connecting to the capsule. Fleischer (1904) had erroneously used the rarer state (rough setae) as a character distinguishing this taxon from *M. concinnum*. The upper laminal cells of *Macromitrium concinnum* had been often described as papillose, a character doubted by Eddy (1996). Here it can be confirmed, after careful examination of the type of *M. concinnum* (*Zollinger itia. Jav. secundi 3716?*, FH), that the cells are mostly smooth and only irregularly papillose. In *M. blumei* the cells are typically smooth also. As such, the character of smooth vs. rough setae and the nature of the laminal cells cannot be used to distinguish these taxa. As they have no real differences, *M. concinnum* is placed here under the synonymy of *M. blumei* var. *blumei*.

Specimens examined:

INDONESIA. Java: *s.loc.*, *s.date*, *Blume s.n.* (isotype of *M. blumei*: BM!); *ibidem*, *Blume s.n. ex Hb. Nees* [*c.fr.*] (holotype of *M. blumei*: BM!); *ibidem*, *Miquel s.n.* [*c.fr.*] (BM!); *ibidem*, *s.coll. ex Hb. Dozy & Molk.* [*c.fr.*] (NY!); *ibidem*, *s.coll. ex Hb. Jaeg.* [*c.fr.*] (NY!); *ibidem*, *s.coll. H681* (BM 2 sheets!); *ibidem*, *Zollinger 1741 ex Hb. Jaeg.* [*c.fr.*] (NY!); *ibidem*, *Zollinger 1742* [*c.fr.*] (BM!); *ibidem*, 1832, *Greville s.n.* [*c.fr.*] (BM!); *ibidem*, 1843, *s.coll. ex Hb. Miquel* (BM!); *ibidem*, 800 m, 15.IX.1899, *Fleischer 33* (NY!); Buitenzorg, *s.date*, *s.coll. ex Hb. Jaeg.* (NY!); Buiternzorg, 1843, *s.coll.* [*c.fr.*] (BM!); Mt. Halimun National Park, Mt. Kendang, 980 m, 9.IX.2005, *Yong 6619* [*c.fr.*] (KLU!); *ibidem*, 1030 m, 10.IX.2005, *Yong 6622*, *6623*, *6624* (KLU!); *ibidem*, 1250 m, *Yong 6627* (KLU!); *ibidem*, 1260 m, *Yong 6628* (KLU!); *ibidem*, 1300 m, *Yong 6629* (KLU!); Mt. Salak, *s.date*, *Lobb s.n.* [*c.fr*.] (NY!); Batavia, NW slopes of Mt. Salak, above Goenoeng Boender, 1400 m, 28.V.1909, *Palmer & Bryant 661* [*c.fr*.] (NY!); Preanger, Montis Pangerango, Tjibodas, 1420 m, IV–V.1894, *Schiffner 77689* (NY!); in montibus Gedeh supra Tjibodas, 2000 m, *Fleischer 1594* [*c.fr*.] (NY! TNS!); im Berggarten von Tjibodas, 1450 m, II.1900, *Fleischer 132* [*c.fr*.] (BM 2 sheets! NY!); Tjibodas, 1450 m, II.1900, *Fleischer s.n.* [*c.fr*.] (NY!); Tjibodas, 2.VII.1898, *Nyman 369864* (NICH!); Tjibodas Forest Reserve, 1400 m, 13.IX.1969, *Eddy* [*c.fr*.] 4149 (BM!); Tugu, slope of Gedeh-Pangerango, above G. Mas, along Djalan Mandalawangi, 1300–1500 m, 3–4.X.1952, *Meijer 6035* (NY!). **Kalimantan:** Borneo in Mt. Sakoembang, *s.date*, *Korthals s.n. ex Herb. Lugd. Batav*. (NICH!). **Lombok:** Rindjani-Vulkangebirde, Nordost-Seite, Sembalun-Hochebene, 1165–1265 m, 30.V.1910, *Elbert 1546* [*c.fr*.] (SING!). **Sulawesi:** Minahassa, Boyong, *Warburg* (NY!); South Sulawesi, Latimojong, forest above Rantelemo, 1950 m, 10.XI.1969, *Jeremy 7612* [*c.fr*.] (BM!). **Sumatra:** Kerinchi-Seblat National Park, *Ho 05-222* (SING); Kerinchi-Seblat National Park, entrance to Mt. Kerinchi-Tujuh, *Tan 05-109* (SING); Kerinchi-Seblat National Park, Mt. Lumut, *Ho 05-169*, *05-170* (SING); Kerinchi-Seblat National Park, Mt. Tujuh, *Ho 05-148*, *05-149*, *05-150*, *05-153* (SING); Mt. Ketambe and vicinity, 8–15 km SW from the mouth of Lau Ketambe, 40 km NW of Kutatjane, 1700–1900 m, 19.VII.1972, *de Wilde & de Wilde-Duyfjes 13793*, [*c.fr*.] (L, NY! TNS!). **MALAYSIA. Johore:** Mt. Ophia [=Mt. Ledang], VI.1892, *Ridley 231* [*c.fr*.] (BM 2 sheets! SING!). **Kedah**: Jitra, Mt. Jerai (Kedah Peak), 2.VIII.1988, *Sadiah et al. s.n.* (KLU!); *ibidem*, 20.VII.1991, *Sani 11* (UKMB!); *ibidem*, 950 m, 26.VIII.1988, *Sadiah et al. 169a*, *170e* (KLU!); *ibidem*, 1200–1400 m, 22.IV.2001, *Hanizawati et al. 2001-8* (UKMB!); Jitra, Mt. Jerai (Kedah Peak), mushrooms cultivating area, 910 m, 26.VIII.1988, *Sadiah et al. 150b* (KLU!); Jitra, Mt. Jerai (Kedah Peak), TV transmitting station, 1130 m, 6.VII.1990, *Sadiah & Zamzuri 1604* (KLU!); *ibidem*, 1140 m, 6.VII.1990, *Sadiah & Zamzuri 1618*

(KLU!). **Kelantan**: Dabong, Mt. Stong, 1105 m, 27.V.2003, 1010–1105 m, *Yong 4133*, *4134* [*c.fr*.], *4150* [*c.fr*.], *4151* [*c.fr*.], *4152* [*c.fr*.], *4153*, *4154* [*c.fr*.] (KLU!); Lojing Highlands, Lojing Forest Reserve, 1150 m, 31.V.2008, *Suleiman 3127* (BORH! KLU!); Taman Negara, Kuala Koh, Mt. Tahan, ATM Camp, 350 m, 12.IX.1999, *Yong 1793a* (KLU!). **Pahang**: Cameron Highlands, Bukit Mentinggi, 19.VI.1988, *Damanhuri s.n*. (UKMB!); Cameron Highlands, Golf Course, 7.VII.1964, *Clear 1281* (KLU!); Cameron Highlands, Mt. Brinchang, 1980 m, 1.I.1989, *Wong & Talib 3998* (KLU!); *ibidem*, 1900 m, 24.IV.1999, *Gunaseelan & Mohamed 92* (KLU!); Cameron Highlands, Mt. Perdah, 18.VI.1988, *Damanhuri s.n*. [*c.fr*.] (UKMB!); Cameron Highlands, Sg. Palas Tea Estate, 1850 m, 19.IX.1985, *Mohamed 8980b* (KLU!); Cameron Highlands, Tanah Rata, Pelangi Aparment, 1375 m, 13.III.2004, *Yong et al*. *4909*, *4911* (KLU!); *ibidem*, 5.XII.2004, *Yong & Goh 6122* (KLU!); Cameron Highland, Tanah Rata, jungle path no. 9 & 9a, 1220 m, 11.VII.2004, *Yong 6050* (KLU!); Fraser's Hill, *s.date*, *Damanhuri s.n*. (UKMB!); *ibidem*, 1120 m, 11.III.2000, *Damanhuri et al*. *200-136* (UKMB!); Fraser's Hill, Alan's Water, 1180 m, 3.I.2008, *Yong 7474* (KLU!); Fraser's Hill, Jeriau Road, 3500–4000 ft [=1067–1219 m], 20.VIII.1960, *Burkill et al*. *HMB 2437* [*c.fr*.] (SING!); Fraser's Hill, water fall, 4000 ft [=1219 m], 5.IX.1965, *Inoue 10698* (TNS!); Genting Highland, Mt. Ulu Kali, 4800 ft [=1463 m], 4.VIII.1982, *Salleh 2* (KLU!); *ibidem*, 5000 ft [=1524 m], 30.VII.1978, *Manuel 2731* [*c.fr*.], *2732b* [*c.fr*.] (KLU!); *ibidem*, 1720 m, 11.X.2003, *Yong et al*. *4694* (KLU!); *ibidem*, 5800 ft [=1768 m], 17.VI.1978, *Manuel 2468* [*c.fr*.] (KLU! NY!); Taman Negara, Merapoh, Mt. Tahan, Bonsai Camp, 1700 m, 17.VI.1995, *Ibrahim 351* [*c.fr*.] (KLU!); Taman Negara, Mt. Tahan, VII.1911, *Ridley 1009* [*c.fr*.] (BM!); *ibidem*, 5000 ft [=1524 m], 30.VIII.1928, *Holttum 20866* [*c.fr*.] (BM! SING!); *ibidem*, 5000 ft [=1524 m], 31.VIII.1928, *Holttum 20868* [*c.fr*.] (BM! SING!), *20869* [*c.fr*.] (SING!); *ibidem*, 6000 ft [=1830 m], 1.IX.1928, *Holttum 20896* (BM! SING!); *ibidem*, 7000 ft [=2134 m], 1922, *Haniff & Nur 7907* (holotype of M.

magnirete: SING! isotype BM!). **Perak**: Taiping, Taiping Hill (Maxwell Hill), 3500 ft [=1067 m], 17.IX.1940, *Spare 3231* [*c.fr*.] (BM!); *ibidem*, 1100 m, 18.IV.1971, *Tixier 5788* (SING!); *ibidem*, 1180 m, 6.VI.1983, *Mohamed et al*. *8140* (KLU!); *ibidem*, 1100–1400 m, 8.III.2004, *Mohamed & Yong 4807* (KLU!); *ibidem*, 11.III.2004, *Mohamed & Yong 4875*, *4877*, *4884* (KLU!); Taiping, Taiping Hill (Maxwell Hill), Mt. Hijau, 3400–4751 ft [=1036–1448 m], 4.III.1980, *Manuel 3211* (KLU!); *ibidem*, 1120 m, 7.III.2004, *Mohamed & Yong 4760* [*c.fr*.] (KLU!); Ulu Perak, Belum Royal Park, Sg. Kenarong, 200–300 m, 30.VII.2003, *Yong 4486* (KLU!). **Sabah**: Lahad Datu, Danum Conservation Area, Mt. Danum, summit area, 1840 m, 9.VI.1989, *Damanhuri s.n*. [*c.fr*.] (UKMB!); *ibidem*, 1850 m, *Damanhuri s.n*. [*c.fr*.] (UKMB!); Long Pasia, Rekong Waterfall, 1308 m, 8.XI.2003, *Suleiman 1369* [*c.fr*.] (BORH! SAN); Ranau, Kinabalu Park, Mt Kinabalu, Timpohon Gate, 1500 m, 8.V.2005, *Yong 6204* (KLU!); Ranau, Kinabalu Park, Park headquater, 1500 m, *Yong 6231* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Mt. Tambuyukon, 1480 m, 14.VIII.2008, *Suleiman 3669* [*c.fr*.] (BORH, KLU! SNP); *ibidem*, 1520 m, 14.VIII.2008, *Suleiman 3676*, *3677* (BORH, KLU! SNP); *ibidem*, 1550 m, 14.VIII.2008, *Suleiman 3680* [*c.fr*.] (BORH, KLU! SNP); *ibidem*, 2200 m, 14.VIII.2008, *Suleiman 3735*, *3737* [*c.fr*.] (BORH, KLU! SNP); Sandakan, Telupid, Ulu Tungud Forest Reserve, Maliau Range, 1000 m, 4.V.2005, *Andi 324* [*c.fr*.], *328* [*c.fr*.] (BORH, KLU! SAN); Sipitang District, Muaya Waterfall, 1031 m, 4.XI.2003, *Suleiman 1298* (BORH! SAN); Tawau, Maliau Basin, *Eucalyptus* Camp, 980–1100 m, 16–24.VI.2006, *Mohamed & Yong 7184*, *7194* (KLU!). **Sarawak**: Kubah National Park, Mt. Serapi, 780 m, 21.VII.1991, *Mohamed & Bakar 3091* (KLU!); Padawan, Penrissen Range, Borneo Highland Resort, 820 m, 16.VII.2005, *Yong 6176* (KLU!). **Selangor:** Genting Highland, 27.X.1983, *Damanhuri 2496* (UKMB!); *ibidem*, 1110 m, 29.VIII.1991, *Mohamed 7666a* (KLU!); Genting Highland, Awana cable car station, 955 m, 22.V.2006, *Yong 6681* (KLU!); *ibidem*, 1000 m, 4.X.2003, *Yong 4528*, *4531a* (KLU!); *ibidem*, 1030 m, 22.V.2006, *Yong 6684* (KLU!); Genting Highland, Gohtong Jaya, 1055 m, 9.IX.2003, *Yong 4742* (KLU!); Genting Highland, water reservoir near Genting Resort, 1240 m, 16.XII.1983, *Damanhuri 3598* (UKMB!); **Terengganu**: Dungun District, Mt. Mandi Angin, Pasir Raja Forest Reserve Compartment 18, 1260 m, 8.VI.2004, *Yong 5946* (KLU!); Dungun District, Mt. Mandi Angin, Pasir Raja Forest Reserve Compartment 16, Sg. Loh, 1000 m, 9.VI.2004, *Yong 6011* (KLU!). **PHILIPPINES. Luzon:** Bataan, Mt. Mariveles, V.1904, Copeland (isotype of *M. copelandii*: NY!); Zambales, Palauig, 1400 m, XI.2003, *Linis 511-03* (SING). **Mindanao:** Bukidnon, Mt. Kalatungan, Pangantucan, 12–14.V.1999, *Lubos K104* (SING!).

3. *Macromitrium blumei* var. *zollingeri* (Mitten ex Bosch & Sande Lacoste) S.-L.Guo, B.C.Tan & V.Virtanen (Figs. 5.16 & 5.17)

Nova Hedwigia 82: 476 (2006). *M. zollingeri* Mitt. *ex* Bosch & Sande Lac., Bryol. Jav. 1: 113, tab. 90 (1859). LECTOTYPE (Touw, 2007): Java, *Zollinger, Iter. jav. sec. 3716* (L; isolectotypes BM! NY!).

M. striatum Mitt. *ex* Bosch & Sande Lac., Bryol. Jav. 1: 134 (1860). ***syn. nov***. TYPE: Borneo, in monte Kina Balloo, *Low s.n.* (holotype L; isotype NY!).

M. assimile Broth., Leafl. Philipp. Bot. 6: 1978 (1913), ***syn. nov***., non Broth. & Dixon (1915). TYPE: Mindanao, Davao, Todaya, Mt. Apo, *Elmer 11663* (holotype NY! isotype BM!).

M. annamense Broth. & Paris in Broth., Nat. Pfl. 11: 39 (1925). LECTOTYPE (Guo et al., 2006): Annam, Lang Bian, 1500 m, 25.XI.1903, *Micholitz 290* (H-BR) — fide Guo et al. (2006).

Plant small to medium-sized, forming short-cushion or mats; young shoots dark-green, gradually turning olive-green to rusty-brown at mature portions, brownish to darker

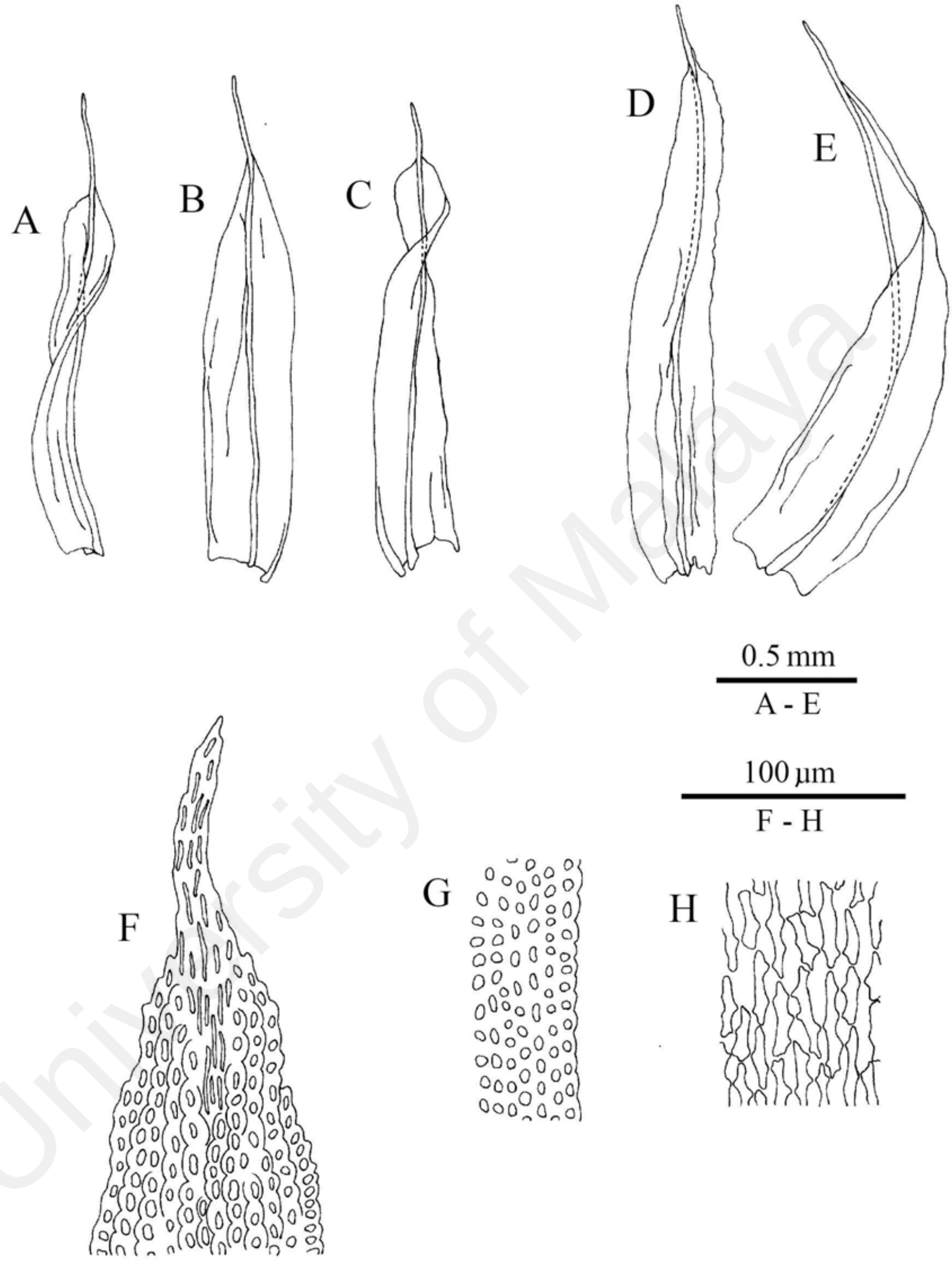

Figure 5.16. Illustrations of *Macromitrium blumei* var. *zollingeri* (Mitt. *ex* Bosch & Sande Lac.) S.L. Guo, B.C. Tan & Virtanen — A-D, branch leaves; **E,** perichaetial leaves; **F,** leaf apex; **G,** mid-leaf cells; **H,** basal laminal cells. [**A** from *Yong 6249* (KLU); **B** from *Yong 6239* (KLU); **C** from *Yong 4149* (KLU); **D-H** from *Holttum 28123* (SING)]

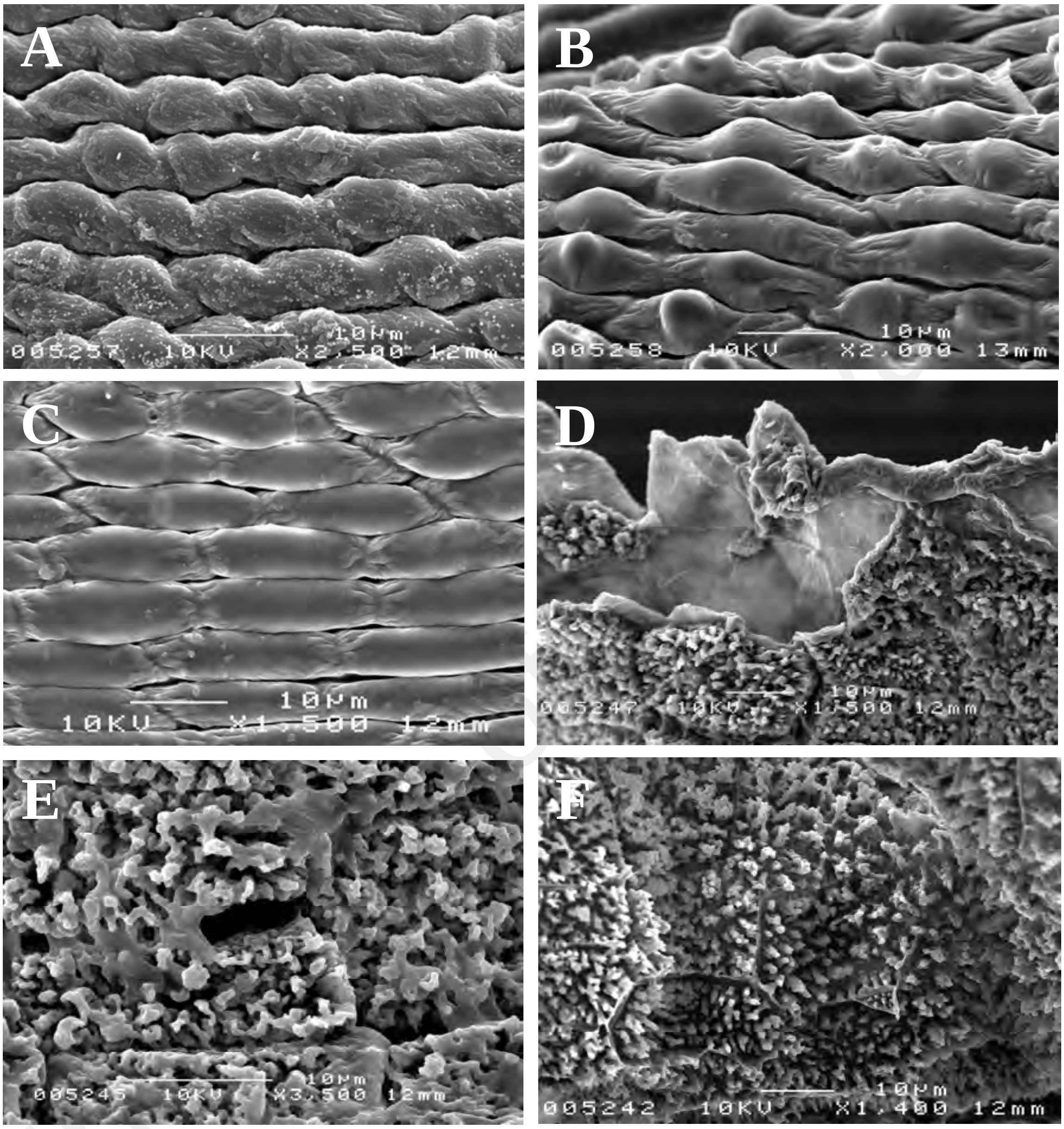

Figure 5.17. SEM images of *Macromitrium blumei* var. *zollingeri* (Mitt. *ex* Bosch & Sande Lac.) S.L. Guo, B.C. Tan & Virtanen — A, upper laminal cells; **B,** basal laminal cells; **C,** basal laminal cells near insertion; **D,** dorsal view of inner peristome layer and part of outer peristome layer; **E,** dorsal view of outer peristome layer; **F,** ventral view of inner peristome layer. [All from *Yong 6231* (KLU)]

below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 1.0–1.5 cm tall and 2–3 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender, triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, densely arranged, distinctly funiculate with leaves spirally wound around branch, each leaf flexuose-twisted (when dry), erect-spreading to wide-spreading (when moist); branch leaves 1.3–1.8 × 0.3–0.4 mm, length-width ratio 4–5:1, slender-lanceolate to lingulate, lamina straight to gently bent, occasionally with deflexed or twisted apex, plane; apex firm, obtuse to broadly acute, cuspidate; margin subentire to crenulate, plane at distal part but deflexed at base; costa excurrent, ending in a distinctive awn, awn 0.2–0.4 mm long. Upper laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, oblate to quadrate, evenly incrassate, not pitted, flat or strongly bulging, smooth, lumina oval; middle laminal cells 10–16 × 8–12 µm, grading from short-rectangular to gradually long-rectangular toward the basal lamina, incrassate, not pitted, with narrow-rhombic lumina, cells flat or strongly bulging, smooth, clear; basal laminal cells 32–70 × 8–12 µm, length-width ratio 4–6:1, long-rectangular, incrassate, walls more or less evenly thickened, lumina 2–3 µm wide, linear, pitted only near juxtacostal region and insertion, cells flat, strongly unipapillose to tuberculate.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, achieving the size of branch leaves or larger, 1.3–2.0 × 0.4–0.5 mm, broad-lanceolate to oblong-lanceolate, upper lamina broad, expanding gradually toward mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender, acute to acuminate, cuspidate; margin subentire, plane; costa short-excurrent, ending in a cusp; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 0.7–1.0 mm long; paraphyses abundant, densely covering the vaginula, 0.5–0.7 mm long, made of 7–10 short- or long-rectangular cells. Seta 15–20 mm long, smooth, sinistrorse-twisted. Capsule urns 1.2–1.5 × 0.7–0.8 mm, short-ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.9–1.1 mm. Peristome double. Exostome teeth fused into a tall, continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal side of teeth densely reticulate-papillose, papillae simple to compound, while ventral side of teeth weakly ornamented; vertical and horizontal cell-wall visible on both side of teeth, marked by low and thin lamellae. Endostome teeth fused into a continuous membrane, fused with exostome at their apical extent; dorsal side of teeth weakly ornamented, while ventral side of teeth densely reticulate-papillose, papillae simple to compound; vertical and horizontal cell-wall visible on both side of teeth, marked by low and thin lamellae. Endostome absent. Spores anisomorphic, larger spores 38–42 µm in diameter, smaller spores 20–28 µm in diameter. Calyptra mitrate, plicate, naked, base fringed or lacerated.

Other descriptions and illustrations: Fleischer (1904) p. 422–424, fig. 77; Eddy (1996) p. 78, fig. 384 as *M. zollingeri*.

Distribution: As. 3: Cambodia, Sri Lanka, Thailand (Peninsula, Southeastern), Vietnam; As. 4: Indonesia (Borneo, Buru, Flores, Java, Lombok, Sulawesi, Sumatra), Malaysia (Malay Peninsula, Borneo).

Habitat and ecology: Epiphytic on tree trunks and lower canopy branches, occasionally on bushes, collected from forested to slightly disturbed sites. The plant has a wide altitudinal range from 300 m to 2500 m.

Notes:

1. *Macromitrium blumei* var. *zollingeri* can be recognized by its a) oblong-lanceolate to lingulate branch leaves with blunt apices and strongly whorled on the branch, giving a rope-like appearance; b) excurrent costa ending in a distinctive awn; c) rounded and smooth, either flat or bulging upper laminal cells; d) long seta; and f) smooth calyptra.

2. This variety is very similar to *M. blumei* var. *blumei* in most aspects, except its larger plant size, with longer and more slender branch leaves, in which the excurrent costa is 2–3 times longer. Eddy (1996) has precisely described an "abruptly excurrent costa forming a long mucro, awn or almost a hair point" for var. *zollingeri*, which is useful for quick diagnosis of the variety, including differentiating it from the closely allied var. *blumei*.

3. *Macromitrium assimile* was formerly placed under the synonym of *M. blumei* var. *blumei* by Bartram (1939). Careful examination of the type material of *M. assimile* showed that its characters fell within the ranges found in *M. blumei* var. *zollingeri* (see Guo et al., 2006), therefore it is considered a synonym of the latter.

4. Fleischer (1904) was the first person who noted that *M. striatum* (from Borneo) was merely a variation of *M. zollingeri* (sensu Fleischer, 1904), which differed by its smaller, flat leaf base, weakly papillose leaf with yet longer, distinctive cuspidate hair ["*schmälere, am blattgrunde flache, kaum papilöse blätter met noch lingerer haarspitze unterscheidet"*]. *Macromitrium striatum*, which is only known from the type collected from Mount Kinabalu, is confirmed here as just a smaller form of *M. blumei* var. *zollingeri*.

Malaysian specimens examined:

INDONESIA. Java: *s.loc.*, *s.date*, *Zollinger s.n. ex Hb. Hook.* (BM!); inter javanicum secundum, *s.date*, *Zollinger 3716* [*c.fr.*] (isolectotypes of *M. zollingeri*: BM! NY!). **Kalimantan:** East Kutai, Peak of B.papan terr. Beul, 600–700 m, 10.VII.1952, *Meijer*

B2046 [*c.fr*.] (SING!). **Sumatra:** Kerinchi-Seblat National Park, Mt. Lumut, *Ho 05-178* (SING); Mt. Dempo, 8000 ft [=2438 m], 9.II.1933, *Holttum 28123* (SING!); Mt. Talaman, *Bunnemeijer 786 ex Hb. Verdoorn* (17879) (BM!). **MALAYSIA. Kedah:** Gurun, Kedah Peak, 3500 ft [=1067 m], 1.IV.1925, *Holttum 14862* [*c.fr*.] (SING!). **Kelantan:** Dabong, Mt. Stong, 1040 m, 27.V.2003, *Yong 4149* (KLU!). **Pahang:** Fraser's Hill, Pine Tree Hill, 4800 ft [=1463 m], 21.III.1929, *Holttum 21562* (SING!); Taman Negara, Mt. Padang, 300 m, 14.IV.1974, *Littke s.n.* [*c.fr*.] (UKMB!). **Sabah**: in monte Kina Balloo, *Low s.n.* [*c.fr*.] (isotype of *M. striatum*: NY!); Maraiparai, 5000 ft [=1524 m], 24.XI.1931, *Holttum 25184* (BM! SING!); Mt. Kinabalu, Colombon Basin, end of Numeruk ridge near Colombon river, 3500 ft [=1067 m], 18.VIII.1933, *Clemens 40012* [*c.fr*.] (NY!); Ranau, Kinabalu Park, Mt. Kinabalu, Panar Laban, 2685 m, 9.V.2005, *Yong 6298* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, Pondok Kandis, 1740 m, 28.XI.2001, *Suleiman 739* (BORH!); Ranau, Kinabalu Park, Mt. Kinabalu, Timpohon Gate, 1550 m, 8.V.2005, *Yong 6201* (KLU!); Ranau, Kinabalu Park, park headquater, 1500 m, *Yong 6228*, *6239*, *6249* (KLU!); Ranau, Kinabalu Park, Mt. Tambuyukon, 1450 m, 14.VIII.2008, *Suleiman 3642* [*c.fr*.] (BORH, KLU! SNP); Tawau, Maliau Basin, *Eucalyptus* Camp, 980–1100 m, 16–24.VI.2006, *Mohamed & Yong 7331* (KLU!). **PHILIPPINES. Luzon:** Zambalas, XI–XII.1907, *Curran & Merrill 8188* [*c.fr*.] (NY!). **Mindanao:** Bukidnon, Mt. Candoon, VI–VII.1920, *Ramos & Edano 37181* [*c.fr*.] (BM!); Davao, Todaya (Mt. Apo), IX.1909, *Elmer 11663* [*c.fr*.] (holotype of *M. assimile*: NY! isotype BM!), 11792 [*c.fr*.] (BM 2 sheets! NY!); Misamis Oriental, Mt. Lumot (via Haruhay Trial), Barangay Lunutan, 1710 m, 25.VIII.1999, *Schumm & Schwarz 4800* (SING!); Nord Cotabato, Mt. Apo, Lake Venado, 2320 m, 10.VIII.1999, *Schumm & Schwarz 4573* (SING!). **Mindoro:** Mt. Halcon, XI.1906, *Merrill 5505* [*c.fr*.] (NY!).

4. *Macromitrium cuspidatum* Hampe (Figs. 5.18, 5.19 & 5.20)

Icon. Musc. 20 (1844). LECTOTYPE (Vitt et al., 1995): In Insula Java legit. diligentissimus *Junghuhn*; ab amicissimo Gottsche communicatum (BM).

M. elongatum Dozy & Molk., Ann. Sci. Nat. Bot., sér. 3, 2: 311 (1844), non Dozy & Molk. *ex* Bosch & Sande Lac. (1859). LECTOTYPE (Vitt et al., 1995): Sumatra, Sakoembang, *Korthals s.n.* (L) — fide Dozy & Molkenboer (1861).

Plant medium-sized to fairly large, forming cushions or mats; young shoots yellowish-green, gradually turning to olive-green and orange-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short to tall, 2–4(–5) cm tall and 4–6(–7) mm wide, loose to tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate on young shoots, becoming more lanceolate at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, laxly to densely arranged, leaves erect-spreading to spreading, with loosely curved or deflexed apices (when dry), wide-spreading to squarrose-spreading with recurved apices (when moist); branch leaves (3.2–)3.6–4.0(4.3) × (0.6–)0.8–1.0(–1.2) mm, length-width ratio 4–6:1, slender to broad lanceolate with an oblong base, lamina mostly recurved, plane; apex firm, slender to rather broad, long, acuminate with a long-cuspidate to aristate awn; margin subentire to crenulate, plane at distal part but reflexed at base; costa long-excurrent, piliferous, ending in a 0.45–0.75 mm long arista. Upper laminal cells 5–28 × 5–8 µm, length-width ratio 1–5:1, size and shape varied on different leaves, from oblate, short- or wide-rectangular to distinctly long-rectangular, incrassate, walls not pitted, shorter cells always densely pluri-papillose for those short-cells, while longer cells often flat or low-bulging, cells mostly obscure due to the dense papillae but clear in latter case; middle

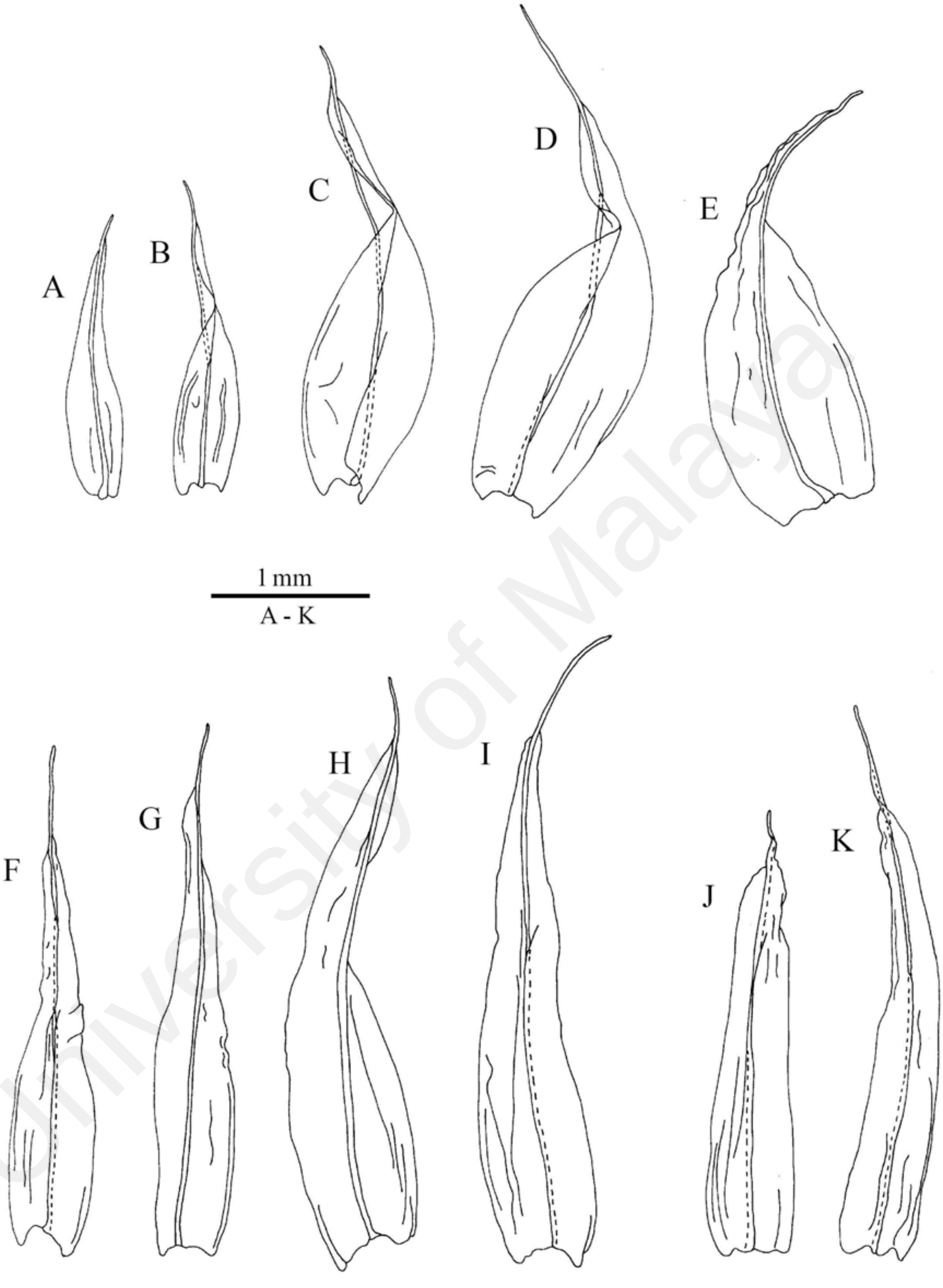

Figure 5.18. Illustrations of *Macromitrium cuspidatum* Hampe — A-I, branch leaves; **J-K,** perichaetial leaves. [**A-B** from *Mohamed 3144c* (KLU); **C** from *Yong 6113* (KLU); **D** from *Mustapeng 254* (SAN); **E** from *Yong 5280* (KLU); **F, J-K** from *Yong 4136* (KLU); **G** from *Yong 6527* (KLU); **H** from *Mohamed 8716* (KLU); **I** from *Damanhuri 2001-22* (UKMB)]

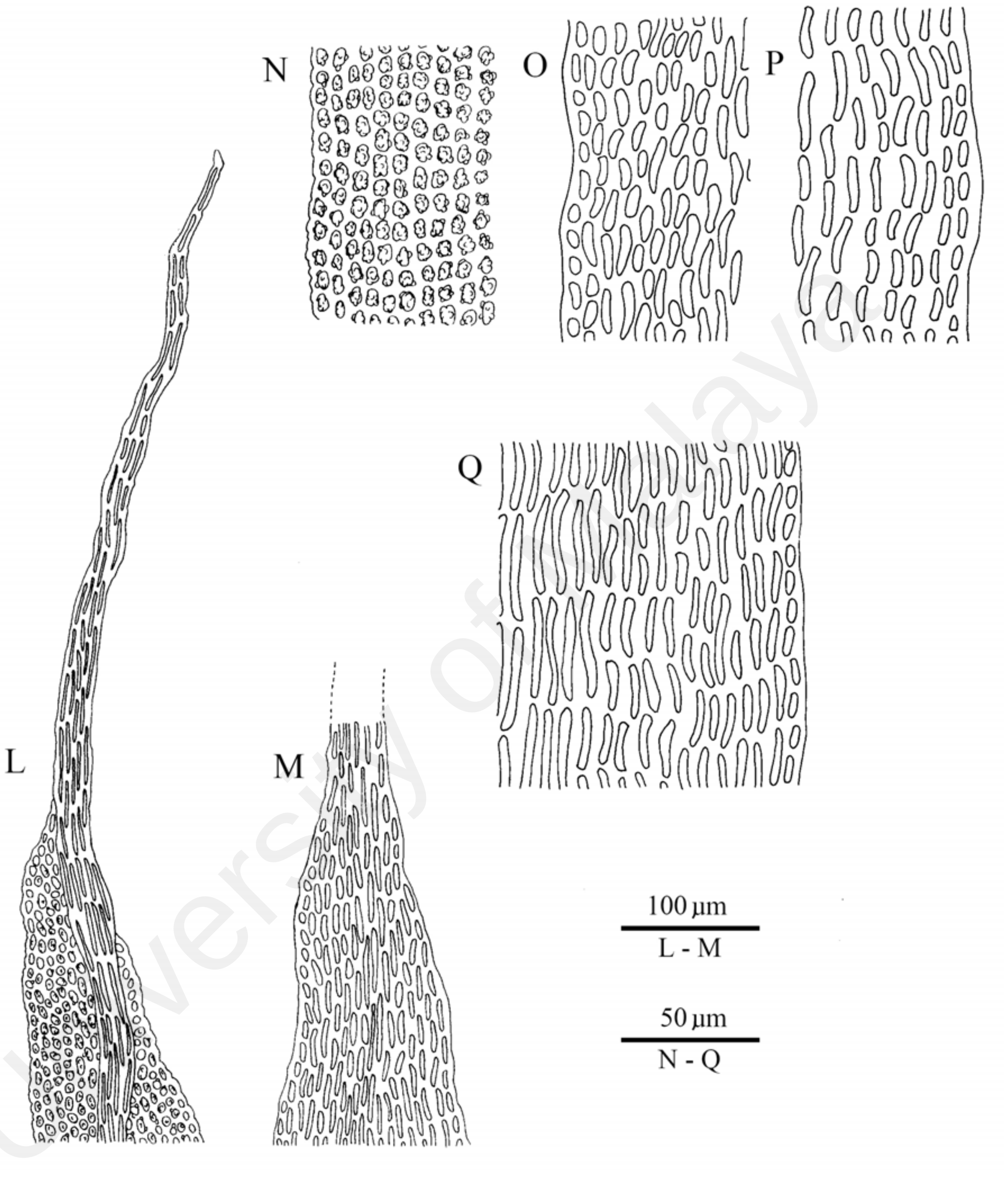

Figure 5.19. Illustrations of *Macromitrium cuspidatum* Hampe — L-M, leaf apices; **N-P,** upper laminal cells; **Q,** basal laminal cells. [**L, O, Q** from *Yong 4136* (KLU); **M, P** from *Sadiah 113* (KLU); **N** from *Yong 6520* (KLU)]

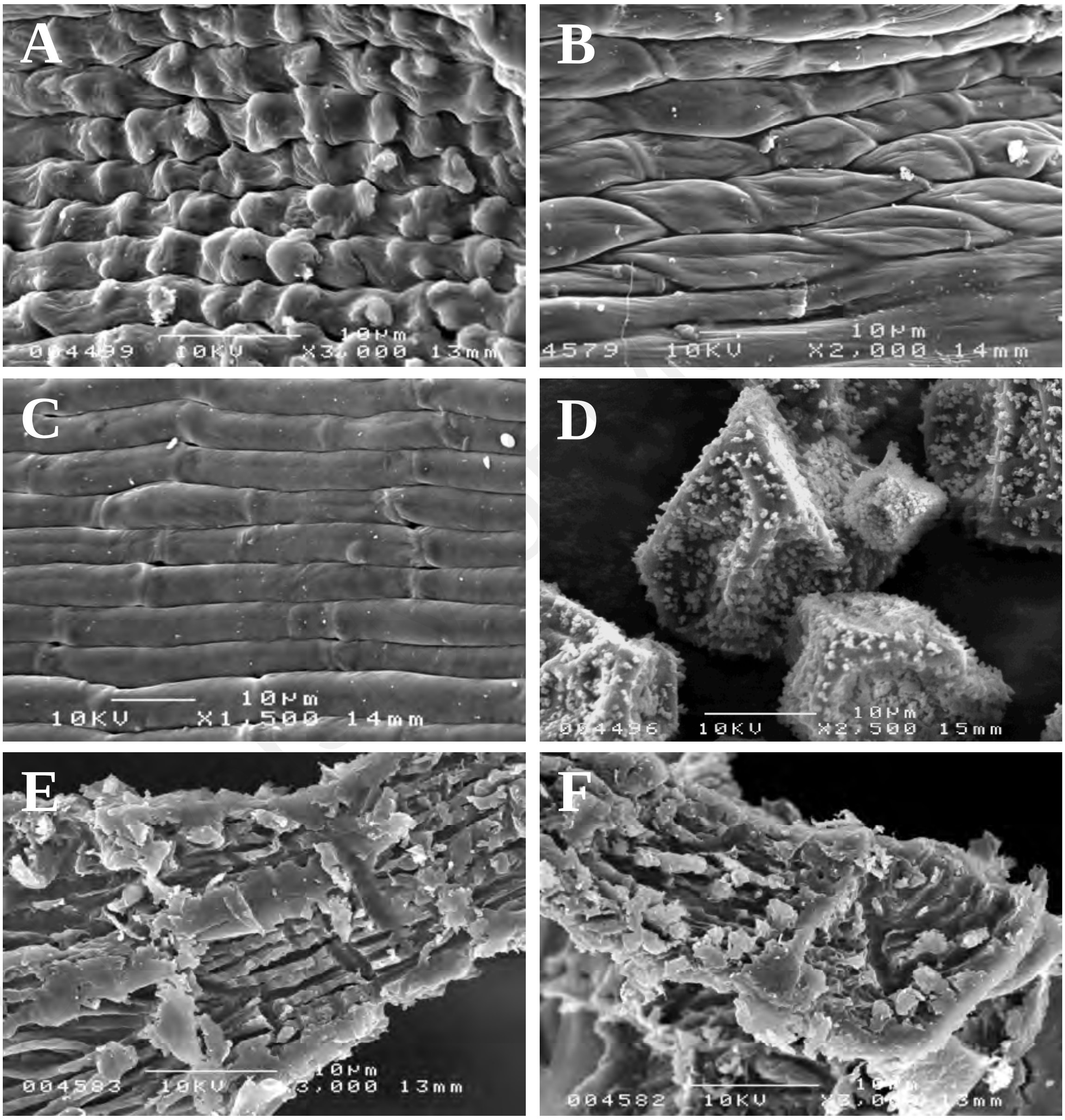

Figure 5.20. SEM images of ***Macromitrium cuspidatum*** **Hampe — A-B,** upper laminal cells; **C,** basal laminal cells; **D,** spores; **E,** dorsal view of peristome teeth; **F,** ventral view of peristome teeth. [All from *Yong 1099* (UKMB)]

laminal cells 9–38 × 6–10 µm, gradually elongate toward the basal lamina, cells not uniform in length, incrassate, with curved to more-or-less straight lumina, cells flat, weakly papillose to smooth, clear; basal laminal cells 28–70 × 8–12 µm, length-width ratio 3–6:1, long-rectangular, incrassate, walls unevenly thickened, lumina 2–3 µm wide, strongly curved to sigmoid in appearance, pitted only near juxtacostal region and insertion, cells flat, smooth.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, smaller than or about the size of branch leaves, 2.5–3.2 × 0.5–0.8 mm, broad-lanceolate to oblong-laceolate, upper lamina narrow, expanding abruptly below apex or gradually toward the mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender acuminate to sometimes cuspidate; margin subentire to entire, plane; costa excurrent, ending in a 0.1–0.25 mm long awn; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 0.8–1.0 mm long; paraphyses abundant, densely covering the vaginula, 0.7–1.0 mm long, made of 13–22 short-rectangular cells. Seta 5–7 mm long, smooth, sinistrorse-twisted. Capsule urns 1.3–1.5 × 1.0–1.1 mm, short-ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.9–1.0 mm. Peristome single. Exostome teeth separated above but connected at their base in a rather tall membrane, erect to slightly incurved at top in both dry and wet conditions; dorsal side of teeth vertically striolate-papillose with simple wart-like papillae, irregularly distributed on coarse vertical to diagnonal ridges; ventral side of teeth irregular striolate-papillose with simple wart-like to compound papillae, on vaguely raised, vertical or diagonal ridges; remains of original cell-walls generally faint on dorsal side, occasionally marked by low and vague trabeculae, but trabeculae distinct on ventral side, marked by low and filmy trabecula. Endostome absent. Spores anisomorphic, larger spores 32–35 µm in diameter, smaller spores 17–20 µm in diameter. Calyptra mitrate, plicate, sparsely hairy, hairs stiff erect, mostly on ridges near to the calyptra base, calyptra base fringed or lacerated.

Other descriptions and illustrations: Müller (1849) p. 731; Dozy & Molkenboer (1861) p. 115–116, tab. 92; Fleischer (1904) p. 454–455; Bartram (1939) p. 180, pl. 13, fig. 224; Vitt et al. (1995) p. 27–29, figs. 1d, 12; Eddy (1996) p. 49–50, fig. 361.

Distribution: As. 3: Cambodia; As. 4: Indonesia (Borneo, Java, Sumatra, Ternate), Malaysia, Papua New Guinea, Philippines (Luzon, Mindoro, Palawan, Panay)

Habitat and ecology: Epiphytic on tree trunks and lower branches, or occasionally on rocks and boulders. The species has been collected from both primary forest and rather open sites, and is especially common on trees growing in gardens on mountains. In Malaysia, the species mostly occurs at 1000–2100 m; not common at lower elevations, although once collected in the lowlands (*Mohamed & Yong 5380*, KLU, collected from a fallen branch in Mulu National Park, Sarawak).

Notes:

1. Touw (2007) indicates a possible mistake in the label of the lectotype of *M. elongatum*, and states that Mount Sakoembang is in Borneo.

2. *Macromitrium cuspidatum* can be rapidly recognized by its a) medium to large plant size; b) piliferous branch leaves, ending in a long-excurrent costa; c) smooth basal laminal cell surfaces; and d) irregularly thickened walls of basal laminal cells that give rise to arched or sigmoid lumina. Only one other *Macromitrium* species, *M. longipilum*, has long-piliferous leaves, but that can be differentiated by its more robust size, distinctly tuberculate basal laminal cells and longer setae.

3. Both short- or long-rectangular upper laminal cells are found in this species, but on

different branches. The shorter cells are always pluripapillate, while the longer cells are smooth.

4. *Yong & Mohamed 5380* from the Mulu National Park lowlands is odd only by its ovate branch leaves (about 3:1 in length-width ratio, and thus very different from the lanceolate leaves of 4–5:1 in length-width ratio typical of the species).

Specimens examined:

INDONESIA. Java: *s.loc.*, *s.date*, *s.coll*. *ex* Hb. Dozy & Molk. [*c.fr*.] (NY!); *s.loc.*, *s.date, s.coll*. *ex* Hb. Hook. (NY!); Gedeh im Berggarten von Tjibodas, IV.1900, *Fleischer 283* (NY!); Megamendong, *s.date*, *Motley s.n*. [*c.fr*.] (NY 3 sheets!); Megamendong Pass, 4000–6000 ft [=1219–1829 m], VII & X.1854, *Motley s.n*. [*c.fr*.] (NY!); Mt. Salak, 3000 ft [=914 m], *s.date,* Kurz 845 [*c.fr*.] (NY!). **Kalimantan:** East Kalimantan, Nunukan, Krayan, Pa' Raye Village, 1040 m, 4.IV.2003, *Suleiman 1088* [*c.fr*.] (BO, BORH!). **Sumatra:** Taman Nasional Kerinchi-Seblat, Mt. Tujuh, *Ho 05-151*, *05-152* (SING!). **MALAYSIA:** *s.loc*., *s.date*, *Robbins 3673* [*c.fr*.] (KLU!). **Johore:** Mt. Muntahak, 2000 ft [=610 m], 1.III.1928, *Holttum 19915* (SING!). **Kedah**: Jitra, Mt. Jerai (Kedah Peak), 2400 ft [=732 m], 20.VIII.1939, *Spare 2341* (SING!); *ibidem*, 1110 m, 26.VIII.1988, *Sadiah et al*. *113*, *115*, *116a* [*c.fr*.] (KLU!); *ibidem*, 1200 m, 21.VII.1983, *Razali RJ1094* (UKMB!); *ibidem*, 1200–1400 m, 22.IV.2001, *Hanizawati et al*. *2001-22* (UKMB!). **Kelantan**: Dabong, Mt. Stong, 1035–1105 m, 27.V.2003, *Yong 4119*, *4120* [*c.fr*.], *4136* [*c.fr*.], *4146* (KLU!). **Pahang**: Cameron Highlands, 6.VII.1964, *Clear 1138* (KLU!); Cameron Highlands, Tanah Rata, garden of Pelangi Apartment, 1375 m, 5.XII.2004, *Yong & Goh 6112*, *6113*, *6117* (KLU!); Cameron Highlands, Tanah Rata Town, 1400 m, 5.XII.2004, *Yong & Goh 6130* (KLU!); Cameron Highlands, Mt. Brinchang, 1880 m, 27.X.1987, *Mohamed & Zamzuri 1059b* (KLU!); Cameron Highlands, Mt. Jasar, 31.XII.1988, *Damanhuri s.n*. [*c.fr*.] (UKMB!); Cameron Highlands, Tanah Rata, Parit Waterfall, 1420 m, 7.XII.2003, *Yong et al*. *4639* [*c.fr*.] (KLU!); Fraser's Hill, 1100 m, 10.III.2000, *Damanhuri et al. 2000-40* (UKMB!); *ibidem*, 1200–1300 m,7.IV.1995, *Ellis BF9521* [*c.fr*.] (BM!); *ibidem*, 4200 ft [=1280 m], 1.V.1957, *Burkill HMB1194* (SING!); Fraser's Hill, Allan's water, 1200 m, 10.III.2000, *Damanhuri et al. 2000-8* [*c.fr*.] (UKMB!); Fraser's Hill, Buona Vista Road, 4100 ft [=1250 m], 30.IV.1957, *Burkill HMB1176* (SING!); Fraser's Hill, Jelai Tower, 1160 m, 11.III.2000, *Damanhuri et al. 2000-155* (UKMB!); Fraser's Hill, Jeriau Waterfall, 680–820 m, 10.III.2000, *Damanhuri et al. 2000-51* [*c.fr*.], *2000-52*, *2000-54* [*c.fr*.], *2000-56*, *2000-57*, *2000-58*, *2000-59* [*c.fr*.], *2000-63*, *2000-65* [*c.fr*.], *2000-66* [*c.fr*.], *2000-67* [*c.fr*.], *2000-68* [*c.fr*.], *2000-69* [*c.fr*.], *2000-71*, *2000-75* [*c.fr*.], *2000-76*, *2000-77* [*c.fr*.] (UKMB!); Fraser's Hill, RHB bungalow, 1100 m, 10.III.2000, *Damanhuri et al. 2000-100* (UKMB!); Fraser's Hill, The Quest, 1120 m, 11.III.2000, *Damanhuri et al. 2000-132* [*c.fr*.] (UKMB!); Fraser's Hill, Ye Old Smoke House, 1120 m, 10.III.2000, *Damanhuri et al. 2000-91*, *2000-96*, *2000-97* (UKMB!); Taman Negara, Merapoh, Mt. Tahan, Bonsai Camp, 1700 m, 15–19.VI.1995, *Ibrahim 343* [*c.fr*.] (KLU!); *ibidem*, 14.VI.1999, *Yong 1099* [*c.fr*.] (UKMB!). **Penang**: Penang Hill, 600 m, XI.1979, *Mohamed 199* (KLU!); Penang Hill, Convalescent Bungalow, 730 m, 21.VIII.2005, *Mohamed & Yong 6520*, *6527* (KLU!). **Sabah:** Crocker Range National Park, Papar, alt. 1150 m, 2.IX.2002, *Akiyama Crocker-176* [*c.fr*.] (BORH! HYO); Long Miao, 1238 m, 24.III.1999, *Ibrahim AI436* (SING!); Mt. Tingkar, 4.IX.1999, *Ibrahim & Kiew AI631 & AI636* (SING!); Ranau, Kinabalu Park, Mt. Kinabalu, Sayap, 860 m, 4.VI.1992, *Mohamed 4550c* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Mt. Tambuyukon, 1400 m, 14.VIII.2008, *Suleiman 3614* [*c.fr*.], *3646* (BORH, KLU! SNP); Sandakan, Telupid, Ulu Tungud Forest Reserve, Maliau Range, 700 m, 4.V.2005, *Andi 238* (KLU!); *ibidem*, 1000 m, 4.V.2005, *Andi 254* (KLU!); Tawau, Maliau Basin, *Eucalyptus* Camp, 980–1100 m, 16–24.VI.2006, *Mohamed & Yong 6806* [*c.fr*.], *7332*, *7405* (KLU!). **Sarawak**: Kubah National Park, Mt. Serapi, 700 m, 21.VII.1991, *Mohamed & Bakar 3114c*

(KLU!); Miri, Mulu National Park, 100–200 m, 12.V.2004, *Mohamed & Yong 5380* (KLU!). **Selangor:** Genting Highland, 1000 m, 29.VIII.1991, *Mohamed 8864* (KLU!); Genting Highland, water reservoir near Genting Resort, 1240 m, 16.XII.1983, *Damanhuri 3604* (UKMB!). **PAPUA NEW GUINEA. West Sepik:** Frieda River Base Camp at Horse Creek, 400 m, 1.VIII.1981, *Koponen 34863* (NY!). **PHILIPPINES. Luzon:** Bataan, top of Mt. Mariveles, *s.date*, *Borden 740* (NY!); Bataan, Upper Lamao, 2.I.1904, *s.coll. 822* [*c.fr.*] (NY!); Upper Ramos River, 1070 m, I.1904, *Williams 822* [*c.fr.*] (NY!). **Mindanao:** Misamis Oriental, Mt. Lumot, SW of Gingoog City, Barangay Lunutan, 1140 m, 24.VIII.1999, *Schumm & Schwarz 4020*, *4133* (SING!); Misamis Occidental, Mt. Malindang, 2070 m, I.2004, *Azuelo 286* (SING!). **Palawan:** *s.loc.*, II.1906, *Curran 3886* (NY!).

5. *Macromitrium densum* Mitt. (Figs. 5.21 & 5.22)

J. Proc. Linn. Soc., Bot., Suppl. 1: 51 (1859). TYPE: Nepal, *Wallich s.n.* (holotype NY!).

M. brevissimum Dixon, J. Siam Soc., Nat. Hist., Suppl. 9: 19 (1932), ***syn. nov***. TYPE: Thailand, Udawn, Nakawn Panom, Muk Dahan, on rock in open deciduous forest, 200 m, II.1924, *Kerr 74* (holotype BM!).

Plant small to medium-sized, forming short-cushion or mats; shoots olive-green to brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5 cm tall and 2–3 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender, triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, densely arranged, distinctly funiculate with leaves spirally wound around branch, each leaf flexuose-twisted (when dry), erect-

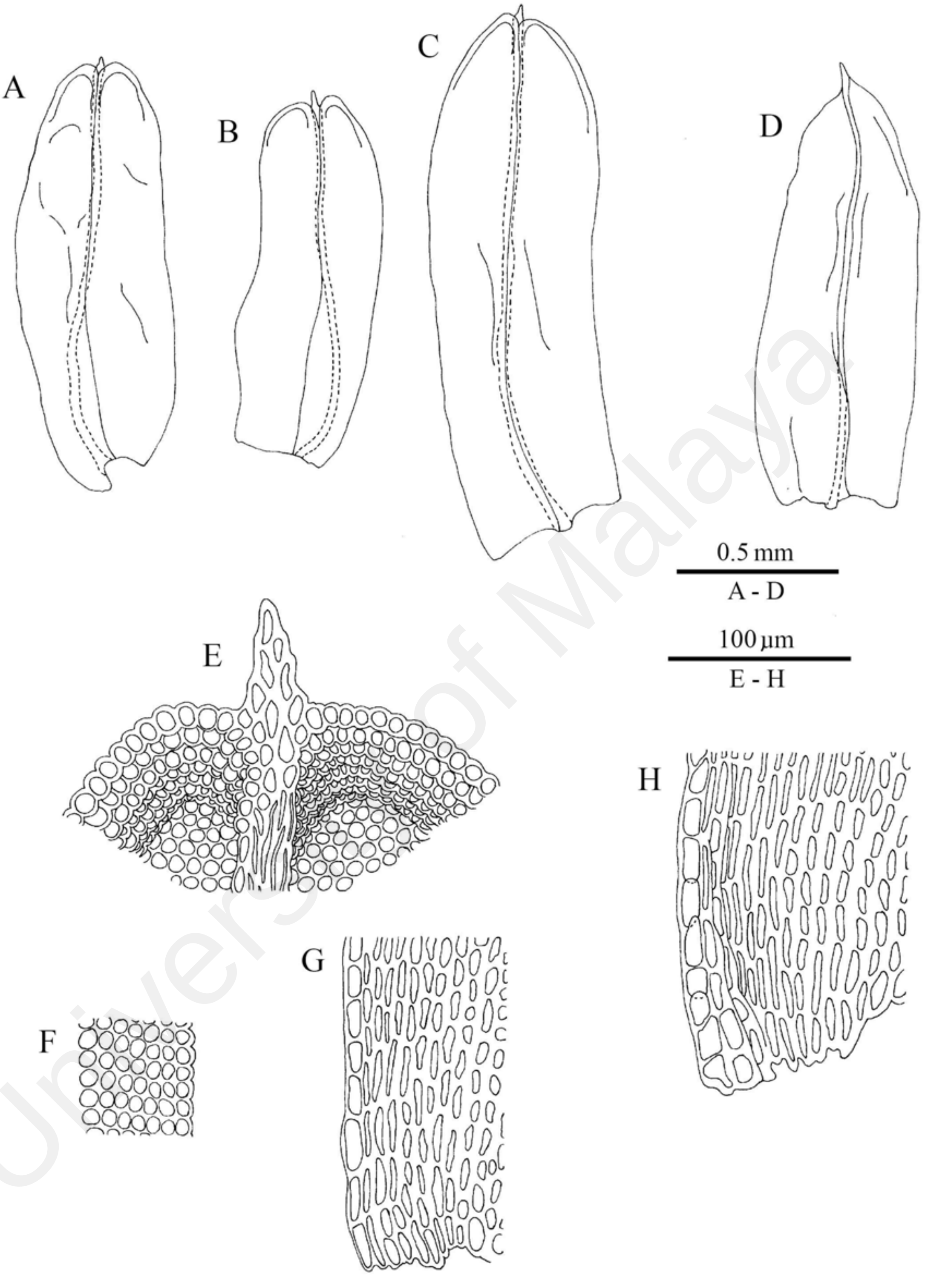

Figure 5.21. Illustrations of *Macromitrium densum* Mitt. — A-C, branch leaves; **D,** perichaetial leaf; **E,** leaf apex; **F,** upper laminal cells; **G-H,** basal laminal cells. [**A, D-G** from *Kerr 74* (BM); **B** from *Kerr 73* (BM); **C & H** from *Damanhuri 99-179* (UKMB)]

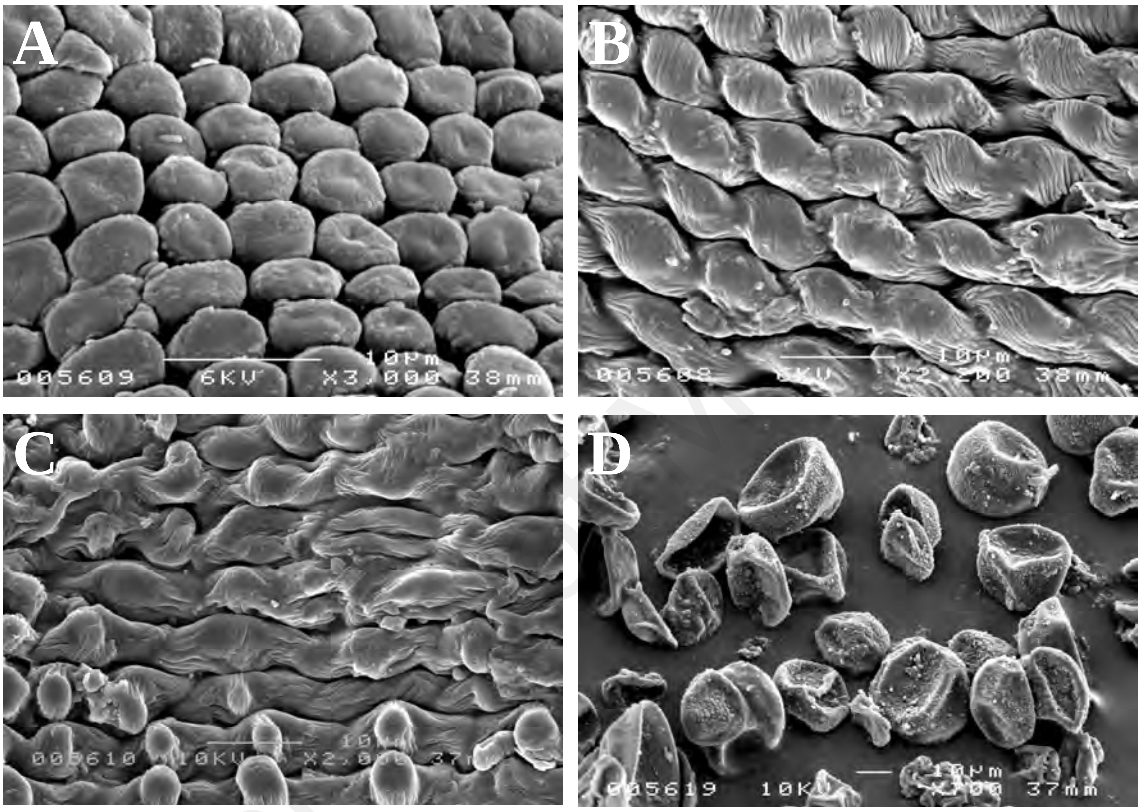

Figure 5.22. SEM images of *Macromitrium densum* Mitt. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** spores. [All from *Kerr 74* (BM)]

spreading to wide-spreading (when moist); branch leaves 1.0–1.4(–1.8) × 0.4–0.6 mm, length-width ratio 2–3:1, oblong-lanceolate to short-lingulate, with margins parallel from apex to leaf base, lamina gently bent, upper lamina concave but plane below; apex firm, broad, cucullate, obtuse to retuse with distinctive mucronate end; margin crenulate, incurved at apex, plane at mid-leaf but deflexed at base; costa short-excurrent with 1–2 cells extending beyond the tip, forming a sharp mucro. Upper laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, oblate to quadrate, moderately thick-walled, not pitted, strongly bulging, smooth, lumina oval; middle laminal cells 10–16 × 10–12 µm, grading from short-rectangular to gradually elongate toward the basal lamina, incrassate, not pitted, with square to rectangular lumina, cells strongly bulging, smooth, clear; basal laminal cells 10–32(–40) × 8–10 µm, length-width ratio 1–3:1, short- to long-rectangular, longer cells confined to region before leaf insertion, incrassate, walls evenly thickened, lumina 4–6 µm wide, linear, not pitted, cells strongly bulging, unipapillose to tuberculate.

Pseudoautoicous, if dwarf male plants present, bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, achieving the size of branch leaves, 1.3–1.5 × 0.4–0.6 mm, oblong-lanceolate, upper lamina broad, plane, leaf base without distinct plications; apex acute-apiculate; margin subentire, plane; costa short-excurrent, with 1–2 cells extending beyond the tip; laminal cells distinctively incrassate with oval to long-rectangular lumen, pitted only at basal lamina. Vaginula 0.9–1.0 mm long; paraphyses 0.4–0.6 mm long, made of 6–10 short- or long-rectangular cells, scarce, scattered on vaginula. Seta 7–9 mm long, smooth, sinistrorse-twisted. Capsule urns 1.2–1.4 × 0.9–1.0 mm, short-ovoid to ellipsoid, smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 4–6, cryptoporous; operculum rostrate, beak 0.7–0.9 mm. Peristome single. Exostome teeth fused into a continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal and ventral side of teeth reticulate-papillose, papillae simple; remains of original cell-wall visible on both side of teeth, marked by low and thin trabeculae. Endostome absent. Spores anisomorphic, larger spores 34–40 µm in diameter, smaller spores 22–24 µm in diameter. Calyptra mitrate, plicate, naked, calyptra base fringed or lacerated.

Other descriptions and illustrations: Gangulee (1976) p. 1175, fig. 569.

Distribution: As. 3: India, Myanmar, East Nepal, Thailand (Northern, Northeastern, Southeastern), Vietnam; As. 4: Malaysia (Malay Peninsula).

Habitat and ecology: Epiphytic on tree trunks and branches, or found on granitic rocks or sandstones, usually in rather open areas. The species is only known in low-elevation sites, from sea level to 600 m.

Notes:

1. Just like many other *Macromitrium* species, *M. densum* is very variable in terms of plant and leaf size. However, the species can easily be recognized by its cucullate leaf apex which is unique to the species. Together with its almost-parallel leaf margins and short-mucronate leaf apex, this species cannot be confused with its congeners. Interestingly, *M. densum* was only documented for northern India and Indochina prior to the present study. The discovery of this species in Perlis, in the extreme northwest of Peninsular Malaysia, appears to be its southernmost limit.

2. The plant was thought to be endemic to eastern Nepal (Gangulee, 1976), until 1932 when it was collected in Thailand as *M. brevissimum* (Dixon, 1932b). In fact, the species is common in Indochina (Noguchi, 1972) but there it has been often mistaken for *M. concinnum* Mitt. ex Bosch & Lac. (synonymous to *M. blumei* in the present study). Other than its cucullate leaf apex, this species is similar to *M. blumei* in plant size, branch leaf shape and its bulging and smooth upper laminal cell features.

<u>Specimens examined</u>:

MALAYSIA. Perlis: Wang Kelian, Wang Mu Forest Reserve, trail to Bukit Pelarit, 220–553 m, 2.X.1999, *Damanhuri 99-179* (UKMB!). **NEPAL:** *s.loc*., *s.date*, *Wallich s.n*. (holotype of *M. densum*: NY!). **THAILAND. Payap:** 20 km N of Bo Luang near Ban Om Khut, 6.VII.1968, *Larsen et al. 2224* [*c.fr*.] (NY!); Chiengmai, Doi Sutep, Dry, dipterocarp forest, on tree, common, 30.IX.1958, *Serensen at al. 5362* [*c.fr*.] (NY!). **Phitsanulok:** Tung Salaeng Luang, 500 m, on boulders near streams, 24.VII.1966, *Larsen et al 860* (NY!). **Rachasima:** Buriram, Nang Rawng, 200 m, I.1924, Kerr 73 (BM!) (identified as *M. brevissimum* by Dixon). **Udawn:** Loi, Dan Sai, 600 m, III.1924, Kerr 100 (BM!) (identified as *M. brevissimum* by Dixon); Nakawn Panom, Muk Dahan, 200 m, II.1924, *Kerr 74* (holotype of *M. brevissimum*: BM!). **VIETNAM:** Yokdon National Park, Daklak, 26.VII.02, *Huong H050* (SING!)

6. *Macromitrium falcatulum* Müll. Hal. (Figs. 5.23 & 5.24)

Linnaea 38: 558 (1874). LECTOTYPE (Vitt et al., 1995): Insulae Philippinae, *Cuming 2212* (NY! isolectotype BM).

M. merrillii Broth., Öfv. Finska Vet.-Soc. Förh. 47 (14): 4 (1905). TYPE: Philippines, Luzon, Tarlac, Concepcion, on branches of *Palaquim latifolium*, *Merrill 3590* (holotype H-BR; isotype NY!) — fide Bartram (1939).

M. winkleri Broth. in Winkler, Bot. Jahrb. 49: 350 (1913). LECTOTYPE (Vitt et al., 1995): SO-Borneo, Hayup, *Winkler 2117* (H-BR; isolectotype H-BR) — fide Vitt et al. (1995).

M. brevirete Dixon, Gard. Bull. Straits Settlem. 4: 18 (1926), *nom nud*.

Plant small, forming cushions or mats; young shoots yellowish-green, gradually turning rusty-brown when mature, brownish to darker below. Stems creeping, covered by

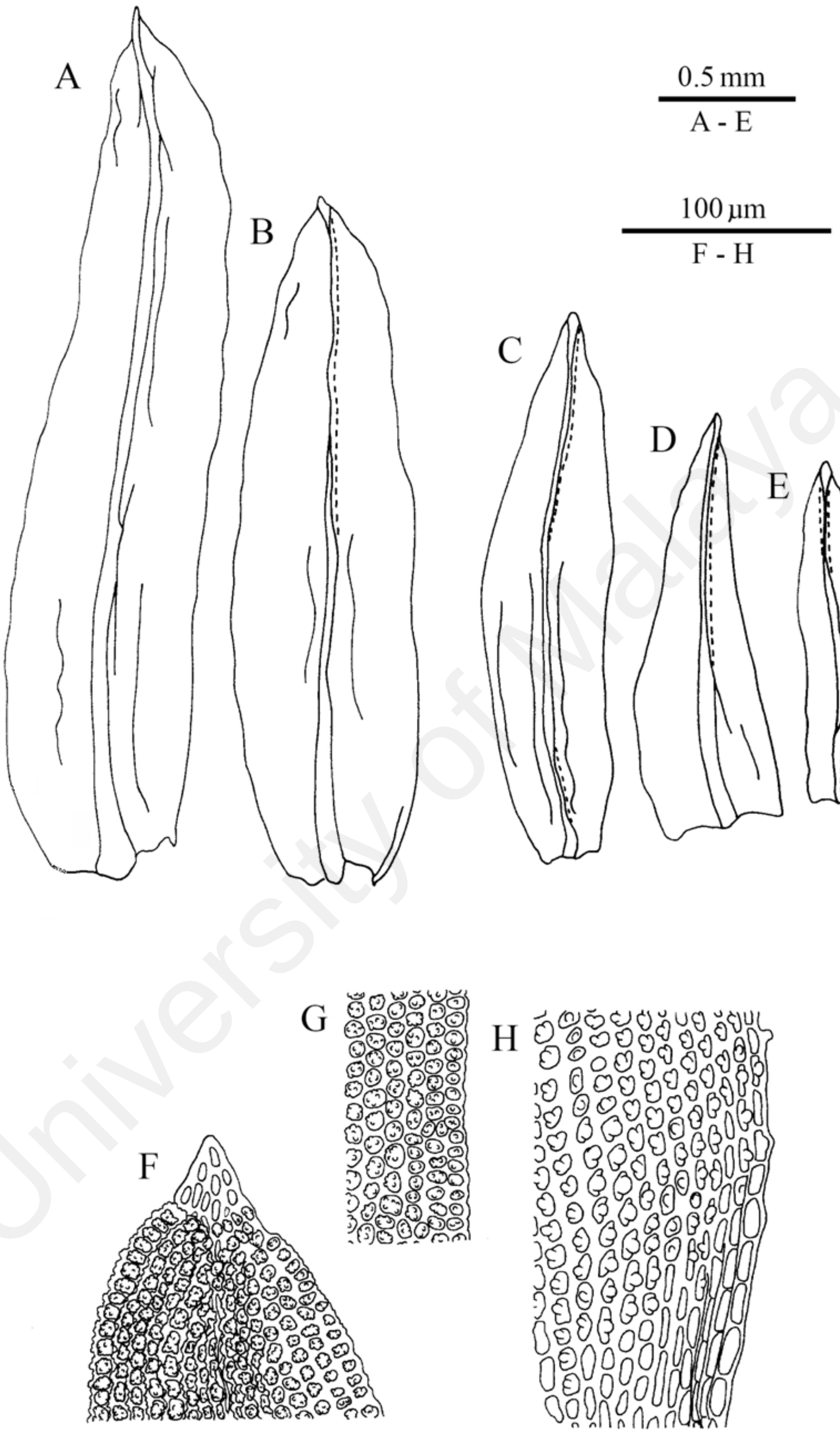

Figure 5.23. Illustrations of *Macromitrium falcatulum* Müll. Hal. — A-B, branch leaves; **C-E,** perichaetial leaves (left to right, from outer to innermost positions); **F,** leaf apex; **G,** mid-leaf cells; **H,** basal laminal cells. [All from *Damanhuri 97-1232* (UKMB)]

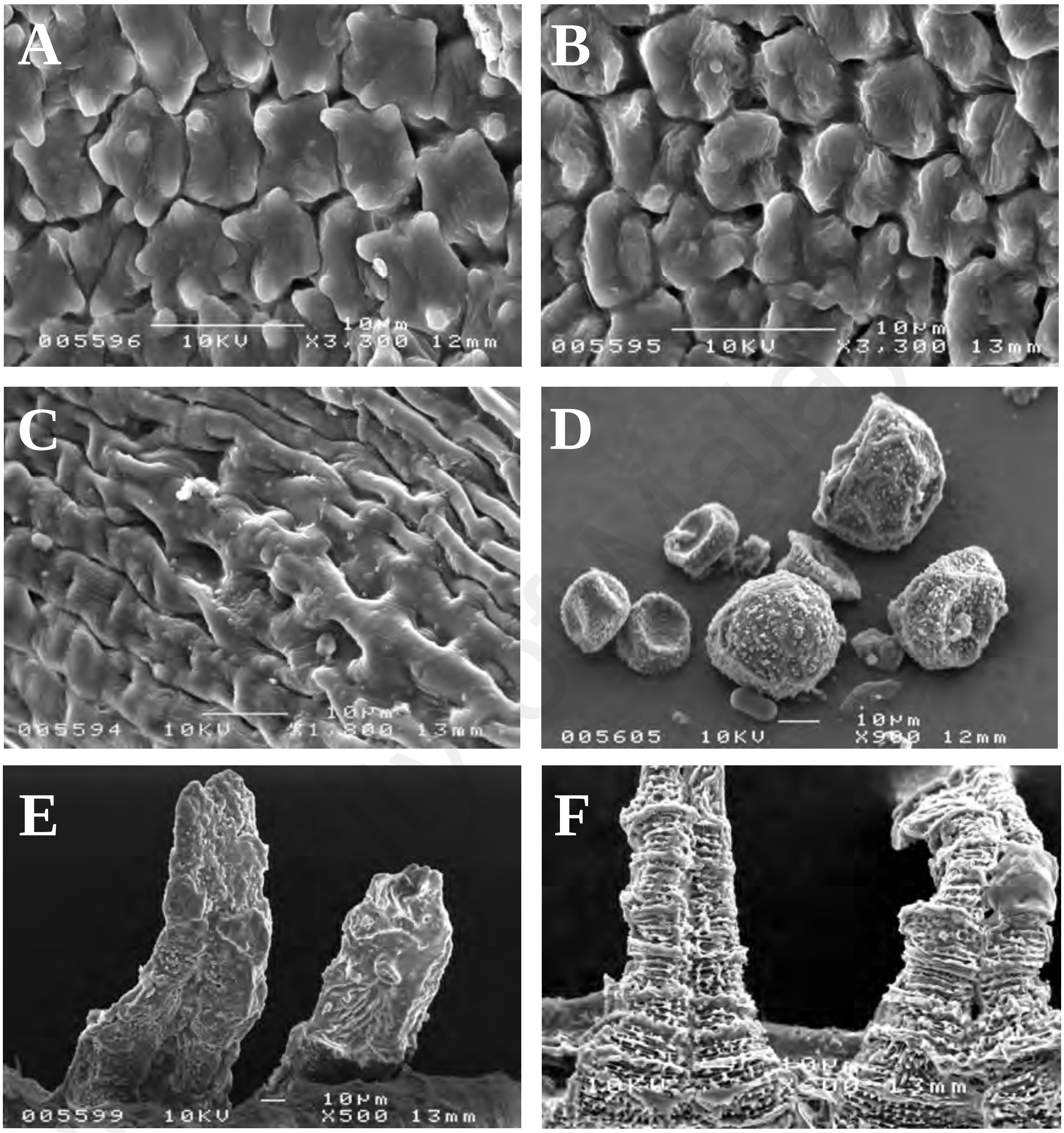

Figure 5.24. SEM images of *Macromitrium falcatulum* Müll. Hal. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** spores; **E,** dorsal view of peristome teeth; **F,** ventral view of peristome teeth. [All from *Burkill 17467* (SING)]

rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches generally short, 0.5–1 cm tall and 1.0–2.5 mm wide, loose or tightly arranged, rarely branched. Stem leaves inconspicuous, small, covered by rhizoids, triangular-lanceolate on young shoots, becoming lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, leaves twisted-contorted, tightly inrolled, often compact, apices almost all hidden by the strongly involute laminae (when dry), erect-spreading to wide-spreading (when moist); branch leaves 1.4–1.8 × 0.3–0.4 mm, length-width ratio 4–5:1, slender lanceolate to linear-lanceolate with an oblong base, lamina straight, plane; apex firm, broadly acute to mucronate; margin subentire to crenulate, plane at distal part but reflexed at base; costa short-excurrent with 1–2 cells extending beyond the tip. Upper and middle laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, rounded to oblate, moderately thick-walled, walls not pitted, cells bulging, pluri-papillose, papillae generally low; basal laminal cells mostly oblate to short-rectangular, 12–15 × 8–12 µm, length-width ratio 1–1.5:1, cells bulging, mostly unipapillose, incrassate, walls evenly thickened, rarely thicker than lumen width, lumina 8–10 µm wide, pitted only near juxtacostal region and insertion, longer cells only restricted to the 3–4 rows before leaf insertion and toward leaf margin, 14–20 µm in length, cells flat and smooth.

Pseudoautoicous, dwarf male plants bud-like, small, perigonial leaves 0.2–0.3 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, usually smaller than branch leaves, 1.0–1.1 × 0.2–0.3 mm, typically lanceolate to broad-laceolate, leaf base often with a few long-plications; apex acute to acuminate; margin subentire to entire, plane; costa percurrent or short-excurrent with 1–2 cells extending beyond the tip; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula

0.9–1.4 mm long; paraphyses abundant, densely covering the vaginula, 0.4–0.5 mm long, made of 8–10 short to long-rectangular cells. Seta 3–5 mm long, smooth, dextrorse or sinistrorse-twisted. Capsule urns 1.2–1.4 × 0.7–0.9 mm, short-ovoid to ellipsoid, smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.7–0.9 mm. Peristome single. Exostome of 16 teeth that are separated above but connected at their base as a low membrane, erect to slightly incurved at top in both dry and wet conditions; dorsal side of teeth rough, "coralloid", with wart-like to simple papillae irregularly distributed, papillae sometime confluent into vertical or diagonal ridges; ventral side of teeth horizontally striolate-papillose with simple to compound papillae, on distinctly raised horizontal ridges; remains of original cell-wall obscure on dorsal side, but marked by thickened trabeculae on ventral side. Endostome absent. Spores anisomorphic, larger spores 32–46 µm in diameter, smaller spores 18–24 µm in diameter. Calyptra mitrate, plicate, densely haired, hairs short, stiff erect, freely distributed on calyptra, hairs twisted only near to calyptra base, base fringed or lacerated.

Other descriptions and illustrations: Bartram (1939) p. 174–175, pl. 13, fig. 215; Vitt et al. (1995) p. 32–33, figs. 1b, 14; Eddy (1996) p. 38–40, fig. 352.

Distribution: As. 3: Thailand (Northern), Vietnam; As. 4: Indonesia (Borneo, West Irian), Malaysia, Papua New Guinea, Philippines (Bataan, Luzon, Mindanao, Palawan).

Habitat and ecology: Epiphytic on tree trunks and branches. In Malaysia, the species is only found in lowland rainforest, although elsewhere it has been reported at 500–2000 m and in rather open habitats, such as savannah forests (Eddy, 1996).

Notes:

1. The small to medium plant size, distinctly convex leaf cells that are pluripapillate on the upper lamina but unipapillate at the leaf base, and densely pilose calyptra easily

distinguish this species from others. However, in Peninsular Malaysia, *M. falcatulum* is also distinctive by its peculiar plant habit, forming many short-monopodial branches with tightly inrolled leaves and neatly arranged on long-creeping stems (this form is, strangely, not consistent in other provenances).

2. Although both dextrorsely and sinitrorsely twisted setae were encountered together in many populations in some Southeast Asian material during the present study, only dextrorsely twisted seta have been documented for New Guinea (Vitt et al., 1995). However, other taxa, viz., *M. longipilum*, *M. nepalense*, *M. parvifolium*, are also known with setae twisted left or right at random. Hence, seta twisting appears not to be reliable for identifying species.

3. Tan (2005) considered this species closely resembling *M. japonicum* Dozy & Molk., a species common in the East Asiatic region with its westernmost extent in Sri Lanka. In the present study, it has been possible to distinguish *M. falcatulum* from *M. japonicum* by its acute leaf apex, compared to the usually blunt to obtuse leaf apex of *M. japonicum*. In addition to this, the perichaetial leaves of *M. falcatulum* are generally small, lanceolate and acute to acuminate, whereas those of *M. japonicum* are large and subulate-lanceolate, with slender elongate apices.

Specimens examined:

MALAYSIA. Johore: Endau-Rompin, Mt. Tiong, 480 m, 25.VII.2002, *Yong & Sabda 2607* (KLU!). **Kelantan**: Taman Negara, Kuala Koh, 200 m, 12.IX.1999, *Yong 1737* (KLU!). **Pahang**: Gua Kechil limestone, 1000 ft [=305 m], 21.VI.1971, *Chin 1185* (KLU!); Jerantut, 7.XII.1924, *Burkill 17467* (original material of *M. brevirete*: SING!); Taman Negara, Merapoh, Sg. Juram, 9.V.1997, *Damanhuri 97-1232* (KLU! UKMB!). **Perak**: Ulu Perak, Belum Forest Reserve, 300–598 m, 18.V.1998, *Damanhuri 98-62* (UKMB!); *ibidem*, 250–420 m, 24.V.1998, *Damanhuri 98-478* (UKMB!); Ulu Perak, Belum Royal Park, Sg. Kenarong area, 200–300 m, 27.VII.2003, *Yong 4332* (KLU!).

Sarawak: *s.loc*., II–VI.1914, *s.coll*. *2725* (NY!). **Selangor**: Langat Basin, Mt. Nuang, 200 m, 24.IV.1997, *Damanhuri & Ahmad 97-374* (UKMB!). **PHILIPPINES:** *s.loc*., *s.date*, *Cuming 2202?* (BM!); *s.loc*., *s.date*, *Cumming 2212* (lectotype of *M. falcatulum*: NY!). **Alabat:** *s.loc*., 21–30.XII.1916, *Merrill 10559* [*c.fr*.] (NY!). **Luzon:** Bataan, Samal, Palili, So. Pilis, 410 m, VI.2004, *Linis 922-04* (SING!); Lamao river, 90 m, I.1904, *Williams 821* [*c.fr*.] (NY!); Rizal, VIII.1913, *Ramos 21343* [*c.fr*.] (NY!); Tarlac, XI.1908, *Merrill 3590* (isotype of *M. merrillii*: NY!); Tayabas, Kabibihan, III.1911, *Foxworthy & Ramos 13149* [*c.fr*.] (BM! NY!); Tayabas, Mt. Pular, I.1913, *Ramos 19396* [*c.fr*.] (NY!). **Mindanao:** Zamboanga, Banga, XI–XII.1907, *Whitford & Hutchinson 9047* [*c.fr*.] (BM! NY!); *ibidem*, XI–XII.1907, *Whitford 9098* [*c.fr*.] (NY!). **Palawan:** Taytay, IV.1913, *E.D. Merrill 8991* [*c.fr*.] (NY! TNS!).

7. *Macromitrium fuscescens* Schwägr. (Figs. 5.25, 5.26 & 5.27)

Sp. Musc. Frond. Suppl. 2, 2 (2): 129, tab. 191 (1827). LECTOTYPE (Vitt et al., 1995): In insulis Marianis lectum misit, *Gaudichaud s.n*. (G; isolectotypes BM! G).

M. semipellucidum Dozy & Molk., Ann. Sci. Nat., Bot. sér. 3 (2): 311 (1844). LECTOTYPE (Vitt et al., 1995): Borneo et Java, *Korthals s.n*. (L; isolectotypes BM! BM! L) — fide Vitt et al. (1995).

M. calvescens Bosch & Sande Lac., Bryol. Jav. 1: 125, tab. CIII (1860). LECTOTYPE (Vitt et al., 1995): Java, prope Tjiburrum, *Hasskarl s.n*. (L) — fide Vitt et al. (1995).

M. glaucum Mitt., J. Linn. Soc., Bot. 10: 167 (1868). LECTOTYPE (Vitt et al., 1995): Samoa, Tutuila, forming extensive mats on Breadfruit trees nearly at sea-level, *Powell 109* (NY! isolectotypes NY) — fide Vitt et al. (1995).

Plant small to medium-sized, forming cushions or mats; young shoots yellowish-green,

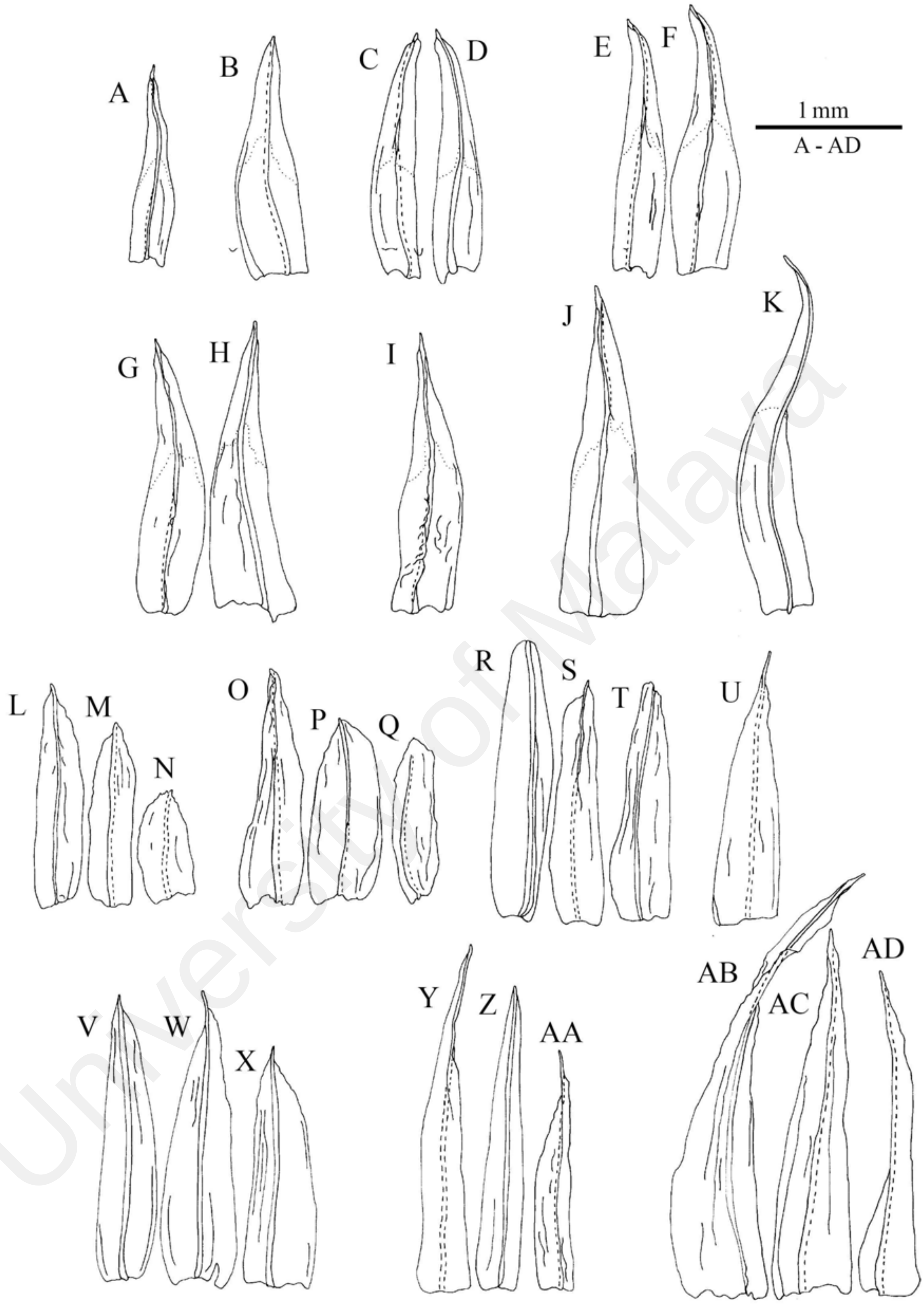

Figure 5.25. Illustrations of *Macromitrium fuscescens* Schwägr. — A-K, branch leaves; **L-AD,** perichaetial leaves (left to right, from outer to inner most position) [**A, K, Y-AA** from *Henderson 19757* (SING); **B, L-N** from *Ridley 178* (SING); **C-D, O-Q** from *Mohamed 9290* (KLU); **E-F, R-T** from *Yong 6613* (KLU); **G-H, V-X** from *Selina s.n.* (KLU); **I, U** from *Henderson 19694* (BM); **J, AB-AD** from *s.coll. B1034* (KLU)]

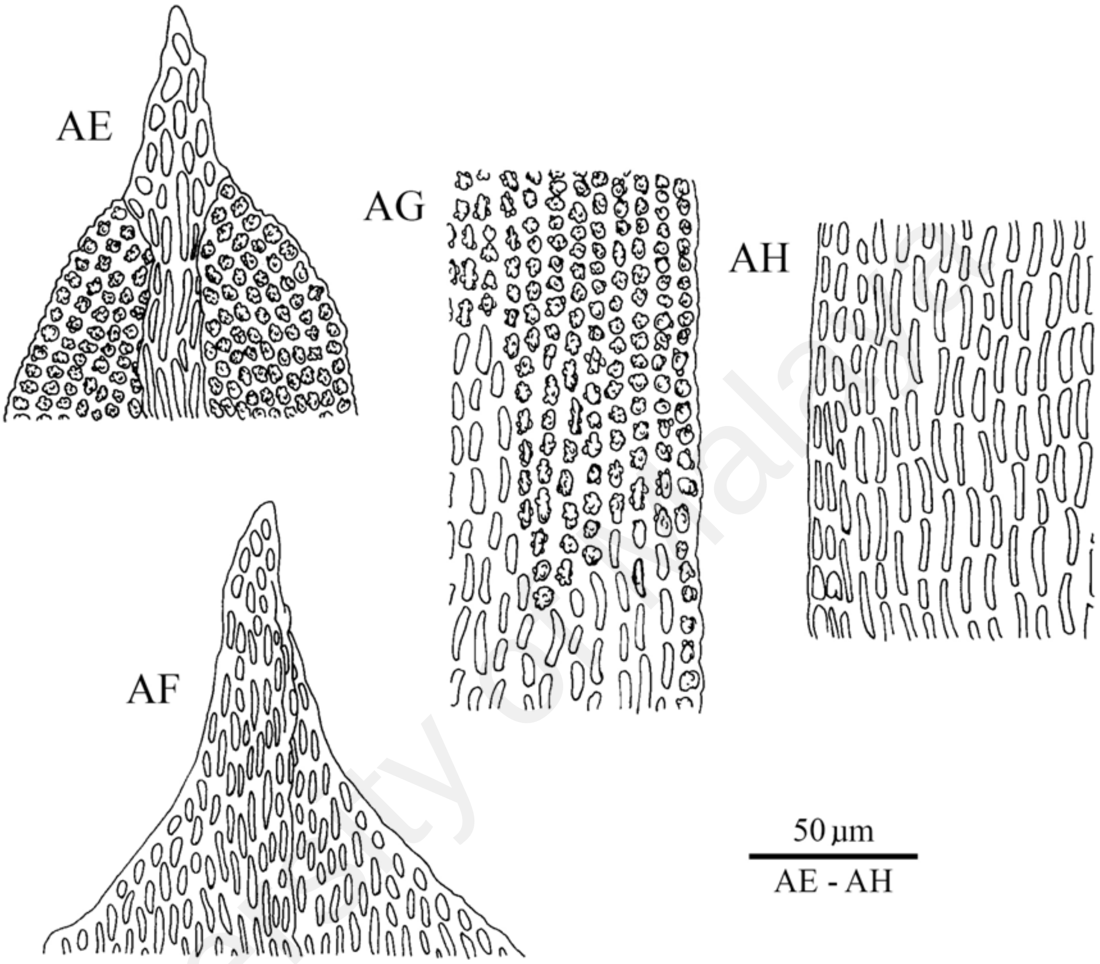

Figure 5.26. Illustrations of *Macromitrium fuscescens* Schwägr. — AE, leaf apex; **AF,** perichaetial leaf apex; **AG,** mid-leaf cells; **AH,** basal laminal cells. [**AE-AH** from *Selina s.n.* (KLU)]

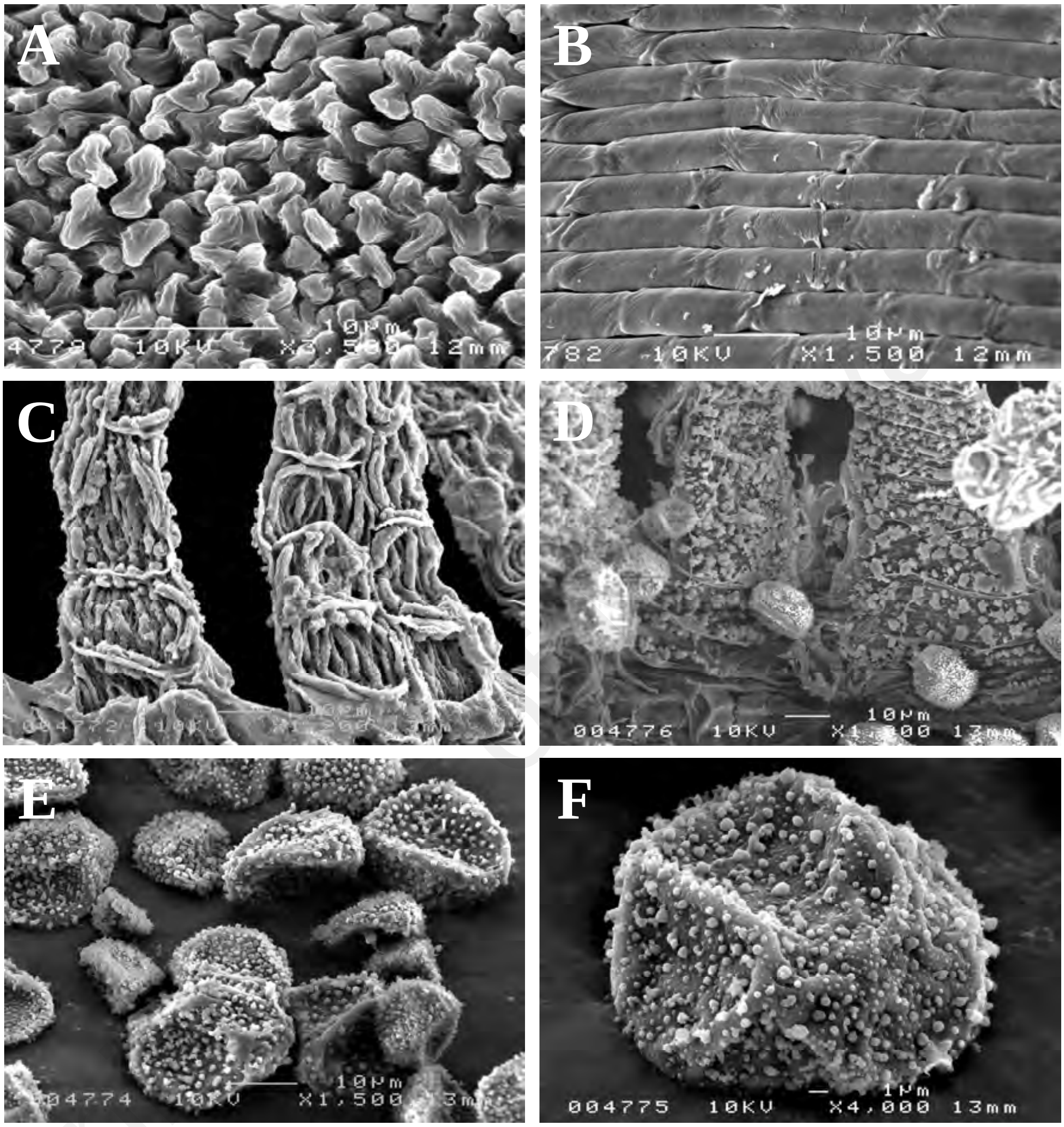

Figure 5.27. SEM images of *Macromitrium fuscescens* Schwägr. — A, upper laminal cells; **B,** basal laminal cells; **C,** dorsal view of peristome teeth; **D,** ventral view of peristome teeth; **E,** spores; **F,** detail of a microspore [All from *Mohamed & Yong 6571* (KLU)]

gradually turning to olive-green and brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5–1.5 cm tall and 1.5–3.0 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate on young shoots, becoming more lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, always densely arranged, indistinctly funiculate with leaves irregularly twisted, with incurved to inrolled apices (when dry), erect-inflexed to wide-spreading with straight or weakly incurved apices (when moist); branch leaves (1.3–)1.5–2.1(–2.4) × 0.4–0.6(–0.8) mm, length-width ratio 3–4:1, broad lanceolate to lingulate-lanceolate with an oblong base, lamina mostly straight, plane; apex firm, slender to rather broad-acuminate, sometime mucronate; margin subentire to crenulate, plane at distal part but reflexed at base; costa percurrent or short-excurrent with 1–2 cells extending beyond the tip. Upper laminal cells 5–6 × 5–6 µm, length-width ratio 1:1, rounded, oblate to short- or wide-rectangular, evenly incrassate, walls not pitted, cells flat, densely pluri-papillose, obscure; middle laminal cells 7–20 × 6–9 µm, abruptly grade from obscure, short, densely papillose cells into clear, long and smooth cells near mid-leaf, forming a more-or-less demarcated line between upper and basal lamina; basal laminal cells 24–36(–40) × 8–12 µm, length-width ratio 3–4:1, long-rectangular, incrassate, walls unevenly thickened, lumina 2–3 µm wide, strongly curved to sigmoid in appearance, pitted only near juxtacostal region and insertion, cells flat, smooth.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.3–0.4 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, about the size or larger than branch leaves, leaf shorter toward inner position, 1.2–2.2 × 0.5–0.7 mm, lingulate, oblong-laceolate to triangular-lanceolate, upper lamina often broad, with parallel margins or expanding gradually toward mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender acuminate to more commonly broadly acute or obtuse; margin subentire to entire, plane; costa percurrent or ending below leaf apex; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 0.8–1.0 mm long; paraphyses abundant, densely covering the vaginula, 0.5–0.8 mm long, made of 10–16 short to long-rectangular cells. Seta 5–7 mm long, smooth, dextrorse-twisted. Capsule urns 1.2–1.4 × 0.9–1.1 mm, short-ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.8–1.1 mm. Peristome single. Exostome of 16 teeth that are separated above but connected at their base as a low membrane, erect to slightly recurved at top in both dry and wet conditions; dorsal side of teeth vertically striolate-papillose with wart-like to relatively large, simple papillae, scattered on coarse vertical ridges; ventral side of teeth horizontally striolate-papillose with small to relatively large, compound papillae, on thin horizontal ridges, or sometime on irregular reticula; remains of original cell wall distinctive on both sides of teeth, marked by tall and thick trabeculae on dorsal side but by tall and filmy trabeculae on the ventral. Endostome absent. Spores anisomorphic, larger spores 22–25 µm in diameter, smaller spores 14–16 µm in diameter. Calyptra mitrate, plicate, sparsely hairy, hairs long, stiff erect and mostly on ridges near to the calyptra base, calyptra base fringed or lacerated.

Other descriptions and illustrations: Müller (1849) p. 743 as *M. semipellucidum*; Dozy & Molkenboer (1861) p. 127–128, tab. 105 as *M. semipellucidum*; Fleischer (1904) p. 437–439 as *M. semipellucidum*; Bartram (1939) p. 178, pl. 13, fig. 221, as *M. semipellucidum*; Vitt et al. (1995) p. 33–36, fig. 15; Eddy (1996) p. 52, fig. 365 as *M. semipellucidum*.

Distribution: As. 3: Sri Lanka, Thailand (Peninsula), Vietnam; As. 4: Indonesia (Borneo, Java, Sulawesi, Sumatra, West Irian), Malaysia (Borneo, Malay Peninsula), Papua New Guinea, Philippines (Luzon, Mindanao, Panay); Oc.: Guam, Hawaii, Samoa, Society Islands, Solomon Islands.

Habitat and ecology: Epiphytic on tree trunks and lower branches or occasionally on rocks and boulders. The species is also often collected from tree buttresses and rotten logs. It is found below 1500 m, mostly near sea level, and is very common in lowland forest and on garden trees at or above mid-montane elevations. It has also been collected from several limestone sites in Malaysia.

Notes:

1. *Macromitrium fuscescens* is the commonest *Macromitrium* in Malaysia, and known to be highly polymorphic. In general, the species is recognized by its a) broad-lanceolate to lingulate-lanceolate branch leaves that are irregularly twisted-contorted when dry, but spreading when moist; b) short and densely papillate upper lamina cells that abruptly transition into long and smooth basal laminal cells at mid-leaf; c) short and smooth seta; d) sparse-hairy calyptra.

2. In general, two forms of branch leaves are found in this species, viz., a) short oblong-lanceolate leaves with broadly acute apex, b) long, slender-lanceolate leaves with relatively narrow apex that ends in an acute point. Leaf variation is continuous and cannot justify placement of taxa in separate varieties, although specimens with the latter leaf form have usually been identified as *M. semipellucidum* (a synonym) and were also easily confused with *M. incurvifolium*.

3. *Macromitrium fuscescens*, most abundant in the lowlands, resembles a smaller form of the typically higher-elevation *M. salakanum*. The more slender forms of *M. fuscescens* have some resemblance to *M. incurvifolium*, another lowland species. The abrupt transition from short-pluripapillate upper laminal cells into long-smooth basal

laminal cells at the mid-leaf region reliably distinguishes *M. fuscescens* from these other species. Other characters may not be so reliable to use. For example, the subtriangular perichaetial leaves in *M. fuscescens* are usually larger than those of *M. incurvifolium* and very different from those in *M. salakanum* in shape and size. However, perichaetial leaves of *M. fuscescens* are as variable as vegetative leaves (Fig. 5.23) and have been inconsistently described by different authors (e.g., Vitt et al., 1995; Eddy, 1996).

4. Vitt et al. (1995) synonymized *M. miquelii* under the present species. However, the original descriptions (Dozy & Molkenboer, 1861) and illustrations of *M. miquelii* show that the upper laminal cells gradually (not abruptly) transition into basal laminal cells at the mid-leaf region. Also, the relatively large perichaetial leaves with rather blunt apices in *M. miquelii* (Dozy & Molkenboer, 1861) more resembles that of *M. salakanum*. Therefore *M. miquelii* has been excluded from the synonymy of *M. fuscescens* in the present study.

<u>Specimens examined</u>:

INDONESIA. Ambon: *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe* [*c.fr*.] (BM!). **Java:** *s.loc*., *s.date*, *s.coll*. [*c.fr*.] (NY 2 sheets!); *s.loc*., *s.date*, *Korthals s.n*. [*c.fr*.] (BM!); Megamendong, *s.date*, *Motley s.n*. [*c.fr*.] (NY!); Megamendong, 25–4500 ft [=762–1372 m], *s.date*, *Kurz 481* [*c.fr*.] (BM!). **Kalimantan:** *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Bescherelle* (BM!); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe ex Lacoste* [*c.fr*.] (BM!); *s.loc*., *s.date*, *Korthals s.n*. [*c.fr*.] (isolectotypes of *M. semipellucidum*: BM 2 sheets!); Kalangau, 1858, *Motleyi 25* [*c.fr*.] (NY!). **Sulawesi**: Tanah Toraja, about 2 km south Rentepoa, Mt. Kongkang limestone, 800–1000 m, 17.VI.1986, *Chin 3645* [*c.fr*.] (KLU!). **Sumatra:** Nias, 1924, *Pieper 26* (BM!); Padang Pandjang, 800 m, IX.1929, *Jacobson s.n*. (SING!). **MALAYSIA. Johore**: Endau Rompin, Mt. Tiong, 480 m, 25.VII.2002, *Yong & Sabda 2599*, *2600*, *2602* (KLU!). **Kedah**: Gulau, Ulu Muda Forest Reserve, Compartment 73, 230 m, 28.III.2003, *Yong 3340* (KLU!); Jitra, Mt. Jerai (Kedah Peak), 2.VIII.1988, *Sadiah et al*. *s.n*. (KLU!); Langkawi Islands, Mt. Raya Forest Reserve, 670 m, 16.IV.2003, *Mohamed & Yong 3684* (KLU!). **Kelantan**: Gua Panjang, Gua Ninik, 1000 ft [=305 m], 27.X.1927, *Henderson 19694* [*c.fr*.], *19757* (BM! SING!); Sg. Rek Forest Reserve, 500 ft [=152 m], 3.VI.1982, *Aishah 252* (KLU!); Taman Negara, Kuala Koh, 100 m, 23.V.1999, *Yong & Damanhuri 843* (UKMB!); *ibidem*, 350 m, 12.IX.1999, *Yong 1793b* [*c.fr*.] (KLU!). **Negeri Sembilan:** Pantai, VI.1890, *Ridley 749* (SING!). Pahang: Gua Tipus, 400 m, 10.VIII.1929, *Henderson 22563* (SING!). **Pahang**: Bukit Serdam limestone hill, 1000 ft [=305 m], 19.VI.1971, *Chin 1045* (KLU!); *ibidem*, 20.VI.1971, *Chin 1138* [*c.fr*.] (KLU!); Cameron Highlands, *s.date*, *Mohamed 33* (KLU!); Cameron Highlands, Iskandar Waterfall, 420 m, 6.X.2003, *Yong et al*. *4541* (KLU!); Cameron Highlands, Robinson Waterfall, 1120 m, *s.date*, *Mohamed & Damanhuri 9764* (KLU!); Cameron Highlands, Tanah Rata, 1440–1500 m, 4.VIII.1988, *Mohamed & Damanhuri 1091* (KLU!); Cameron Highlands, Tanah Rata, jungle path no.10, 1500 m, 13.III.2004, *Yong et al*. *4907* (KLU!); Fraser's Hill, *s.date*, *s.coll*. *B1034* (KLU!); Fraser's Hill, Alan's Water, 1180 m, 3.I.2008, *Yong 7475* (KLU!); Fraser's Hill, Jalan Sekolah, 1110 m, 10.III.2000, *Damanhuri et al*. *2000-14* [*c.fr*.] (UKMB!); Fraser's Hill, Temerloh Bungalow, *M.E.D.P*. *s.n*. (KLU!); Genting Highlands, Awana Resort, 1000 m, 4.X.2003, *Yong 4527* (KLU!); Grik-Jeli Highway, Paya Bungor, 40 m, 30.VI.1986, *Mohamed 9290* (KLU!); Gua Tipus, 10.VIII.1929, *Henderson 22563* [*c.fr*.] (KLU! SING!); Sg. Sat, 20.VII.1929, *Henderson 22021* [*c.fr*.] (SING!); Taman Negara, Kuala Tahan, Perkai, 250 ft [=76 m], 20.III.1983, *Razali RJ1533* (UKMB!); Taman Negara, Merapoh, Gua Peningat, 7.V.1997, *Damanhuri & Ahmad 97-944*, *97-954*, *97-985*, *97-1016*, *97-1091*, *97-1123*, *97-1128*, *97-1133* (UKMB!). **Penang**: Penang Hill, Convalescent Bungalow, 730 m, 21.VIII.2005, *Mohamed & Yong 6510* [*c.fr*.], *6517* [*c.fr*.] (KLU!); Penang Hill, Crag Hotel, 665 m, 21.VIII.2005, *Mohamed & Yong 6594* [*c.fr*.] (KLU!). **Perak:** Kuala Kenering, VIII.1909, *Ridley 208* [*c.fr*.] (BM! SING!);

Taiping, *s.date*, *Johnson 382* (SING!); Taiping, Taiping Hill (Maxwell Hill), 1120 m, 7.III.2004, *Mohamed & Yong 4743* (KLU!); Taiping, Taiping Lake, 120 m, 9.III.2004, *Mohamed & Yong 4842* (KLU!); Temengok, VIII.1909, *Ridley 178* (SING!); Ulu Perak, Belum Forest Reserve, Sg. Lebur, 250–420 m, 24.V.1998, *Damanhuri 98-406*, *98-460* [*c.fr*.], *98-462* (UKMB!); Ulu Perak, Belum Royal Park, Sg. Kenarong, 200–300 m, 27.VII.2003, *Yong 4319*, *4320*, *4321*, *4324* (KLU!); *ibidem*, 29.VII.2003, *Yong 4420*, *4422*, *4429*, *4434* (KLU!); *ibidem*, 30.VII.2003, *Yong 4483*, *4490*, *4493* [*c.fr*.], *4494* (KLU!); Upper Perak, Kulim Hot Spring, 14.VI.1930, *Henderson 23861* [*c.fr*.] (SING!). **Sabah**: Danum Valley, Borneo Rainforest Lodge Canopy Walkway, 760 m, 6.IX.1997, *Ellis DAM629* [*c.fr*.] (BM!); Danum Valley, Main Trail West, 760 m, 29.VIII.1997, *Ellis DAM341* [*c.fr*.] (BM!); Lahad Datu, Danum Conservation Area, Sg. Purut, 220 m, 7.VI.1989, *Damanhuri s.n.* [*c.fr*.] (UKMB!); Lahad Datu, Danum Conservation Area, Sg. Sabrau, 220 m,.18.X.1989, *Damanhuri s.n.* [*c.fr*.] (UKMB!); Mt. Tingkar, 4.IX.1999, *Ibrahim & Kiew AI641* (SING!); Ranau, Kinabalu Park, Bukit Tupai Trail, 1460 m, 13.V.2005, *Yong 6440* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, *Damanhuri s.n.* (UKMB!); Sandakan, Telupid, Ulu Tungud Forest Reserve, Maliau Range, 120 m, 4.V.2005, *Andi 196, 326* (KLU! SAN); Sipitang, Mt. Lumaku, Muaya Waterfall, 850 m, 30.VII.2008, *Suleiman 3457* [*c.fr*.] (BORH, KLU!). **Sarawak**: *s.loc*., II–VI.1914, *native collector 2738*, *2740* [*c.fr*.] (NY!); Bau, 100 m, 23.VII.1991, *Mohamed & Bakar 3208b* (KLU!); Bau, Bukit Sarang, 160 m, X.2004, *S.Lee s.n.* [*c.fr*.] (KLU!); Bau, Fairy Cave, 50 m, 16.VII.2005, *Yong 6471* (KLU!); Kuching, near District office, 20 m, *Mohamed 9509* (KLU!). **Selangor:** Klang, Telok Reserve, 28.IX.1921, *Burkill 6613* (SING!). **Terengganu**: Dungun District, Kampung Pasir Raja, Pasir Raja Forest Reserve Compartment 5, 150 m, 6.VI.2004, *Yong 5761* [*c.fr*.], *5762*, *5763*, *5764* [*c.fr*.] (KLU!); Dungun District, Kampung Pasir Raja, Sg. Pertang, 60 m, 27.V.1989, *Mohamed 9688* [*c.fr*.] (KLU!); Dungun District, Mt. Mandi Angin, Pasir Raja Forest Reserve, Compartment 16, Sg. Loh, lowland forest zone, 100 m, 9.VI.2004, *Yong 5985* [*c.fr*.], *6000* [*c.fr*.] (KLU!); Kuala Berang, 14.V.1925, *Holttum 15333* (BM! SING!); Ulu Terengganu District, Hutan Lipur Sekayu, 23.V.1989, *Mohamed 9528* [*c.fr*.] (KLU!); *ibidem*, 31.VIII.1990, *Damanhuri 182* [*c.fr*.], *282* [*c.fr*.] (UKMB!). **MARIANA ISLANDS:** *s.loc*., *s.date*, *Gaudichaud 101* (isolectotype of *M. fuscescens*: BM!); *s.loc*., *s.date*, *s.coll ex Hb. Wilson ex Schwaegrichen H727* (*3*) [*c.fr*.] (?isolectotype of *M. fuscescens*: BM!). **PAPUA NEW GUINEA:** *s.loc*., *s.date*, *Naumann 43* [*c.fr*.], *57* [*c.fr*.] (BM!). **Madang:** Lower Ramu-Atitau Area, near Mirap village, 14.X.1958, *Robbins 1880a* [*c.fr*.] (NY!). **Milne Bay:** Sagarai, between Wegulani and Badili Rivers, 40 m, 16.I.1985, *Kumei 130* [*c.fr*.] (ALTA, ASU, LAE, MO, NICH, NY! TBA); Kulumadau, Woodlark Island, Kaurai logging area, 100 m, 9.X.1984, *Kumei 75* [*c.fr*.] (ALTA, LAE, NICH, NY!); Kulumadau, woodlark Island, Kaurai Road, 80 m, 6.XI.1984, *Kumei 121* (TNS!). **Morobe:** Garaina, Kasu Village, 720 m, 2.I.1983, *Kairo 575* (NY!); Lae, Labu Swamp, 1 m, 2.XI.1982, *Streimann 25700* [*c.fr*.] (ALTA, KRAM, LAE, MO, NICH, NY!); Lae, Sangkwep logging area, 200–270 m, 13.III.1975, *Touw 14728* [*c.fr*.] (NY!). **New Britain:** Geleo-Lasilai logging area at Latili Mt., Nakanai Mts., 40 km SE of Hoskins, 220 m, 21.II.1989, *Streimann 41115* [*c.fr*.] (ALTA, LAE, NY!); Ibana Logging Area, slopes of Mt. Ulawun (The Father), 10 km SSE of Ulamona Mission, 250 m, 23.II.1989, *Streimann 41433* (ALTA, LAE, NY!). **New Ireland:** Dangu Valley, *s.date*, *Eddy 6049 pp* [*c.fr*.] (BM!). **West Sepik:** Frieda River Base Camp at Horse Creek, 400 m, 1.VIII.1981, *Koponen 34864* (H, HSC, NY!); headwaters of Kong Kong Creek, 5 km S of Vanimo, 250 m, 24.II.1986, *Mundua 271* [*c.fr*.] (ALTA, NY!). **PHILIPPINES. Luzon:** Bataan: Morong, Bakyas River, 180 m, VII.2004, *Linis 930-04* (SING!); Laguna, San Antonio, II.1913, *Ramos 20613* [*c.fr*.] (NY!); Mt. Marvineles, 400 m, VII.1904, *Leiberg 1215a* [*c.fr*.] (NY!); Pampanga, Mt. Arayat, Southern Peak, 400 m, XII.2003, *Linis 739-03* (SING!). **Mindanao:** Camp Keithley, Lake Lanao, V.1907, *Clemens s.n.* [*c.fr.*] (NY!); *ibidem*, VI.1907, *Clemens s.n.* [*c.fr.*] (NY 2 sheets!); *ibidem*, VII.1907, *Clemens s.n.* [*c.fr.*] (NY!); Caraga, Butuan, III–VII.1911, *Weber 1301* (NY!), *1305* [*c.fr.*] (NY!). **Panay:** Capiz, Libacao, V–VI.1919, *Martelino & Edano 35782* (NY!); Iloilo, 1–11.I.1913, *Robinson 18260* [*c.fr.*] (NY!). **SINGAPORE:** Kranji, 2.X.1910, *Ridley 308* (SING!); Sungei Buloh, 1893, *Ridley 244* (SING!). **SOLOMON ISLANDS:** *s.loc.*, *s.date*, *Norman s.n.* [*c.fr.*] (BM!); Faisi, 1914, *Lee 897* [*c.fr.*] (BM!). **SRI LANKA, Anuradhapura:** Ritigala Strict Natural Reserve, 2400 ft [=732 m], 13.IX.1975, *Jayasuriya et al. 2309* [*c.fr.*] (TNS!). **THAILAND. Nakhon Si Thammarat:** Khao (Mt.) Luang, Camp I, 600 m, 3.II.1966, *Touw 11499* (NY!). **Surat:** Na Sak, Langsuan, 50 m, 6.II.1927, *Kerr 182* [*c.fr.*] (BM!).

8. *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr. (Figs. 5.28 & 5.29)

Sp. Musc. Frond., Suppl. 2, 2 (2): 144 (1827). *Orthotrichum incurvifolium* Hook. & Grev., Edinb. J. Sci. 1: 117 (1824). *Leiotheca incurvifolia* (Hook. & Grev.) Brid., Bryol. Univ. 1: 732 (1826). LECTOTYPE (Vitt & Ramsay, 1985a): Island of Ternate, and in King George's Sound, *s. coll*. (E-Grev.; isolectotype BM!).

Orthotrichum undulatum Hook. & Grev., Edinb. J. Sci. 1: 117, pl. 4 (1824). *Leiotheca undulata* (Hook. & Grev.) Brid., Bryol. Univ. 1: 733 (1826). *Macromitrium undulatum* (Hook. & Grev.) Schwägr., Sp. Musc. Frond., Suppl. 2, 2 (2): 137 (1827). LECTOTYPE (Reese, 1997): 92. Ternate, *Dickson s.n.* (BM! isolectotypes, BM! E) — fide Reese (1997).

M. subtile Schwägr., Spec. Musc. Frond., Suppl. 2, 2 (2): 140, tab. 192 (1827). LECTOTYPE (Vitt & Ramsay, 1985a): In insula Otaheite legit et dedit *Menzies s.n.* (G; isolectotype G) — fide Vitt & Ramsay (1985)

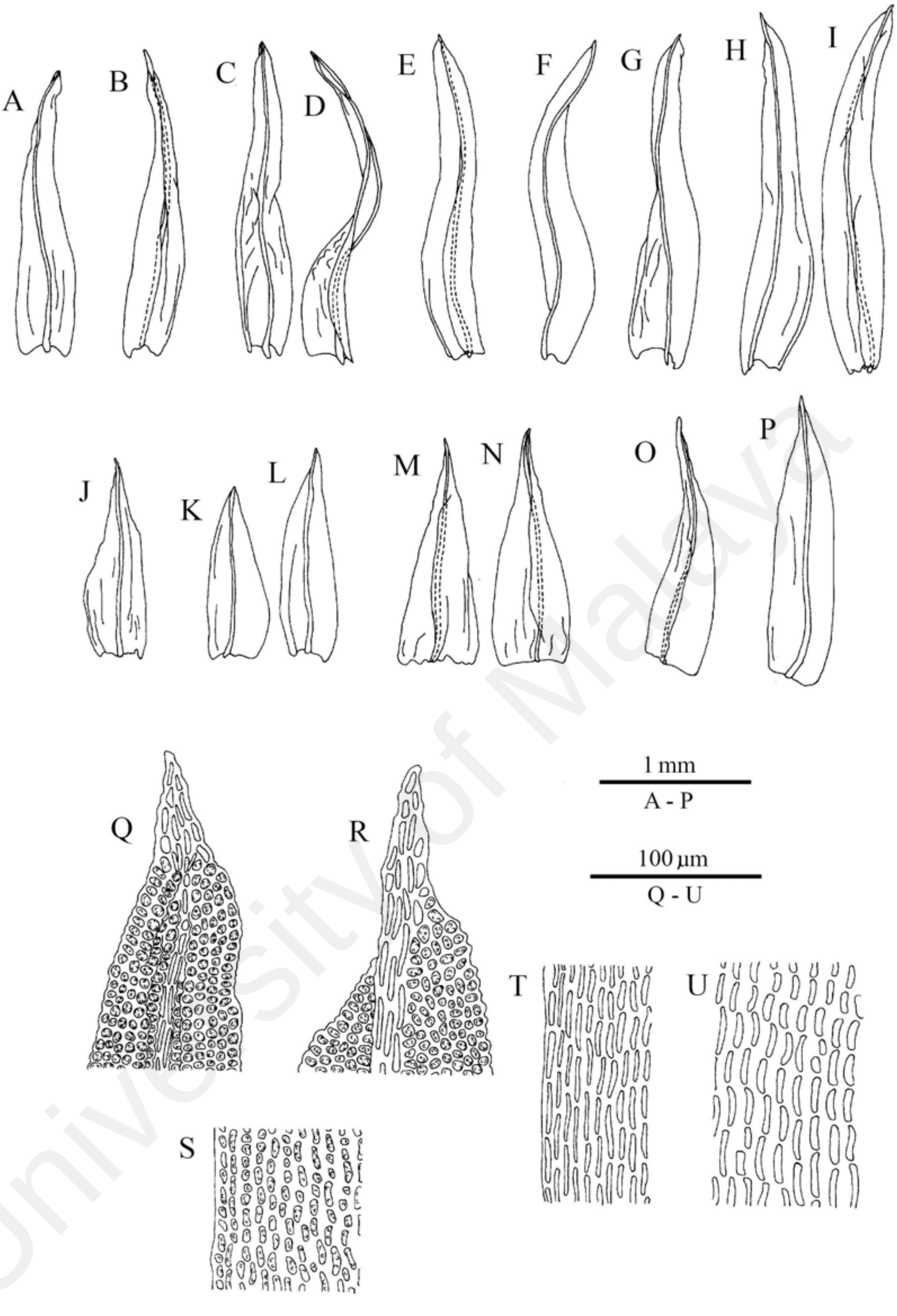

Figure 5.28. Illustrations of *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr. — **A-I,** branch leaves; **J-P,** perichaetial leaves; **Q-R,** leaf apices; **S,** mid-leaf cells; **T-U,** basal laminal cells. [**A, O** from *Foxworthy 1932* (NY, type); **B, J** from *Chin 1631* (KLU); **C-D, K-L** from *Ramos 16671* (NY); **E, P** from *Tan 92-197* (KLU); **F, M-N** from *Mohamed 9543* (KLU); **G** from *Touw 18626* (NY); **H, Q-U** from *Yong 6476* (KLU); **I** from *Yong et al. 4542* (KLU)]

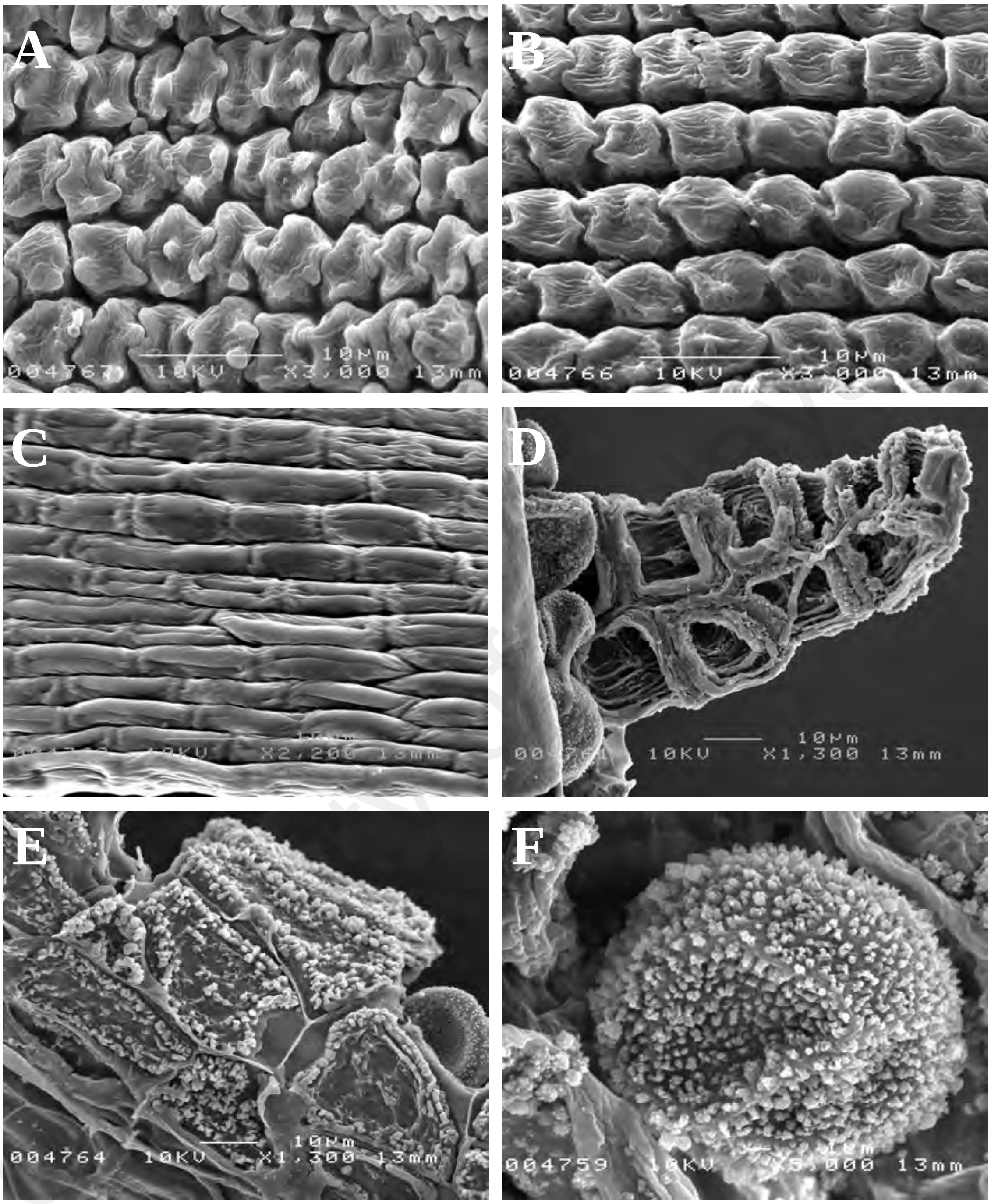

Figure 5.29. SEM images of *Macromitrium incurvifolium* (Hook. & Grev.) Schwägr. — **A,** upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** dorsal view of peristome teeth; **E,** ventral view of peristome teeth; **F,** detail of a microspore. [All from *Yong et al. 4542* (KLU)]

M. javanicum Bosch & Sande Lac., Bryol. Jav. 1: 123, tab. CI (1860). LECTOTYPE (Vitt et al., 1995): Java, *s. coll. ex Hb. Reg. Lugd. Bat.* (L.) — fide Fleischer (1904).

M. subuligerum Bosch & Sande Lac., Bryol. Jav. 1: 124, tab. CII (1860). LECTOTYPE (Vitt et al., 1995): Java, in montibus Gedé et Salak, 1859, *Teysmann s.n.* (L.) — fide Vitt et al. (1995).

M. zippelii Bosch & Sande Lac., Bryol. Jav. 1: 123, tab. C (1860). LECTOTYPE (Vitt et al., 1995): Amboina, belokar, *Zippelius s.n. ex Hb. Reg. Lugd. Bat.* (L; isolectotypes BM! BM!) — fide Vitt et al. (1995).

M. plano-caespitosum Müll. Hal., Linnaea 38: 560 (1874). LECTOTYPE (Vitt et al., 1995): Insulae Philippinae, Luzon, Mahahai, reg. Montosa, *Wallis 1871* (H-BR) — fide Vitt et al. (1995).

M. cumingii Müll. Hal., Flora 82: 452 (1896). HOLOTYPE: Insulae Hawaiieae, *Cuming 2214* (B) — fide Staples et al. (2004).

M. kaernbachii Broth. in Schumann & Lauterb., Fl. Schutzgeb. Südsee 86 (1900). TYPE: Kaiser Wilhelmsland, Sattelberg, Nuselang, am Wege nach Lukube, im Busch bei 850 m ü. M., 11.XII.1893, *Kaernbach 62* (holotype H-BR) — fide Vitt et al. (1995).

M. leucoblastum Müll. Hal *ex* Broth., Fl. Schutzgeb. Südsee 87 (1900). TYPE: New Guinea, Madang, Kaiser Wilhelmsland, Gogolexpedition, XI.1890, *Kaernbach s.n.* (holotype H-BR!) — fide Vitt et al. (1995).

M. foxworthyi Broth., Philipp. J. Sci. 3: 16 (1908), ***syn. nov***. TYPE: Philippines, Pampangan Province, Luzon, Mt. Abu, Dec. 1908, *Foxworthy 1932* (holotype H-BR; isotype NY!).

Plant medium-sized, forming cushions or mats; young shoots yellowish-green, gradually turning to olive-green and rusty-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches generally short, 0.5–1(–1.5) cm tall and 3–5 mm wide, loose or tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, lanceolate on young shoots, becoming long-lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, lax or densely arranged, leaves irregularly twisted, flexuose-contorted, with strongly incurved to involute apices (when dry), erect-spreading to wide-spreading with incurved apices (when moist); branch leaves (2.2–)2.4–2.8 × 0.4–0.5 mm, length-width ratio 5–7:1, long, slender lanceolate to ligulate-lanceolate with an oblong base, lamina straight to often flexuose, plane; apex firm, broadly acute to acuminate, mucronate; margin subentire to crenulate, plane at distal part but reflexed at base; costa mostly percurrent, occasionally ending in a short mucro. Upper and middle laminal cells 5–6 × 5–8 µm, length-width ratio 1:1, oblate to short- or more commonly wide-rectangular, evenly incrassate, walls not pitted, cells flat to low-bulging, pluri-papillose, papillae generally weak; basal laminal cells short to elongate, 10–35 × 8–12 µm, length-width ratio 1–4:1, short-rectangular, or long-rectangular cells more commonly found at region close to leaf insertion, incrassate, walls either even or unevenly thickened, lumina 4–5 µm wide, appearing linear with even thickened walls but strongly curved to sigmoid with uneven walls, pitted only near juxtacostal region and insertion, cells flat, smooth.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.5–0.6 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, usually much smaller than branch leaves, 0.8–1.6 × 0.5–0.6 mm, oblong-laceolate to triangular-lanceolate, upper lamina narrow, expanding gradually towards mid-leaf to an oblong base, leaf base often with a few long-plications; apex slender, acuminate, apiculate; margin subentire to entire, plane; costa percurrent or short-excurrent that ending in a stout apiculus; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 0.8–1.0 mm long; paraphyses abundant, densely covering the vaginula, 0.4–0.9 mm long, made of 8–12 short to long-rectangular cells. Seta 5–6 mm long, smooth, dextrorse-twisted. Capsule urns 1.1–1.2 × 0.7–0.8 mm, ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 2–4, cryptoporous; operculum rostrate, beak 0.9–1.1 mm. Peristome single. Exostome of 16 teeth that are separated above but connected at their base as a low membrane, erect to recurved at top in both dry and wet conditions; dorsal side of teeth with many thickened and papillose anticlinal ridges, each of them emerging like a frame surrounding a lower central portion, central portion vertically striolate-papillose with simple wart-like papillae; ventral side of teeth reticulate-papillose with fine, coronate papillae, on vaguely raised, irregular reticula; both vertical and horizontal cell wall clearly seen on both sides of teeth, marked by thick and papillose ridges on dorsal side while by thin and smooth ridges at the ventral. Endostome absent. Spores anisomorphic, larger spores 30–34 µm in diameter, smaller spores 18–22 µm in diameter. Calyptra mitrate, plicate, sparsely hairy, hairs long, stiff erect and mostly on ridges near to the calyptra base, calyptra base fringed or lacerated.

Other descriptions and illustrations: Müller (1849) p. 750; Fleischer (1904) p. 436–437 as *M. incurvifolium*, p. 439–440 as *M. subuligerum*; Brotherus (1925) p. 41, fig. 443H as *M. javanicum*; Bartram (1939) p. 177, pl. 13, fig. 219, as *M. foxworthyi*, p. 177–178, pl. 13, fig. 220, as *M. subuligerum*; Vitt & Ramsay (1985) p. 415–419, figs. 268–269, 271–273, 275–284; Vitt et al. (1995) p. 36–39, fig. 16; Eddy (1996) p. 46–49, fig. 359 as *M. incurvifolium*, p. 49, fig. 363 as *M. subtile*.

Distribution: As. 2: China; As. 3: Sri Lanka; As. 4: Indonesia (Ambon, Java, Sulawesi, Sumatra, Ternate), Malaysia (Malay Peninsula), New Guinea, Philippines (Bohol, Luzon, Mindanao, Mindoro, Panay); Oc.: Fiji, Hawaii, Samoa, Society Islands, Tahiti, Vanuatu; Austr. 1: North & West Australia.

Habitat and ecology: Epiphytic on tree trunks and lower branches and, occasionally on buttresses and rotten logs. The species adapts well to a wide range of habitats. Besides its usual forested habitat, it has also been collected from limestone sites, gardens and roadside trees, and from fruit trees in orchards. In Malaysia, the plant is most commonly found at low elevations, although elsewhere it is known to occur up to the lower montane zone (Vitt et al., 1995; Eddy, 1996).

Notes:

1. *Macromitrium incurvifolium* is characterized by its a) long, slender to ligulate-lanceolate leaves, with rather blunt or broadly acute apices; b) quadrate or short-rectangular and pluripapillate cells covering most of the leaf lamina (leaving only a short basal region of long-rectangular and smooth cells); c) minute, triangular-lanceolate perichaetial leaves (unique to the species). In addition to this, the exostome teeth of this species are uniquely ornamented by thickened and jointed, anticlinal and periclinal ridges that appear like open boxes fringing the lower central regions. This feature can be readily observed under a light microscope.

2. Sometimes, the species may be confused with *M. falcatulum* because both are restricted to lowlands and share a similar leaf form. However, *M. falcatulum* is always smaller in plant size, with shorter branch leaves, unipapillate basal laminal cells and densely hairy calyptra. In contrast, *M. incurvifolium* plants are bigger, with longer branch leaves, smooth basal laminal cells and sparsely hairy calyptra.

3. I have examined the type materials of *M. foxworthyi* and could not detect any morphological differences from *M. incurvifolium*, so that name is reduced to synonymy.

<u>Specimens examined</u>:

AUSTRALIA: King George's Sound, *s.date, s.coll. H726 ex Hb. Wilson* [*c.fr.*] (isolectotype of M. incurvifolium: BM 4 sheets!). **INDONESIA. Irian Jaya:** Paniai, Rouffaer rivier, VIII.1926, *Leeuwen 9888* (*2634*) [*c.fr.*] (BM!). **Java:** *s.loc., s.date, s.coll.* [*c.fr.*] (NY!); *s.loc., s.date, s.coll. ex Hb. Hampe ex Lacoste* (BM!). **Ternate:** *s.loc., s.date, s.coll. 654*(*92*) *ex Hb. Hooker ex Dickson* [*c.fr.*] (lectotype of *Orthotrichum undulatum*: BM!); *s.loc., s.date, s.coll. ex Hb. Hooker ex Turner ex Dickson* [*c.fr.*] (isolectotype of *Orthotrichum undulatum*: BM!); *s.loc., s.date, s.coll. H654 ex Hb. Wilson ex Dickson* [*c.fr.*] (isolectotype of *Orthotrichum undulatum*: BM!); *s.loc., s.date, s.coll. H724 ex Hb. Wilson ex Dickson* [*c.fr.*] (BM 5 sheets!); *s.loc., s.date, s.coll. H725 ex Hb. Wilson ex Dickson* [*c.fr.*] (BM 2 sheets!); *s.loc., s.date, s.coll. H729ex Hb. Wilson* (BM!). **MALAYSIA. Kedah**: Jitra, Mt. Jerai (Kedah Peak), 950 m, 26.VIII.1988, *Sadiah et al. 166b, 170a* (KLU!). **Kelantan**: Dabong, Mt. Stong Forest Reserve, Mt. Stong, 1105 m, 27.V.2003, *Yong 4154* [*c.fr.*] (KLU!); Gua Musang, Gua Tapah limestone, 600 ft [=183 m], 16.VIII.1971, *Chin 1631* [*c.fr.*] (KLU!); Gua Musang, summit of Batu Neng limestone hill, 800 ft [=244 m], 14.VIII.1971, *Chin 1578* [*c.fr.*] (KLU!). **Pahang**: Cameron Highlands, Batu Mentiggi, trail 13/14, 19.VI.1989, *Damanhuri s.n.* (UKMB!); Cameron Highlands, Iskandar Waterfall, 420 m, 6.X.2003, *Yong et al. 4542* [*c.fr.*] (KLU!); Cameron Highlands, Ringlet, 1100 m, 5.VIII.1988, *Mohamed & Damanhuri 1053* (KLU!); Fraser's Hill, 4000 ft [1219 m], 19.III.1929, *Holttum 21521* (SING!); Sungai Sat, 20.VII.1929, *Henderson 22018* [*c.fr.*] (SING!); Taman Negara, Merapoh, Gua Peningat, 7.V.1997, *Damanhuri & Ahmad 97-981, 97-1028* (KLU! UKMB!). **Penang**: Penang Hill, Convalescent Bungalow, 730 m, 21.VIII.2005, *Mohamed & Yong 6514* (KLU!). **Perak**: Taiping, Taiping Lake, 120 m, 9.III.2004, *Mohamed & Yong 4848* (KLU!); Ulu Perak, Belum Royal Park, Sg. Kenarong area, 200–300 m, 29.VII.2003, *Yong 4335* (KLU!). **Sabah**: Danum Valley

Conservation Area, Nature Trail, 760 m, 3.IX.1997, *Ellis DAM572ii* (BM!); Lahad Datu, Danum Conservation Area, Sg. Purut, 18.X.1989, *Damanhuri s.n.* (UKMB!). **Sarawak**: First Division, Bau, 100 m, 23.VII.1991, *Mohamed & Bakar 3242c*, *3247* (KLU!); First Division, Bau, Fairy Cave, 50 m, 16.VII.2005, *Yong 6476* (KLU!). **Selangor**: Genting Highlands, water reservoir near Genting Resort, 1420 m, 14.XII.1983, *Damanhuri s.n.* (UKMB!); Langat Basin, Mt. Nuang, 350 m, 10.VIII.1997, *N.Abdullah 11* (UKMB!). **Terengganu**: Dungun District, Kampung Pasir Raja, Pasir Raja Forest Reserve Compartment 5 (N 04^0 43’ E 102^0 57.5’), lowland foret zone, 150 m, 6.VI.2004, *Yong 5766* [*c.fr.*] (KLU!); Ulu Terengganu District, Sekayu Forest Reserve, 31.VIII.1990, *N.Azian 3* [*c.fr.*] (UKMB!); *ibidem*, 200 m, 3.II.1989, *Bakar 204* (KLU!); *ibidem*, 250 m, 31.VIII.1990, *Rosada 1* [*c.fr.*] (KLU! UKMB!); Ulu Terengganu District, Sg. Berua, off Jalan Tapah Road, 60 m, 24.V.1989, *Mohamed 9529*, *9543* (KLU!). **PAPUA NEW GUINEA. Central Prov.:** Near Sogeri, on Musgrave River Road, 700 m, 12.II.1981, *Streimann & Naoni 16035* [*c.fr.*] (H, LAE, NY!); Varirata National Park, Sogeri, 22 km ENE of Port Moresby, 600 m, 5.II.1981, *Streimann & Vinnas 14511* (H, LAE, NY 2 sheets! UPNG). **Eastern Highlands:** Wopeia, Aiyura-Omara Road., 10 km SE of Aiyura, 1550 m, 10.IV.1982, *Streimann 18320* [*c.fr.*] (ALTA, H, LAE, NICH, NY!). **Gulf:** Werr River, 640 m, 24.I.1983, *Streimann 33585* (ALTA, NY!). **Milne Bay:** Kulumadau Forestry Station, Woodlark Island, 25.XII.1982, *Kolema 14* [*c.fr.*] (NY!); Simeada Agriculture Station, Gurney Airstrip, 10 m, 18.XII.1982, *Kolema 11* (H, NICH, NY! TBA); Sineada Agriculture Station, Gurney Airstrip, 10 m, 12.XII.1982, *Kolema 1* (H, LAE, NICH, NY!); Sinkwari, 18 km SE of Kulumadau, Woodlark Island, 280 m, 26.XII.1982, *Kolema 16* [*c.fr.*] (NY!). **Morobe:** Bulolo Forestry College, 650 m, 7.X.1983, *Bellamy 1304* [*c.fr.*] (ALTA, NY! TBA); *ibidem*, 730 m, 31.I.1981, *Streimann 14075* [*c.fr.*] (H, LAE, NICH, NY!); Bulolo-Watut Divide, 9 km SSW of Bulolo, 1420 m, 14.X.1982, *Streimann 25210* [*c.fr.*] (ALTA, NICH, NY!); Buso River, 26 km

ENE of Lae, 160 m, 16.I.1981, *Streimann & Tamba 11593* [*c.fr*.] (GRO, LAE, NY!); Heads Hump, 6 km SE of Bulolo, 1000 m, 7.III.1982, *Streimann 17412* [*c.fr*.] (NY!); Lae Botanic Garden, 20 m, 9.III.1975, *Touw 14660* [*c.fr*.] (NY!); *ibidem*, 28.V.1975, *Touw 18626* [*c.fr*.] (NY! TNS!); Menyamya, 1250 m, 30.IV.1982, *Streimann 19748* (H, LAE, NICH, NY!); Middle Creek-Watut River Divide, 8 km NW of Bulolo, 950 m, 2.II.1981, *Streimann 14293* [*c.fr*.] (H, LAE, NY!); Pouyu Village, 2 km SE of Aseki, 1500 m, 24.I.1981, *Streimann & Tamba 12577* [*c.fr*.], *12734* [*c.fr*.] (H, LAE, NICH, NY!); Yinimba, 9 km N of Menyamya, 1500 m, 30.IV.1982, *Streimann 19137* (ALTA, H, KRAM, LAE, MO, NICH, NY! TBA). **New Britain:** Evil River, 30 km SSW of Bialla, 300 m, 25.II.1989, *Streimann 41622* [*c.fr*.] (ALTA, LAE, NY!); Numunda Plantation, 8 km NW of Kimbe, 10 m, 26.II.1989, *Streimann 41644* [*c.fr*.] (NY!). **PHILIPPINES. Luzon:** *s.loc*., *s.date*, *Semper s.n*. [*c.fr*.] (BM 3 sheets!); Isabela, Palanan Municipality, Palanan Wilderness, 300–500 ft [=92–152 m], 19.V.1992, *Tan 92-197* [*c.fr*.] (SING!); Laguna, Mt. Maquiling, 300 ft. (= 91 m), XII.1930, *Herklots 312* (BM!); Laguna, San Antonio, VI.1912, *Ramos 14928* [*c.fr*.] (BM! NY!); *ibidem*, IX–X.1912, *Ramos 16671* [*c.fr*.] (NY!); Mt. Abu, XII.1908, *Foxworthy 1932* [*c.fr*.] (isotype of *M. foxworthyi*: NY!); Sorsogon, Irosin, Mt. Bulusan, *s.date*, *Elmer 15101* [*c.fr*.] (BM!); *ibidem*, VIII.1916, *Elmer 16973* [*c.fr*.] (BM 3 sheets!); *ibidem*, VIII.1916, *Elmer 16973* (*2122*) [*c.fr*.] (BM!); Tayabas, Mt. Pular, I.1913, *Ramos 19393* [*c.fr*.] (NY!); Tayabas, Umiray, V–VI.1917, *Ramos & Edano 29085* [*c.fr*.] (NY!). **Mindanao:** Alag River, XI.1906, *Merill 5688* [*c.fr*.] (NY!). **Panay:** Iloilo, 1–11.I.1913, *Robinson 18167* [*c.fr*.] (BM! NY!). **SINGAPORE:** Chua Chu Kang, 1896, *Ridley 462* [*c.fr*.] (NY! SING!); *ibidem*, IX.1959, *Johnson 258* (KLU!); Kranji, 1892, *Ridley 261* (SING!).

9. ***Macromitrium longicaule*** **Müll. Hal.** (Figs. 5.30 & 5.31)

Syn. Musc. Frond. 1: 742 (1849). LECTOTYPE (Vitt et al., 1995): Java, *Miquel s.n.* (L-Miquel; isotype L-Miquel).

M. brachystele Dixon in Forbes, J. Bot. 61: 62 (1923). TYPE: Papua New Guinea, Central, Sogere, 2000 ft [=610 m], epidendric, *Forbes 515a* (holotype BM) — fide Vitt et al. (1995).

Plant medium-sized to large, forming cushions or mats; young shoots yellowish-green, gradually turning to olive-green at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches tall, (2–)3–5 cm tall and 4–7 mm wide, loose or tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender-lanceolate on young shoots, elongate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, lax to densely arranged, leaves individually curled, crisped or twisted-contorted from erect base that clasp on branch (when dry), erect-spreading, wide-spreading to flexuose-spreading (when moist); branch leaves 3.1–4.2(–4.8) × 0.6–0.8(–0.9) mm, length-width ratio 5–6:1, slender-lanceolate to ligulate-lanceolate with an oblong base, lamina straight or recurved, plane; apex firm, weakly incurved, slender, long, broadly acute or occasionally acuminate; margin denticulate at acumen but crenulate below, plane at distal part but reflexed at base; costa percurrent or ending just below the extreme tips. Upper laminal cells 6–10 × 8–10 µm, length-width ratio 1:1, oblate to short- or wide-rectangular, evenly incrassate, walls not pitted, cells flat or low-bulging, densely pluri-papillose, cells mostly obscure due to the papillae; middle laminal cells 8–16 × 8–10 µm, grading from oblate or short-rectangular

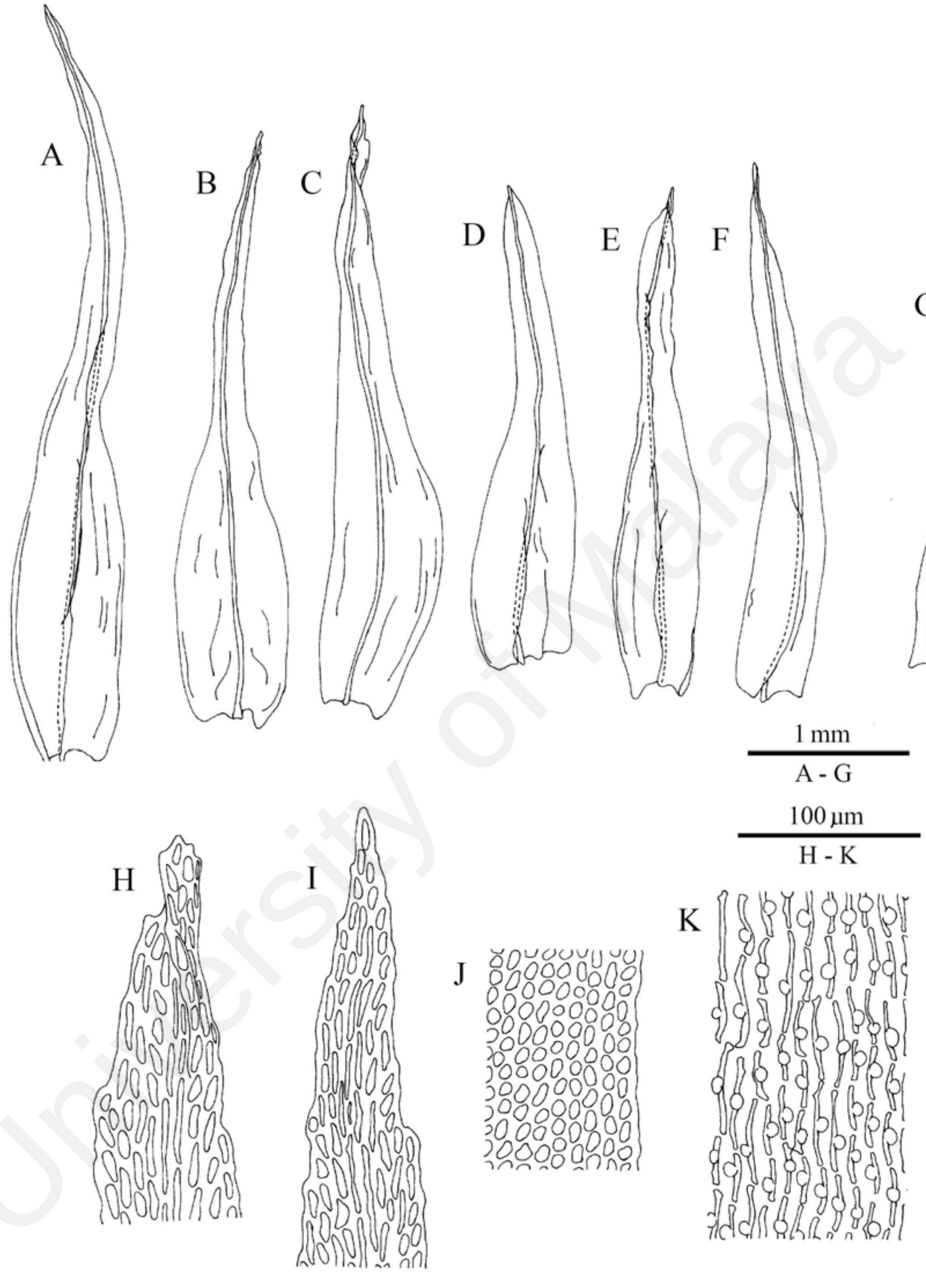

Figure 5.30. Illustrations of *Macromitrium longicaule* Müll. Hal. — **A-F,** branch leaves; **G,** perichaetial leaf; **H-I,** leaf apices; **J,** mid-leaf cells; **K,** basal laminal cells. [**A** from *Damanhuri s.n.* (UKMB); **B, H** from *Yong 6212* (KLU); **C** from *Yong 6061* (KLU); **D** from *Damanhuri 2000-82* (UKMB); **E** from *Yong 6129* (KLU); **F-G, I-K** from *Yong 4657* (KLU)]

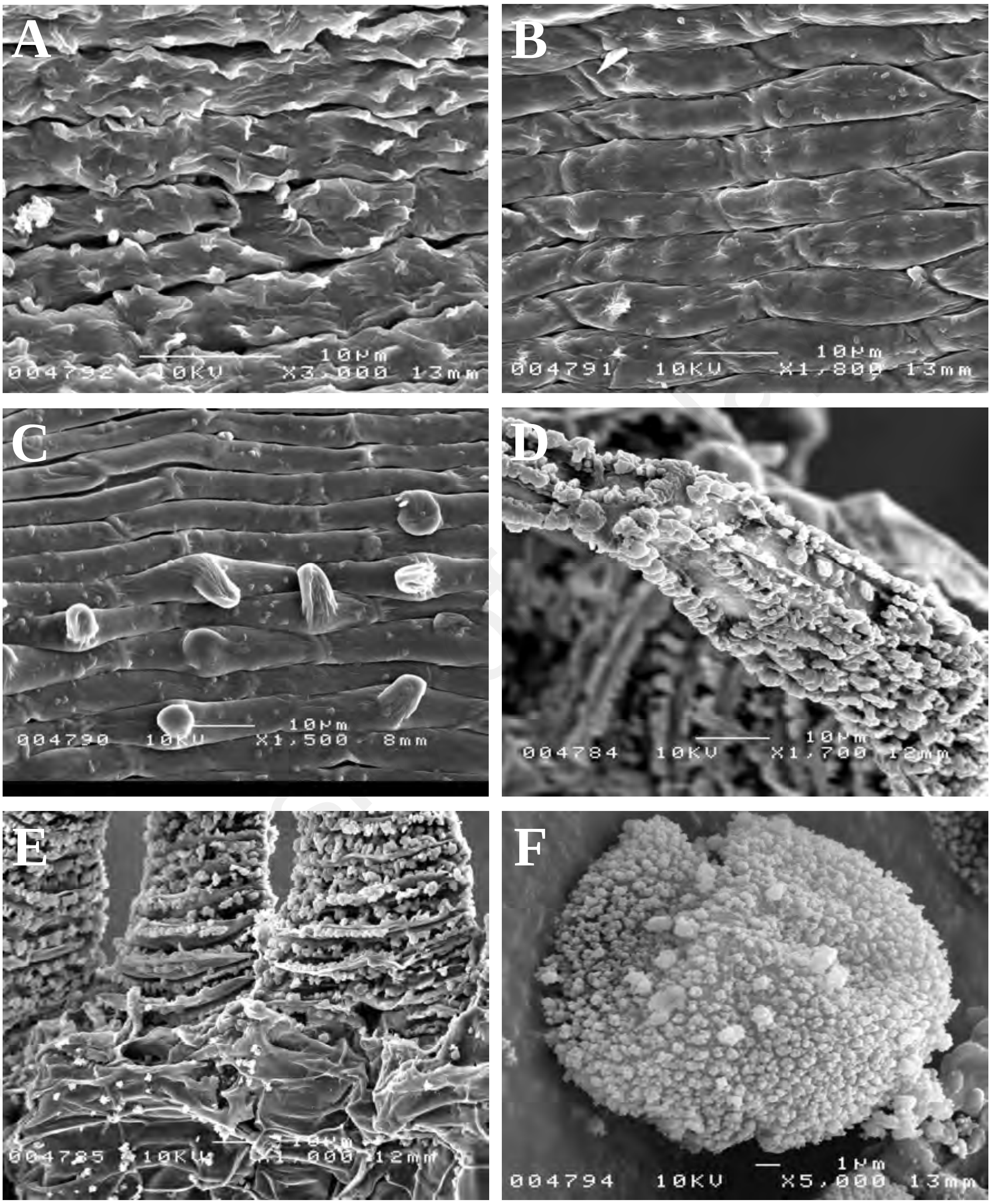

Figure 5.31. SEM images of *Macromitrium longicaule* Müll. Hal. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** dorsal view of peristome teeth; **E,** ventral view of peristome teeth; **F,** detail of a microspore. [All from *Yong 6202* (KLU)]

to gradually elongate toward the basal lamina, cells not uniform in length, incrassate, with curved to more-or-less straight lumina, cells flat, weakly papillose to smooth, clear; basal laminal cells 45–72(–80) × 12–14 µm, length-width ratio 4–6:1, long-rectangular, incrassate, walls either even or unevenly thickened, lumina 3–4 µm wide, appearing linear with even thickened walls but strongly curved to sigmoid with uneven walls, pitted only near juxtacostal region and insertion, cells flat, unipapillose to tuberculate, papillae weakened toward the leaf margin.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, usually much shorter than branch leaves, 2.6–3.4 × 0.4–0.6 mm, slender-lanceolate, upper lamina long and narrow, expanding gradually toward slender, long-oblong leaf base, leaf base often with a few long-plications; apex slender, long-acuminate; margin subentire to entire, plane; costa percurrent or vanish a few cells below tip; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 0.7–0.9 mm long; paraphyses abundant, densely covering the vaginula, 0.5–0.7 mm long, made of 8–14 short- or long-rectangular cells. Seta 4–5 mm long, smooth, sinistrorse-twisted. Capsule urns 1.2–1.3 × 0.8–1.0 mm, short-ovoid to ellipsoid, smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.9–1.1 mm. Peristome single. Exostome of 16 teeth that are separated above but connected at their base as a low membrane, erect to recurved at top in both dry and wet conditions; dorsal side of teeth striolate-papillose in various directions, papillae simple to compound, on coarse vertical or diagonal ridges, occasionally on irregular reticula; ventral side of teeth horizontally striolate-papillose with simple to compound papillae, on distinctly raised, thin horizontal ridges; remnants of original cell-wall obscure on dorsal side, hidden by papillae, but visible on the ventral and marked by low and filmy trabecula. Endostome absent. Spores anisomorphic, larger spores 30–42 µm in diameter, smaller spores 18–24 µm in diameter. Calyptra mitrate, plicate, sparsely hairy, hairs long, stiff erect, mostly on ridges near to the calyptra base, calyptra base fringed or lacerated.

Other descriptions and illustrations: Dozy & Molkenboer (1861) p. 119, tab. 96; Fleischer (1904) p. 451–453, fig. 83; Vitt et al. (1995) p. 39–42, figs. 17, 39; Eddy (1996) p. 64–66, fig. 374.

Distribution: As. 4: Indonesia (Java, Seram, Sulawesi), Malaysia, Papua New Guinea, Philippines (Luzon, Mindanao).

Habitat and ecology: Epiphytic on tree trunks and lower branches, occasionally on rocks and boulders. The species occurs in rather open sites on mountains, especially common on trees growing in gardens, heath forest and limestone vegetation. In Malaysia, it is most common in the lower montane zone (1000–1700 m).

Notes:

1. *Macromitrium longicaule* can be recognised through a combination of characters: a) broadly acute apex of branch leaves; b) entire leaf margins below the denticulate leaf apex; c) short, pluripapillate upper laminal cells compared to the longer tuberculate basal laminal cells; and d) long, slender-triangular perichaetial leaves with a long-flexuose apex (unique to the species).

2. The branch leaves of *M. longicaule* appear to be very variable. A slender, smaller leaf form, with narrow-acuminate apex, is common among Kinabalu collections from Sabah. Both slender and normal leaf forms are also common among New Guinea collections.

Specimens examined:

INDONESIA, Kalimantan: Nunukan, Krayan, Pa’ Raye Village, 970 m, 3.IV.2003, *Suleiman 1046* (BO, BORH!). **Sulawesi:** Latimojong Mountains, Mt. Rantemario, 1900 m, 15.XI.1969, *Eddy 5431 pp* [*c.fr*.] (BM!); Ujung Pandang, Fundort, Gunung Lompobatang bei Malino, XI.1993, *Muller s.n*. [*c.fr*.] (NY!). **Sumatra:** Kerinchi-Seblat National Park, Mt. Kerinchi-Tujuh, *Tan 05-102*, *05-104* (SING!). **MALAYSIA. Malaya**: 6.VII.1964, *IDC 1134* [*c.fr*.] (KLU!). **Kedah**: Jitra, Mt. Jerai (Kedah Peak), 950 m, 26.VIII.1988, *Damanhuri & Zamzuri 169c* (KLU!). **Kelantan**: Lojing Highlands, Mt. Warpu, 1450 m, 29.V.2008, *Suleiman 3092* (BORH!). **Pahang**: Cameron Highlands, 1440 m, 12.III.1989, *Mohamed 9089* (KLU!); Cameron Highlands, Brinchang, Kampung Teria, 1610 m, 6.XII.2004, *Yong & Goh 6135* (KLU!); *ibidem*, 1700 m, 6.XII.2004, *Yong & Goh 6134* (KLU!); Cameron Highlands, Brinchang, Mt. Brinchang, 23.XI.1990, *Damanhuri s.n.* (UKMB!); *ibidem*, 1440 m, 12.III.1989, *Mohamed & Zamzuri 9158* (KLU!); *ibidem*, 1620 m, 12.IV.1987, *Mohamed et al*. *9363* (KLU!); *ibídem*, 1910 m, VIII.1994, *Seki 91* (KLU!); *ibidem*, 1950–1980 m, 3.VIII.1988, *Mohamed & Damanhuri 1030d* (KLU!); Cameron Highland, Brinchang, Rose Garden, 1540 m, 12.IV.1987, *Mohamed et al 9179*, *9238b* (KLU!); Cameron Highlands, Bukit Mentinggi, 19.VI.1988, *Damanhuri s.n.* [*c.fr*.] (UKMB!); Cameron Highlands, Golf Course, 7.VII.1964, *Clear 1280* [*c.fr*.], *1291* [*c.fr*.] (KLU!); Cameron Highlands, Habu, 1450 m, 24.IV.1999, *Gunaseelan & Mohamed 43* [*c.fr*.], *46*, *51* (KLU!); Cameron Highlands, Tanah Rata Town, 1400 m, 5.XII.2004, *Yong & Goh 6129*, *6131*, *6132* (KLU!); *ibidem*, 1450 m, 24–25.IV.1999, *Gunaseelan & Mohamed 124*, *132a*, *139*, *143b*, *153* [*c.fr*.], *154b* (KLU!); Cameron Highlands, Tanah Rata, Forestry Department, 1440 m, 7.X.2003, *Yong et al*. *4657* [*c.fr*.] (KLU!); *ibidem*, 1450 m, 9.X.1999, *Gunaseelan & Ponniah 476* (KLU!); *ibidem*, 10.XI.1999, *Gunaseelan & Ponniah 333* (KLU!); Cameron Highlands, Tanah Rata, Heritage Hotel, 1450 m, 2.XI.2004, *Yong 6061*, *6062*, *6063*, *6065* (KLU!); Cameron Highlands, Tanah Rata, Mt. Jasar, 1580–1640 m, 4.VIII.1988, *Mohamed & Damanhuri 1012* [*c.fr*.] (KLU!); Cameron Highlands, Tanah Rata, Mt. Jasar, jungle path no. 11, 31.XII.1988, *Damanhuri s.n.* [*c.fr*.] (UKMB!);

Cameron Highlands, Tanah Rata, Robinson Waterfall, 1.VI.1988, *Damanhuri l5* (UKMB!); *ibidem*, 1200 m, 11.VII.2004, *Yong 6046* [*c.fr*.], *6047*, *6051* (KLU!); *ibidem*, 1360 m, 7.VII.1993, *Ibrahim & Mohamed 40* [*c.fr*.] (KLU!); *ibidem*, 1400 m, 4.IX.1999, *Gunaseelan & Ponniah 5a* (KLU!); *ibidem*, 1420 m, 7.X.2003, *Yong et al*. *4614*, *4643* (KLU!); *ibidem*, 1430 m, 7.X.2003, *Yong et al*. *4577*, *4676*, *4680*, *4681* [*c.fr*.], *4686* (KLU!); Cameron Highlands, Tanah Rata, Parit Waterfall, 1420 m, 7.X.2003, *Yong et al*. *4613*, *4638* (KLU!); Cameron Highlands, Tanah Rata, garden of Pelangi Apartment, 1375m, 5.XII.2004, *Yong & Goh 6114*, *6115*, *6118*, *6119*, *6126* [*c.fr*.], *6127* [*c.fr*.] (KLU!); Cameron Highlands, Tanah Rata, Strawberry Park Hotel, 1500 m, 2.VIII.1988, *Mohamed & Damanhuri 1074*, *1094* [*c.fr*.], *1099a* (KLU!); Fraser's Hill, Jeriau Waterfall, 860 m, 10.III.2000, *Damanhuri et al*. *2000-70* (UKMB!); Fraser's Hill, The Quest, 1100 m, 11.III.2000, *Damanhuri et al*. *2000-120* (UKMB!); Fraser's Hill, Temerloh Bungalow, 1180 m, 10.III.2000, *Damanhuri et al*. *2000-17*, *2000-20* (UKMB!); Fraser's Hill, Ye Olde Smoke House, 1120 m, 10.III.2000, *Damanhuri et al*. *2000-82* (UKMB!); Genting Highland, Mt. Ulu Kali, 4000 ft (=1219 m), 16.XII.1979, *Manuel 3170b* (KLU!); *ibidem*, 1500 m, 28.IV.1982, *Mohamed s.n*. (KLU!); *ibidem*, 2.III.1980, *Mohamed 2997* (KLU!); *ibidem*, 1750 m, 11.X.2003, *Yong et al*. *4690* (KLU!). **Sabah:** Crocker Range Park, Alab Pass, alt. 1600–1650 m, 15.IX.2002, *Akiyama Crocker-450* (BORH! HYO); Crocker Range Park, Ulu Kimanis, Rinangisan Hill, 1341 m, 28.VII.2002, *Suleiman 944* [*c.fr*.] (BORH! SNP); Long Miao, 1238 m, 24.III.1999, *Ibrahim AI 436* (SING!); Long Pasia, Rekong Waterfall, 1458 m, 8.XI.2003, *Suleiman 1377* [*c.fr*.] (BORH! SAN); Long Pasia, Rimau Hill, 1131 m, 7.XI.2003, *Suleiman 1348* [*c.fr*.] (BORH! SAN); Ranau, Mt. Kinabalu, below Dallas, 2500 ft [=762 m], 9.XI.1931, *Holttum 25371* [*c.fr*.] (SING!); Ranau, Kinabalu Park, Bukit Tupai Trail, 1455 m, 13.V.2005, *Yong 6444* (KLU!); Ranau, Kinabalu Park, Liwagu Trail, 1780 m, 19.I.1997, *Akiyama et al*. *797* (BORH! T. Yamaguchi); Ranau, Kinabalu

Park, Mesilau East River, 1900 m, 3.IX.1986, *Menzel et al. 4757*, *4930* (NY!); Ranau, Kinabalu Park, road from park headquarter to multipurpose hall, 1500 m, 8.V.2005, *Yong 6234*, *6240*, *6243*, *6244* (KLU!); Ranau, Kinabalu Park, road from park headquater to Timpohon Gate, 1490 m, 8.V.2005, *Yong 6207*, *6210*, *6212* [*c.fr*.], *6213*, *6214* (KLU!); *ibidem*, 1500 m, 8.V.2005, *Yong 6202* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Sayap, Sg. Kemantis, 870m, 3.VI.1992, *Mohamed 4544a* [*c.fr*.] (KLU!); Ranau, Mt. Kinabalu, Tenompok, 4700 ft [=1433 m], 11.XI.1931, *Holttum 25692* (SING!); Sipitang, Mt. Lumaku, 1600 m, 29.VII.2008, *Suleiman 3381* (BORH, KLU!); *ibidem*, 1650 m, 29.VII.2008, *Suleiman 3457* [*c.fr.*] (BORH, KLU!); Tambunan, Mahua Waterfall, 1131 m, 8.VII.2003, *Suleiman 1242* [*c.fr*.] (BORH! SNP); *ibidem*, 1200 m, 19.VII.2003, *Michael s.n*. [*c.fr*.] (BORH! SNP); Tambunan, Mahua, Mt. Minduk Sirung, 1200 m, 3.IV.2008, *Suleiman & Masundang 2717* [*c.fr*.] (BORH!); *ibidem*, 1710 m, 2.IV.2008, *Suleiman & Masundang 2623* [*c.fr*.] (BORH!); Tambunan, Mile 32 to Longkogungan Village, 830 m, 22.IX.2008, *Suleiman & Masundang 3980* (BORH!); Tambunan, road from Longkogungan to Kuyungon Village, 600 m, 23.IX.2008, *Suleiman & Masundang 4002* (BORH!). **Selangor:** Genting Highland, Gothong Jaya, water treatment plant, 940 m, 11.X.2003, *Yong et al. 4717* (KLU!); Genting Highland, water reservoir near Genting Resort, 1240 m, 16.IX.1983, *Damanhuri 3570*, *3679* (UKMB!); *ibidem*, 1420 m, 14.IX.1983, *Damanhuri 3210* (UKMB!). **PAPUA NEW GUINEA. Eastern Highlands:** Keglsugl, 3250 m, 24.II.1965, *Eddy 2450* [*c.fr*.] (BM!). **Madang:** Finisterre Range, Daimandi, 1150 m, X.1964, *Eddy 367 pp* [*c.fr*.] (BM!); Finisterre Range, Mt Abilala, 2500 m, 17.XI.1964, *Eddy 1339* [*c.fr*.] (BM!); NE of Teptep, 2950–3100 m, 28.VII.1981, *Norris 65160* [*c.fr*.] (TNS!). **Morobe:** Aseki, Aiuwa-Bakia Track, 1500 m, 22.I.1981, *Streimann & Tamba 12308* [*c.fr*.] (H, LAE, NY!); Aseki, Koke Village, 1500 m, 20.I.1981, *Streimann & Tamba 11659* (GRO, LAE, NICH, NY!); Aseki, Pouyu Village, 1500 m, 24.I.1981, *Streimann & Tamba 12715* (H, LAE, NICH, NY!); Bulolo, Bulolo-Watut Divide, 1530 m, 7.X.1982, *Streimann 24948* [*c.fr*.] (ALTA, NY!); Herzog Mts., Wago, 1150 m, 6.I.1965, *Eddy 1636 pp* [*c.fr*.] (BM!); Rawlinson Range near Ogeramnang airstrip, 1500–1600 m, 18.V.1981, *Koponen 28497* (H, HSC, NY!); Yakwoi River, Menyamya, 1300 m, 1.V.1982, *Streimann 19243* (NY!). **Simbu:** Gumine, Mt. Makaua, 1800 m, 11.XII.1982, *Toia 2A* [*c.fr*.] (H, LAE, NICH, NY!); Mt. Wilhelm, vicinity of Lake Pin(da)unde, 3475 m, 5.VIII.1994, *Tan 94-4320* (SING!). **Southern Highlands:** Anga River, Mendi-Mount Hagen Road, 1700 m, 13.XII.1982, *Streimannn 26949* [*c.fr*.] (ALTA, KRAM, LAE, MO, NY! TALL); Tambul, Kaguba, 2650 m, 12.XI.1968, *Coode 3657* [*c.fr*.] (BM!). **Victoria:** Boridi, Owen Stanley Range, 4700 ft [=1433 m], 22.IX.1935, *Carr 13309* [*c.fr*.] (BM 3 sheets! NY!). **West Sepik:** Star Mountains, Busilmin, 1500 m, 26.III.1975, *Touw 15009* (NY!). **Western Highlands:** Mount Hagen, Karpena Plantation, 1650 m, 1.VII.1982, *Streimann 21859* (H, LAE, NY!). **PHILIPPINES, Luzon:** Bontoc, IV.1910, *Vanoverber 398* (NY!). **Mindanao:** Bukidnon, Mt. Kalatungan, Pangantucan, 12–14.V.1999, *Lubos K181* [*c.fr*.] (SING!); Jordaya, Mt. Apo, 1070 m, IV.1905, *Williams 2673* [*c.fr*.] (NY!); Misamis Oriental, Mt. Lumot, Barangay Lunutan, 1110 m, 24.VIII.1999, *Schumm & Schwarz 5024* (SING!); Nord Cotabato, Lake Agko camping site, 1240 m, 7.VIII.1999, *Schumm & Schwarz 4641* (SING!). **Panay:** Antique, Culasi, Mt. Madja-as, 1050 m, 27.I.2001, *Schwarz 7746* [*c.fr*.] (SING!).

10. *Macromitrium longipilum* A. Braun ex Müll. Hal. var. *longipilum*

(Figs. 5.32, 5.33, 5.34 & 5.35)

Syn. Musc. Frond. 2: 642. 1851. TYPE: Java, *Blume s.n.* (B).

M. crinale Broth. & Geh. in Geh., Biblioth. Bot. 44: 11, tab. 10 (1898), ***syn. nov.*** LECTOTYPE (Vitt, 1995): Indonesia, West Irian, Manokwari, Mt. Arfak ad Hatam, 5000–7000 ft [=1524–2134 m], VII.1875, *Beccari 186* (H-BR).

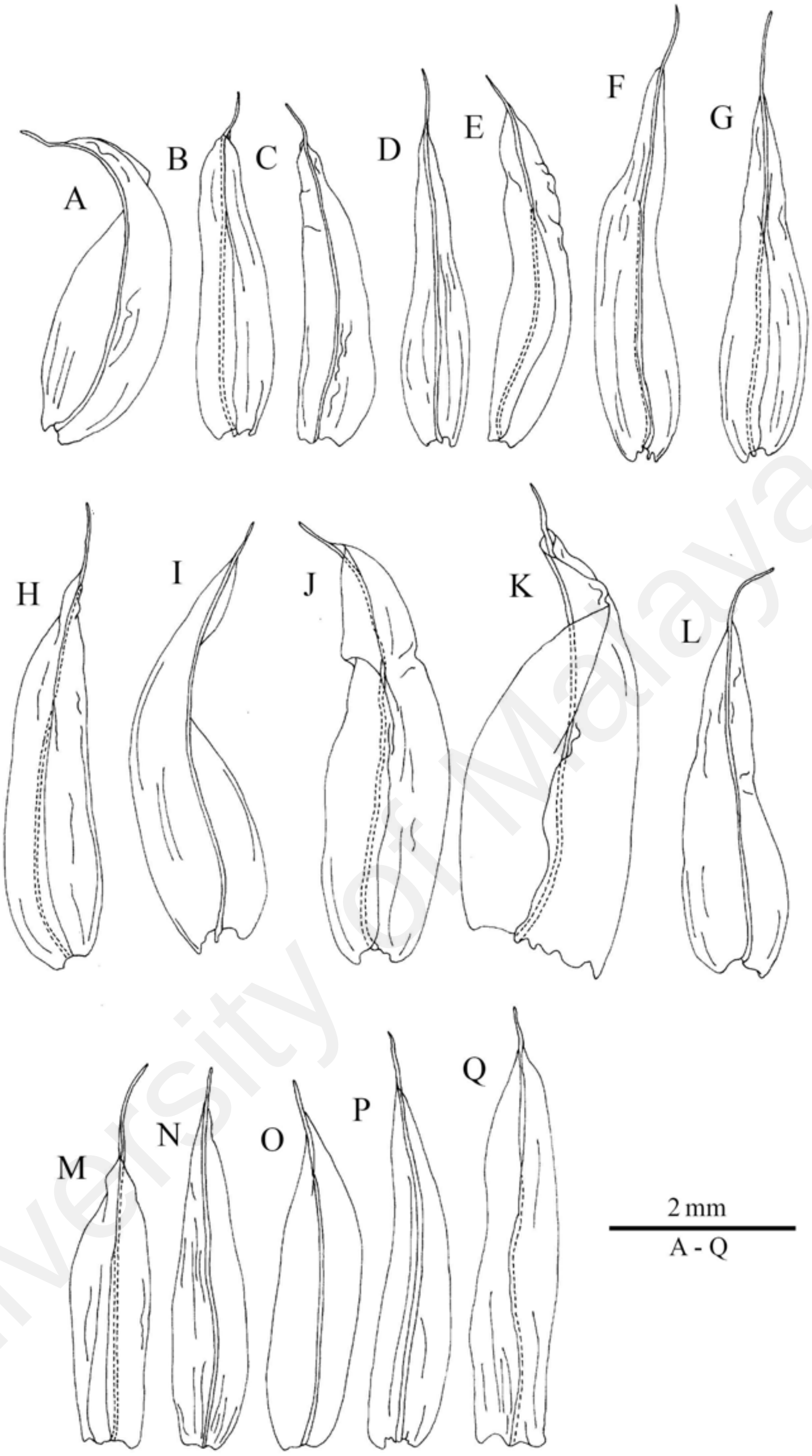

Figure 5.32. Illustrations of *Macromitrium longipilum* A. Braun *ex* Müll. Hal. var. *longipilum* — A-L, branch leaves; **M-Q,** perichaetial leaves. [**A** from *Damanhuri s.n.*, Mt. Danum (UKMB); **B** from *Juri 48* (BORH); **C & N** from *Endert 4535* (Isotype of *M. perdensifolium*, SING); **D** from *Damanhuri 101* (UKMB); **E, O-P** from *Suleiman 123* (BORH); **F** from *Damanhuri 3106* (UKMB); **G** from *Mohamed 52* (KLU); **H** from *Yong 6294* (KLU); **I** from *Streimann 33253* (NY); **J-K, Q** from *Teo 35* (KLU); **L-M** from *Veldhuis 10847* (BM)]

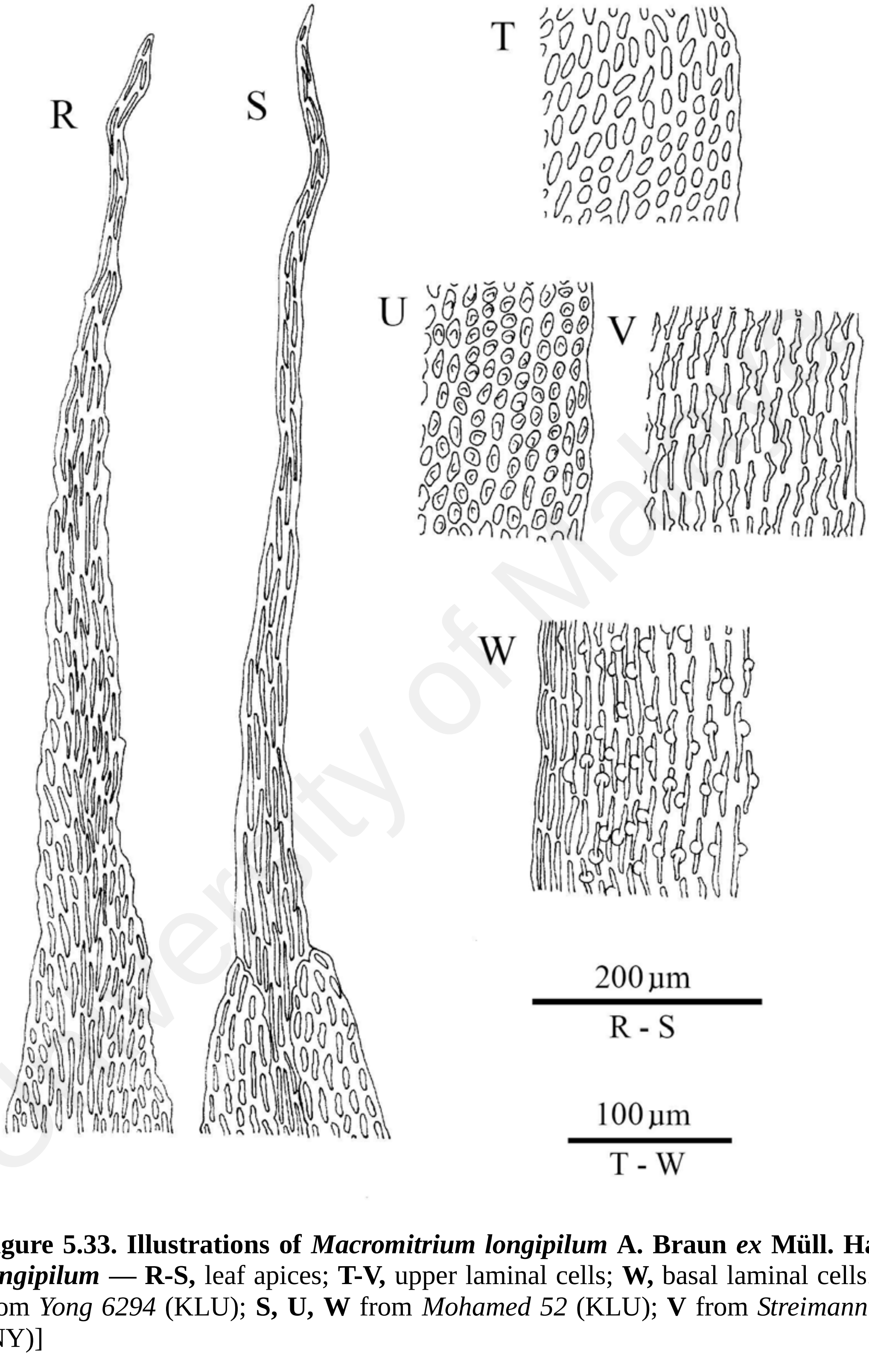

Figure 5.33. Illustrations of *Macromitrium longipilum* A. Braun *ex* Müll. Hal. var. *longipilum* — R-S, leaf apices; **T-V,** upper laminal cells; **W,** basal laminal cells. [**R, T** from *Yong 6294* (KLU); **S, U, W** from *Mohamed 52* (KLU); **V** from *Streimann 33253* (NY)]

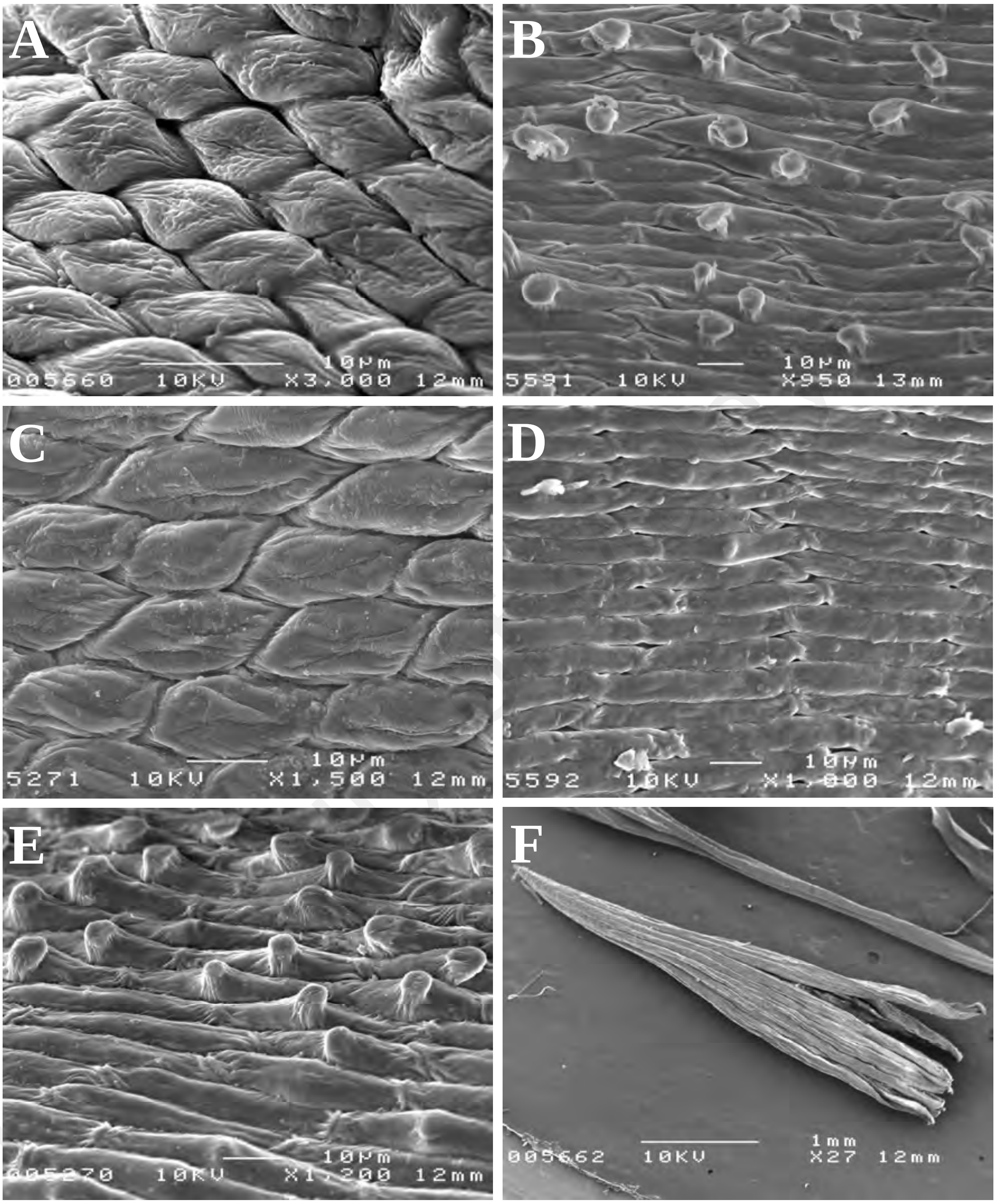

Figure 5.34. SEM images of *Macromitrium longipilum* A. Braun *ex* Müll. Hal. var. *longipilum* — A-B, upper laminal cells; **C-D,** mid-leaf cells; **E,** basal laminal cells; **F,** calyptra. [**A, C** from *Mohamed 52* (KLU); **B, D, E-F** from *Bellamy 1542* (NY)]

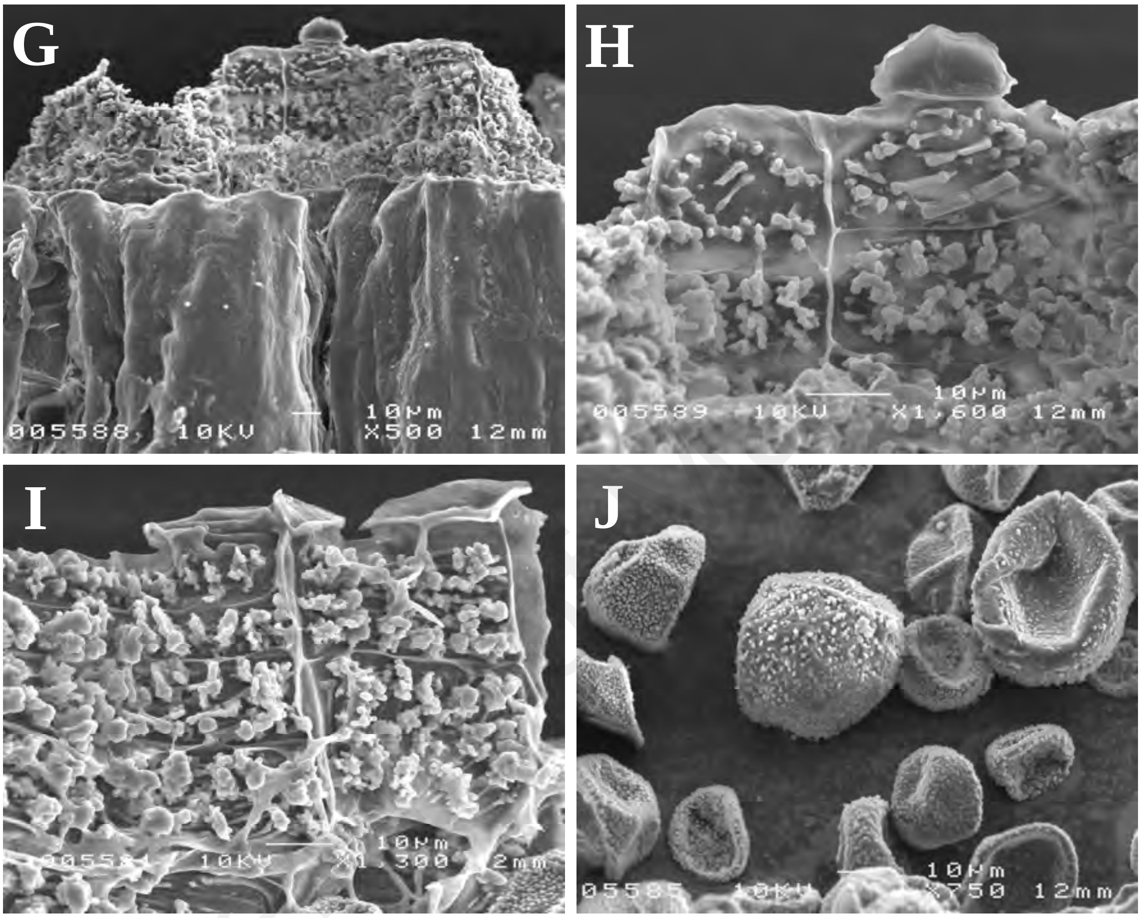

Figure 5.35. SEM images of *Macromitrium longipilum* A. Braun *ex* Müll. Hal. var. *longipilum* — G, capsule with peristome teeth; **H,** dorsal view of peristome teeth; **I,** ventral view of peristome teeth; **J,** spores. [**G-J** from *Bellamy 1542* (NY)]

M. perdensifolium Dixon, J. Linn. Soc., Bot. 50: 90 (1935), ***syn. nov***. TYPE: Borneo, Koetai, Kemoel, in silvis primig., in terra siliciosa, 1700 m, X.1925, *Endert 4535* (holotype BM; isotypes BM! NY! SING!).

Plant robust, forming short-cushions or mats; young shoots olive-green, gradually turning to brownish and reddish-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches stiff, 1–2(–3) cm tall and 8–10 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender-lanceolate on young shoots, elongate at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, densely arranged, indistinctly funiculate, leaves flexuose, more or less spiral on branch, with curved to occasionally deflexed apices (when dry), erect-spreading to wide-spreading with flexuose lamina (when moist); branch leaves (3.4–)4.0–5.4 × 0.9–1.2(–1.6) mm, length-width ratio 3–5:1, ovate-lanceolate to oblong-lanceolate, lamina straight to strongly recurved, plane or occasionally rugose; apex firm, slender to broad, long, acute to acuminate, piliferous; margin subentire to crenulate, plane at distal part but reflexed at base; costa long-excurrent, ending in a 0.5–1.4 mm long hyaline arista. Upper laminal cells 8–40 × 8–12 µm, length-width ratio 1–4:1, size and shape varied on different leaves, from oblate, short to distinctly long-rhombic, shorter cells usually evenly thick-walled, not pitted, strongly bulging, unipapillose, to occasionally pluripapillose, while the longer cells often irregularly thick-walled, pitted and flat, lumen narrow, linear to vermicular; middle laminal cells 10–30 × 8–12 µm, grading from rhombic to gradually long-rectangular toward the basal lamina, incrassate, pitted, with curved to sigmoid-curved lumina, cells smooth, bulging to unipapillose, clear; basal laminal cells 38–64(–72) × 8–

12 µm, length-width ratio 4–7:1, long-rectangular, incrassate, walls either even or unevenly thickened, lumina 3–4 µm wide, appearing linear with even thickened walls but strongly curved to sigmoid with uneven walls, pitted, cells flat, unipapillose to tuberculate.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, about the size of the branch leaves, 3.5–4.8 × 0.6–1.1 mm, broad-lanceolate to oblong-laceolate, upper lamina narrow, expanding abruptly below apex or gradually toward the mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender acuminate, cuspidate to piliferous; margin entire, plane; costa short to long-excurrent, ending in a cusp or hyaline arista; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 1.4–1.8 mm long; paraphyses abundant, densely covering the vaginula, 0.5–0.6 mm long, made of 10–13 short- or long-rectangular cells. Seta 22–30 mm long, smooth, dextrorse or sinistrorse-twisted. Capsule urns 1.8–2.0 × 1.0–1.2 mm, ovoid to long-ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, phaneroporous; operculum rostrate, beak 0.9–1.2 mm. Peristome single. Exostome teeth fused into a continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal side of teeth variously papillose, papillae simple to compound, sometime confluent into transverse or diagonal striate, sparsely distributed on teeth; ventral side of teeth densely reticulate-papillose, with relatively large, compound papillae; remnants of original cell-wall distinct on both sides of teeth, marked by low and filmy trabeculae. Endostome absent. Spores anisomorphic, larger spores 32–40 µm in diameter, smaller spores 20–28 µm in diameter. Calyptra mitrate, plicate, naked, calyptra base fringed or lacerated.

Other descriptions and illustrations: Dozy & Molkenboer (1861) p. 114–115, tab. 91; Fleischer (1904) p. 418–420; Eddy (1996) p. 61–62, fig. 372 as *M. longipilum*, p. 72–74, fig. 381 as *M. perdensifolium*.

Distribution: As. 4: Indonesia (Borneo, Java, New Guinea, Sumatra), Malaysia (Borneo, Malay Peninsula), Papua New Guinea, Philippines (Mindanao).

Habitat and ecology: Canopy epiphyte, often collected from recently fallen branches. This species is restricted to lower montane forest above 1000 m.

Notes:

1. *Macromitrium longipilum* plants are the largest in the genus in Malesia. However, it is apparently not common in Malaysia or neighbouring regions, except in New Guinea, where it has been collected many times (as *M. crinale* in Vitt et al., 1995). The species is easily recognized by the following combination of characters: a) piliferous branch leaves (ending in a long-excurrent costa); b) strongly tuberculate basal laminal cells; and c) long seta. However, the species is very polymorphic, in both its leaf shape and upper laminal cell characters. Traditionally, plants with generally smooth, long-rhomboid to linear upper laminal cells were recognized as *M. crinale* Broth. & Geh., whereas those with papillate and short-rhomboid upper laminal cells were identified as *M. longipilum*. Apart from these, the two taxa are similar in every other aspect. However, the noted differences are often inconsistent and intergrade when more specimens are examined. (Moreover, a similar kind of variation in upper laminal cell characteristics has been shown to be present in a different species, *M. cuspidatum*.) Therefore a wider concept treating *M. crinale* as a synonym of *M. longipilum* is accepted here.

2. Although the species is known to be very variable in leaf shape, three more-or-less consistent variant forms have been recognized in this study, which warrant infraspecific recognition. Specimens identified as *M. longipilum* var. *longipilum* are characterized by

ovate-lanceolate to oblong-lanceolate branch leaves, generally smooth leaf lamina, and unevenly thickened basal laminal cell walls with arched or sigmoid lumina. Further differences among this variety and *M. longipilum* var. *rugosum* and *M. longipilum* var. *ligulatum* are discussed under latter two taxa.

3. Both Dozy & Molkenboer (1861) and Eddy (1996) described the species as having minutely prorate setae. However, in the present study, the setae were found to be mostly smooth and only occasionally prorate at the distal portion.

4. Eddy (1996) considered *M. perdensifolium* (a synonym of *M. longipilum* var. *longipilum*) closely related to *M. yuleanum* Broth. & Geh., a highly variable species which is locally common in, and endemic to, New Guinea and the Solomon Islands. In fact, *M. yuleanum* is more closely related to *M. ochraceum* in many aspects, but can be easily distinguished from *M. longipilum* and its associates by its serrulate leaf margins and percurrent costae.

<u>Specimens examined</u>:

INDONESIA, Kalimantan: W Koetai, Kemoel, 1700 m, X.1925, *Endert 4535* (isotype of *M. perdensifolium*: BM! NY! SING!). **Java:** Preanger, Pengantes pr. Tjibiloe, 2000 m, V.1929, *Veldhuis 10847* (BM!). **Sumatra:** Dolok Soeroengan, Habinsaran, 18.V.1927, *Bartlett 7982* [*c.fr*.] (BM 2 sheets!). **MALAYSIA. Pahang**: Cameron Highland, Mt. Brinchang, 23.XI.1990, *Damanhuri 101* (UKMB!); Genting Highland, 10.IX.1987, *Mohamed s.n*. (KLU!); Genting Highland, Mt. Ulu Kali, 1700 m, 23.VI.1986, *Mohamed 52* (KLU!); *ibidem*, 1730 m, 13.XII.1983, *Damanhuri 3089*, *3106* (UKMB!); *ibidem*, 1745 m, 5.XII.1983, *Damanhuri 2804*, *2842* (UKMB!); *ibidem*, 1770 m, 11.I.1983, *Damanhuri 3817* (UKMB!). **Sabah:** Lahad Datu, Danum Conservation Area, Mt. Danum, 1810 m, 9.VI.1989, Damanhuri s.n. (UKMB!); Ranau, Mt. Kinabalu, trail from Timpohon Gate, 1870 m, 9.V.2005, *Yong 6276* (KLU!); 1990 m, *Yong 6294* (KLU!); Tambunan, Crocker Range Park, Mt. Alab, 1542 m, 13.IV.2002, *Juri 48* (BORH, KLU!, SAN); 1618 m, 17.IV.2002, *Juri 147* [*c.fr*.] (BORH, KLU!, SAN); 1730 m, 9.IX.2008, *Suleiman & Masundang 3837* (BORH, KLU!, SNP); 1780 m, 20.I.2008, *Masundang 106* [*c.fr*.] (BORH, KLU!, SNP); 1800 m, 8.IX.2008, *Suleiman & Masundang 3793*, *3800* [*c.fr*.] (BORH, KLU!, SNP); Tambunan, Mt. Trus Madi, 173 m, 11.IX.1996, *Suleiman 123* [*c.fr*.] (BORH, KLU!, MANCH); Tawau, Maliau Basin, *Eucalyptus* Camp, 970 m, 16–24.VI.2006, *Mohamed & Yong 7188a* [*c.fr*.], *7188b* [*c.fr*.] (KLU!). **Sarawak:** Baram, Mt. Dulit, *s.date*, *Synge 1875* [*c.fr*.] (BM!); Usun Apau Plateau, VII–VIII.2002, *S.P.Teo 30*, *33*, *37*, *40* (KLU!). **PAPUA NEW GUINEA. Central:** Boridi, below the Gap, 7000 ft [=2134 m], 8.I.1936, *Carr 15032* [*c.fr*.] (NY!); Boridi, Uniri [Enili] stream, 6500 ft [= 1981 m], 26.I.1936, *Carr 15255* [*c.fr*.] (NY!). **Eastern Highlands:** Daulo Pass, 8175–8500 ft [= 2492–2591 m], 23.VI.1968, *Weber & McVean B-34131* (COLO, NY!). **Morobe:** Aseki, Aiuwa-Bakia Track, 1500 m, 23.I.1981, *Streimann & Tamba 12369* (H, LAE, NICH, NY!, TBA); Bulolo, Mt. Missim, 3.IV.1984, *Bellamy 1542* [*c.fr*.] (ALTA, CBG, LAE, NICH, NY!); Bulolo, Slate Creek and Gumi Creek Divide, 2100 m, 30.I.1981, *Streimann 13776* (H, LAE, NY!); Siwea, Cromwell Mts., 1800–2100 m, 14.VI.1981, *Norris 62026* (H, HSC, NY!); *ibidem*, 2100–2200 m, 11.VI.1981, *Norris 61400* (TNS!); *ibidem*, 2200–2250 m, 11.VI.1981, *Koponen 30240* [*c.fr*.] (H, HSC, NY!); Wau, Mt. Kaindi, 9.I.1983, *Streimann 33253* (H, NY!); *ibidem*, 2000 m, 13.II.1983, *Streimann 33998* [*c.fr*.] (H, NY!). **West Sepik:** Star Mts., Mt. Antares, 2600 m, 22.VII.1959, *Zanten 656* [*c.fr*.] (L, NY!); *ibidem*, 3000 m, 20.VII.1959, *Zanten 648* (L, NY!). **PHILIPPINES. Mindanao:** Misamis Oriental, Mt. Lumot, Barangay Lunutan, 1300 m, 24.VIII.1999, *Bernabe & Schumm 4023* (SING!).

11. ***Macromitrium longipilum*** **var.** ***ligulatum*** **var. nov. ined. prop.** (Figs. 5.36 & 5.37)

PROPOSED TYPE: Crocker Range Park, Mt. Alab, 1780 m, 20.I.2008, *Masundang 106* (holotype BORH!; isotypes KLU! SNP).

Plant robust, forming short-cushions or mats; young shoots yellowish-green, gradually turning to olive-green and brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5–1.0 cm tall and 6–8 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender-lanceolate on young shoots, elongate at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, densely arranged, indistinctly funiculate, leaves flexuose, more or less spiral on branch, with curved to occasionally deflexed apices (when dry), erect-spreading to wide-spreading with flexuose lamina (when moist); branch leaves 4.6–5.2 × 0.5–0.6 mm, length-width ratio 8–10:1, slender lanceolate to ligulate-lanceolate, lamina straight, twisted, plane; apex firm, long, slender-acuminate; margin subentire to crenulate, plane at distal part but reflexed at base; costa long-excurrent, piliferous, ending in a 0.5–0.9 mm long hyaline arista. Upper laminal cells 12–20 × 8–10 µm, length-width ratio 1.5–2:1, rhombic to long-rectangular, evenly thick-walled, occasionally pitted, flat, smooth, lumen linear; middle laminal cells 12–30 × 8–10 µm, grading from narrow-rhombic to gradually long-rectangular toward the basal lamina, incrassate, pitted, with linear lumina, cells smooth, clear; basal laminal cells 38–68 × 9–14 µm, length-width ratio 4–6:1, long-rectangular, incrassate, walls mostly evenly thickened, lumina 3–4 µm wide, linear, pitted, cells flat, unipapillose, low, sparsely found at basal lamina, more often seen near leaf insertion and juxtacostal region.

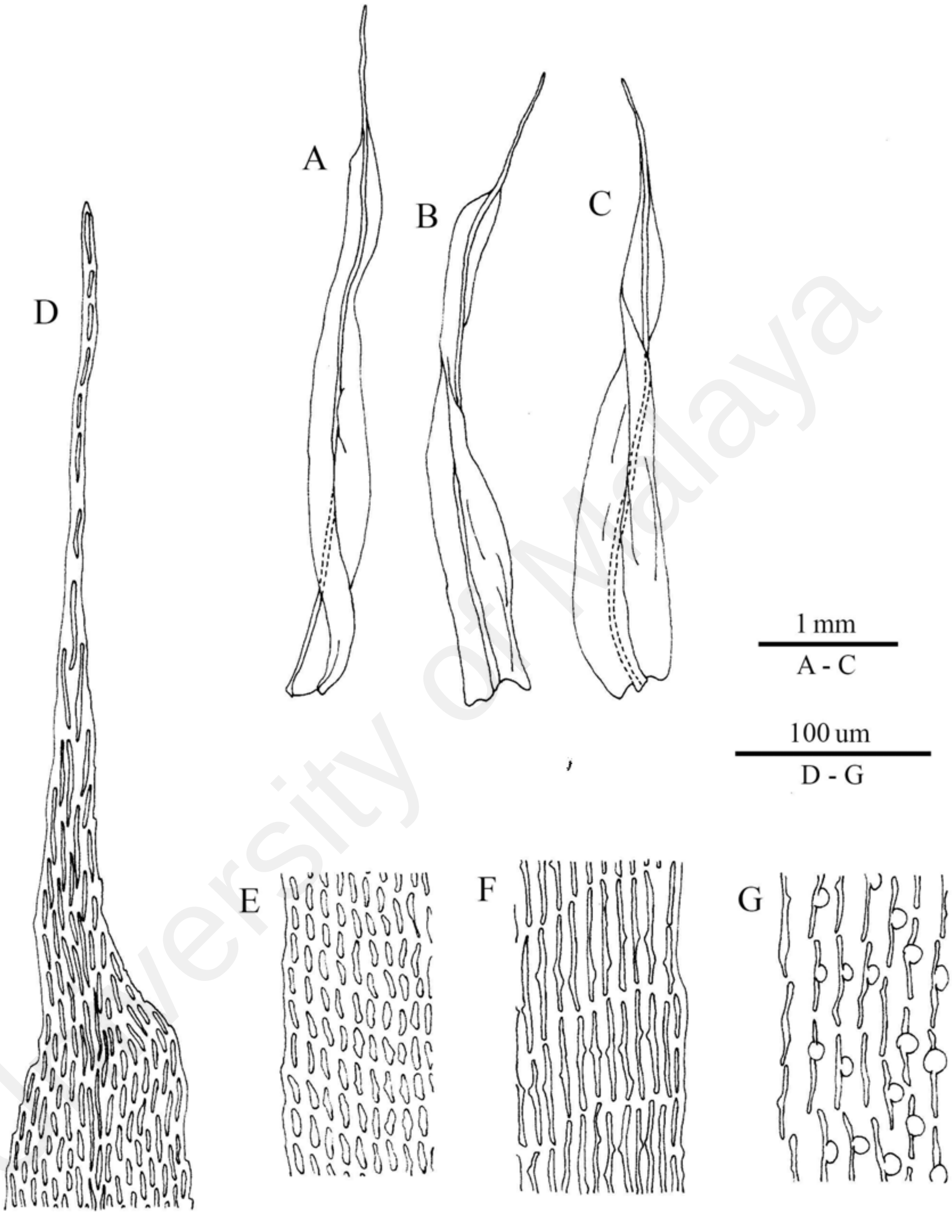

Figure 5.36. Illustrations of *Macromitrium longipilum* var. *ligulatum* var. nov. ined. prop. — A-C, branch leaves; **D,** leaf apex; **E,** upper laminal cells; **F,** mid-leaf cells; **G,** basal laminal cells [**A-B, D-G** from *Holttum 20844* (KLU); **C** from *Damanhuri 102* (UKMB)]

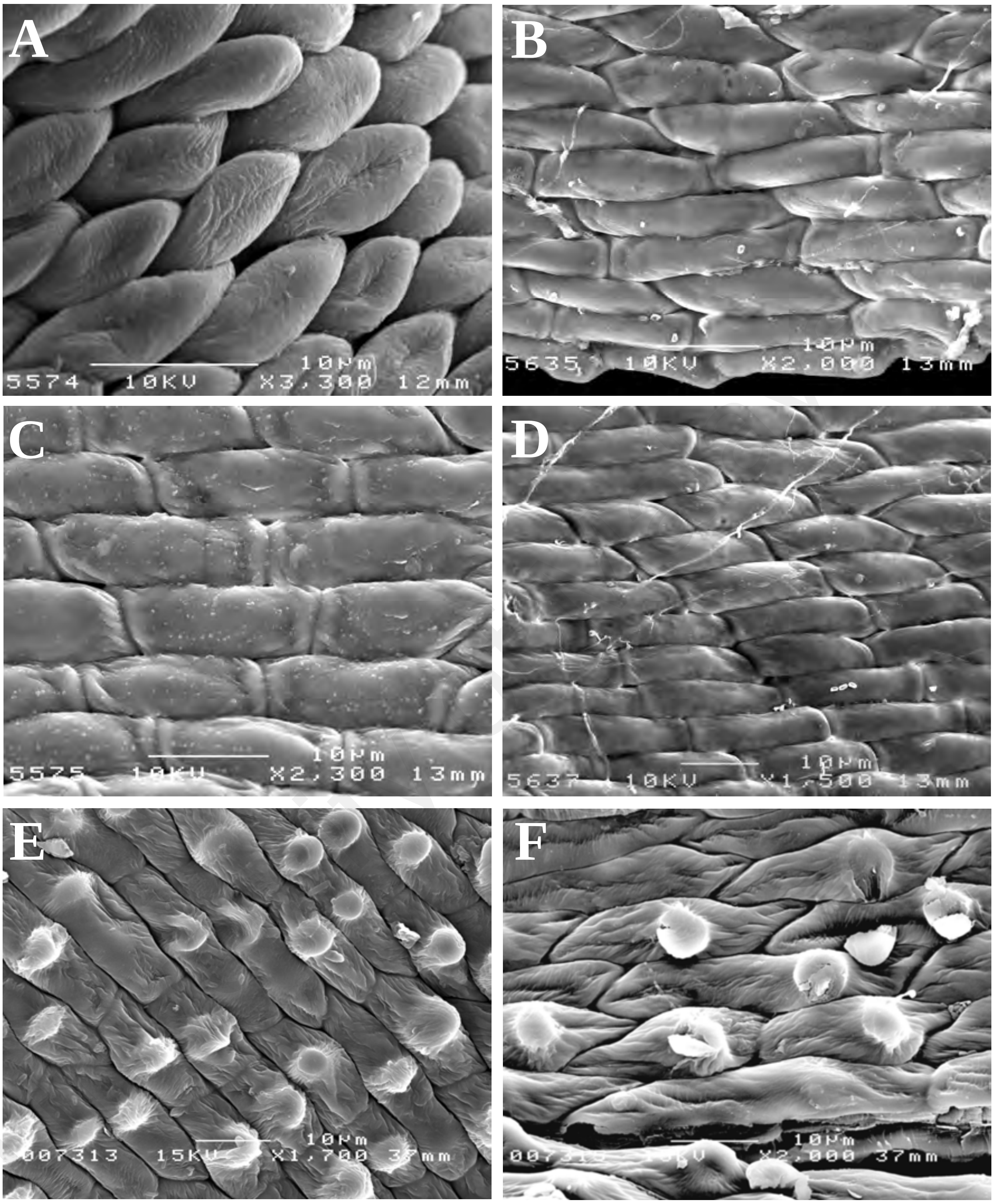

Figure 5.37. SEM images of *Macromitrium longipilum* var. *rugosum* var. nov. ined. prop. (A, C, E) and *Macromitrium longipilum* var. *ligulatum* var. nov. ined. prop. (B, D, F) — A-B, upper laminal cells; **C-D,** mid-leaf cells; **E-F,** basal laminal cells. [**A, C & E** from *Mohamed & Bakar 3093b* (KLU); **B, D & F** from *Holttum 20844* (KLU)]

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, about the size of the branch leaves, 4.5–4.8 × 0.6–0.7 mm, slender-laceolate, upper lamina narrow, expanding gradually toward mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender acuminate, cuspidate or piliferous; margin subentire, plane; costa short to long-excurrent, ending in a cusp or hyaline arista; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 1.5–1.6 mm long; paraphyses abundant, densely covering the vaginula, 0.5–0.6 mm long, made of 10–13 short- or long-rectangular cells. Seta 25–28 mm long, smooth, dextrorse or sinistrorse-twisted. Capsule urns 1.7–1.9 × 1.0–1.2 mm, short-ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, phaneroporous; operculum rostrate, beak 0.9–1.1 mm. Peristome single. Exostome teeth fused into a continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal side of teeth variously papillose, papillae simple to compound, sometime confluent into transverse or diagonal striate, sparsely distributed on teeth; ventral side of teeth densely reticulate-papillose, with relatively large, compound papillae; remnants of original cell-wall distinct on both sides of teeth, marked by low and filmy trabeculae. Endostome absent. Spores anisomorphic, larger spores 30–38 µm in diameter, smaller spores 22–28 µm in diameter. Calyptra mitrate, plicate, naked, calyptra base fringed or lacerated.

Distribution: Endemic to Malay Peninsula and Borneo (Sabah and Kalimantan) (As. 4).

Habitat and ecology: Epiphytic on tree branches and buttresses. The variety occurs at 1000–1800 m in the lower montane and upper montane zones, mostly collected from mossy forest sites.

<u>Note</u>:

Macromitrium longipilum var. *ligulatum* is characterized by its distinctly narrow, ligulate-lanceolate branch leaves, which clearly differentiates it from var. *longipilum* and var. *rugosum*. On the other hand, the almost smooth basal lamina, where cells are irregularly smooth or unipapillate, also helps to separate this variety from the other two varieties, which have consistently unipapillate to tuberculate basal laminal cells.

<u>Specimens examined</u>:

INDONESIA. Kalimantan: East Kutai, Peak of Bt. Papan, Sulau Mandau, 1000 m, 7.VII.1952, *Meijer B181* [*c.fr.*] (SING!). **MALAYSIA. Pahang:** Cameron Highlands, Mt. Brinchang, 1810 m, 23.XI.1990, *Damanhuri 102* (UKMB!); Taman Negara, Kuala Tahan, Mt. Tahan, Sg. Reriang, 27.VIII.1928, *Holttum 20844* (SING!). **Sabah:** Crocker Range Park, Mt. Alab, 1780 m, 20.I.2008, *Masundang 106* [*c.fr.*] (holotype of *M. longipilum* var. *ligulatum*: BORH! isotype KLU! SNP); Crocker Range Park, Papar, Between Ulu Kimanis basecamp and telecommunication tower, 1150 m, 2.IX.2002, *Akiyama Crocker-227* (BORH! HYO); Ranau, Kinabalu Park, Mt. Tambuyukon, Musang Camp (km 10) to the summit, 1450 m, 14.VIII.2008, *Suleiman 3658* (BORH, KLU! SNP); *ibidem*, 1470 m, 14.VIII.2008, *Suleiman 3663* (BORH, KLU! SNP); *ibidem*, 1550 m, 14.VIII.2008, *Suleiman 3678* (BORH, KLU! SNP).

12. *Macromitrium longipilum* var. *rugosum* var. nov. ined. prop. (Figs. 5.37 & 5.38)

PROPOSED TYPE: Malaysia, Penang, Penang Hill, summit area, vicinity of Convalescent Bungalow, 730 m, 21.VIII.2005, *Mohamed & Yong 6526* (holotype KLU!).

Plant robust, forming short-cushions or mats; young shoots yellowish-green, gradually turning to olive-green and brownish at mature portions, brownish to darker below.

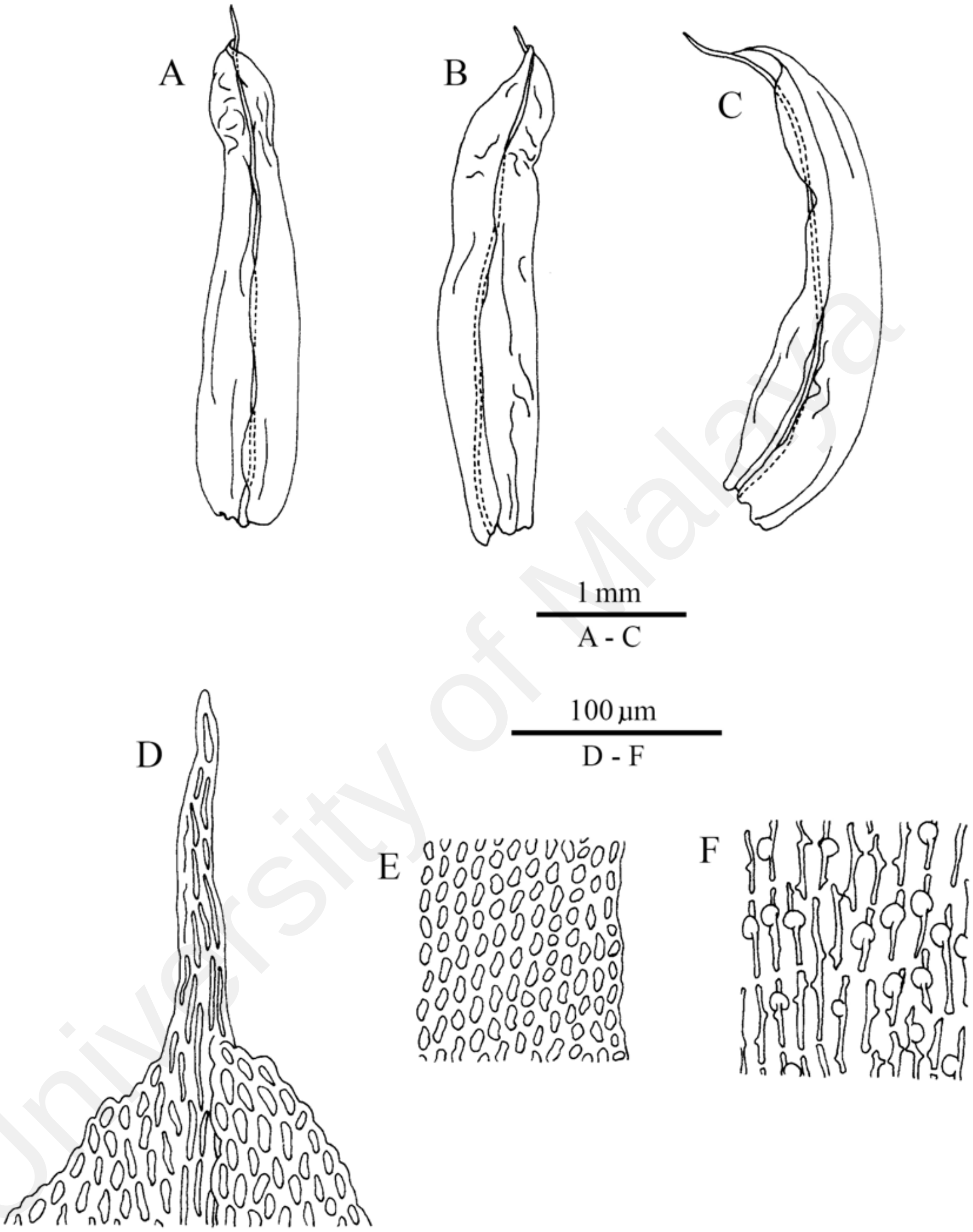

Figure 5.38. Illustrations of *Macromitrium longipilum* var. *rugosum* var. nov. ined. prop. — A-C, branch leaves; **D,** leaf apex; **E,** mid-leaf cells; **F,** basal laminal cells [**A, D-F** from *Mohamed & Bakar 3093b* (KLU); **B** from *Mohamed & Yong 6526* (KLU); **C** from *Juri 162* (BORH)]

Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5–1.0 cm tall and 5–7 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender-lanceolate on young shoots, elongate at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, densely arranged, indistinctly funiculate, leaves flexuose, more or less spiral on branch, with curved to occasionally deflexed apices (when dry), erect-spreading to wide-spreading with flexuose lamina (when moist); branch leaves 3.5–3.8 × 0.7–0.8 mm, length-width ratio 5:1, slender lanceolate to lingulate, lamina straight, distinctly rugose at upper lamina; apex firm, slender to broad, acute to acuminate, cuspidate; margin subentire to crenulate, plane at distal part but reflexed at base; costa excurrent, ending in a 0.1–0.2 mm long cusp. Upper laminal cells 14–18 × 8–10 µm, length-width ratio 1.5–2:1, short-rhombic, evenly thick-walled, not pitted, flat or low-bulging, lumen elliptic; middle laminal cells 10–14 × 8–10 µm, grading from rhombic to gradually long-rectangular toward the basal lamina, incrassate, not pitted, with long-elliptic lumina, cells smooth or low-bulging, clear; basal laminal cells 36–60 × 10–14 µm, length-width ratio 4–6:1, long-rectangular, incrassate, walls mostly evenly thickened, lumina 3–4 µm wide, linear, pitted, cells flat, unipapillose, low, papillae more pronounced only near leaf insertion.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, 3.5–3.6 × 0.6–0.7 mm, slender-laceolate, upper lamina narrow, expanding gradually toward mid-leaf to form a long-oblong leaf base, leaf base often with a few long-plications; apex slender acuminate, cuspidate; margin subentire, plane; costa short-excurrent ending in a cusp; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Sporophytic structure not available.

Distribution: Endemic to Malaysia. As. 4: Malaysia (Borneo, Malay Peninsula).

Habitat and ecology: Epiphytic on tree trunks, occasionally collected from rotten logs. The variety is documented from 730–1620 m in the submontane and lower montane zones. It has been collected from primary forest and garden trees in rather open sites.

Note:

Macromitrium longipilum var. *rugosum* is distinguished from var. *longipilum* and var. *ligulatum* by its distinctly rugose upper lamina. In the other varieties, the branch leaves are smooth. Also, the leaf costa of this variety is always shorter than those found in the two other varieties, and gives rise to a cuspidate, but not long-piliferous apex.

Specimens examined:

MALAYSIA. Penang: Penang Hill, summit area, Convalescent Bungalow, 730 m, 21.VIII.2005, *Mohamed & Yong 6526* (holotype of *M. longipilum* var. *rugosum*: KLU!). **Sabah:** Tambunan, Mt. Alab, 1620 m, 17.IV.2002, *Juri 152* (BORH!, KLU!, SAN). **Sarawak:** Kuching, Kubah National Park, Mt. Serapi, summit, 21.VII.1991, *Mohamed & Bakar 3093b* (KLU!).

13. *Macromitrium macrosporum* Broth. (Figs. 5.39 & 5.40)

Oefvers. Förh. Finska Vetensk.-Soc. 40: 168 (1898). LECTOTYPE (Vitt et al., 1995): British New Guinea, Mt. Scratchley, 12200 ft [=3719 m], *Giulianetti s.n.* (H-BR; isolectotype BM!).

M. goniostomum Broth., Philipp. J. Sci. 5: 145 (1910). LECTOTYPE (Vitt et al., 1995): Philippines, Luzon, Benguet, Pauai, 2100 m, VI.1909, *McGregor 8697* (H-BR; isolectotype BM!) — fide Vitt et al. (1995).

M. aspericuspis Dixon, Ann. Bryol. 12: 51 (1939). TYPE: Indonesia, Sumatra, Mt. Losir, on bark of tree, 3250–3400 m, 4.II.1937, *van Steenis 10156* (holotype L; isotype BM) — fide Vitt et al. (1995).

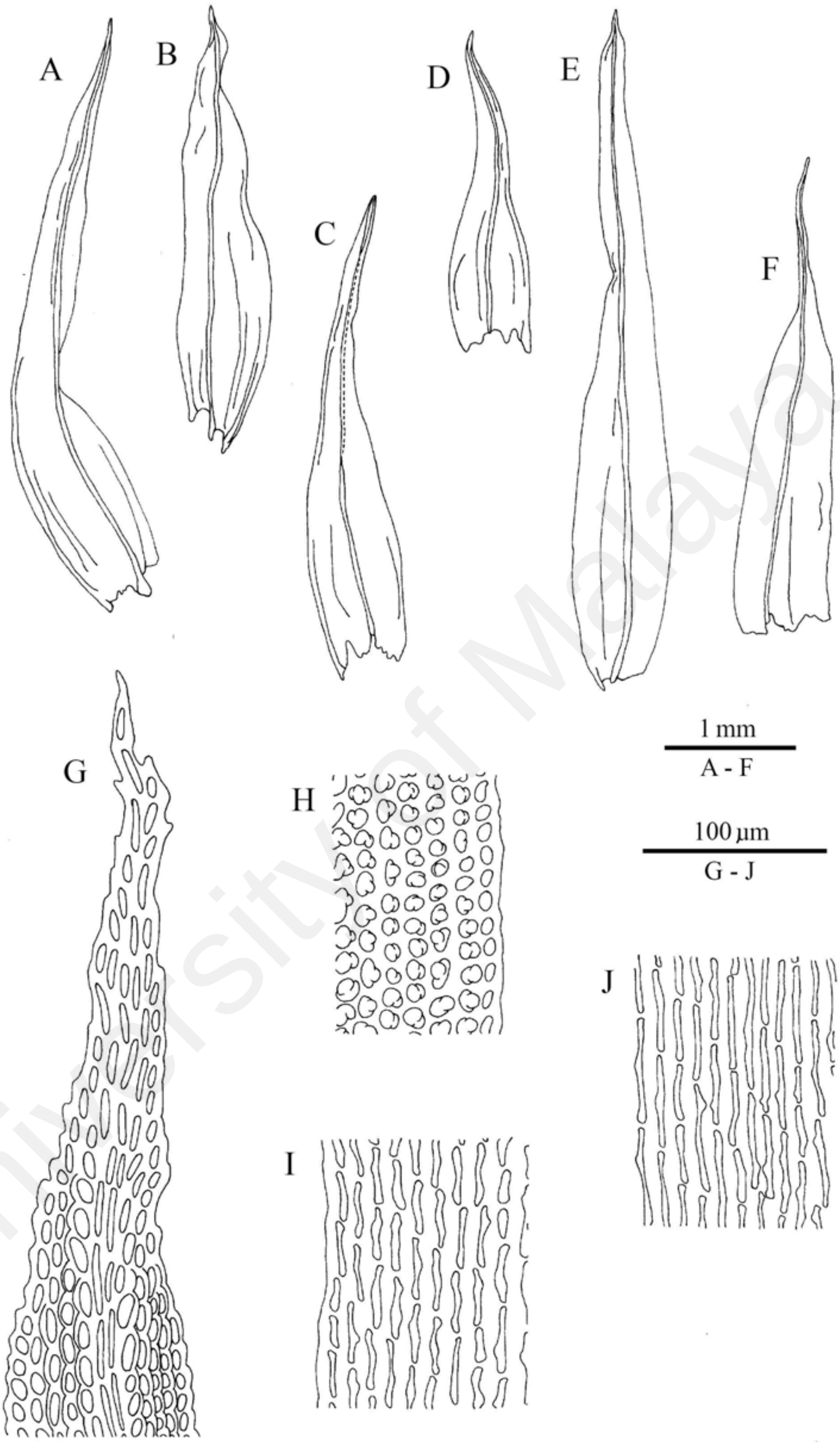

Figure 5.39. Illustrations of *Macromitrium macrosporum* Broth. — A-E, branch leaves; **F,** perichaetial leaf; **G,** leaf apex; **H,** upper laminal cells; **I,** mid-leaf cells; **J,** basal laminal cells. [**A, F** from *Akiyama et al. 183* (BORH); **B** from *Eddy 121* (BM); **C** from *Sinclair et al. 9149* (SING); **D** from *Giulianetti s.n.* (BM, lectotype); **E, G-J** from *Yong 6373* (KLU)]

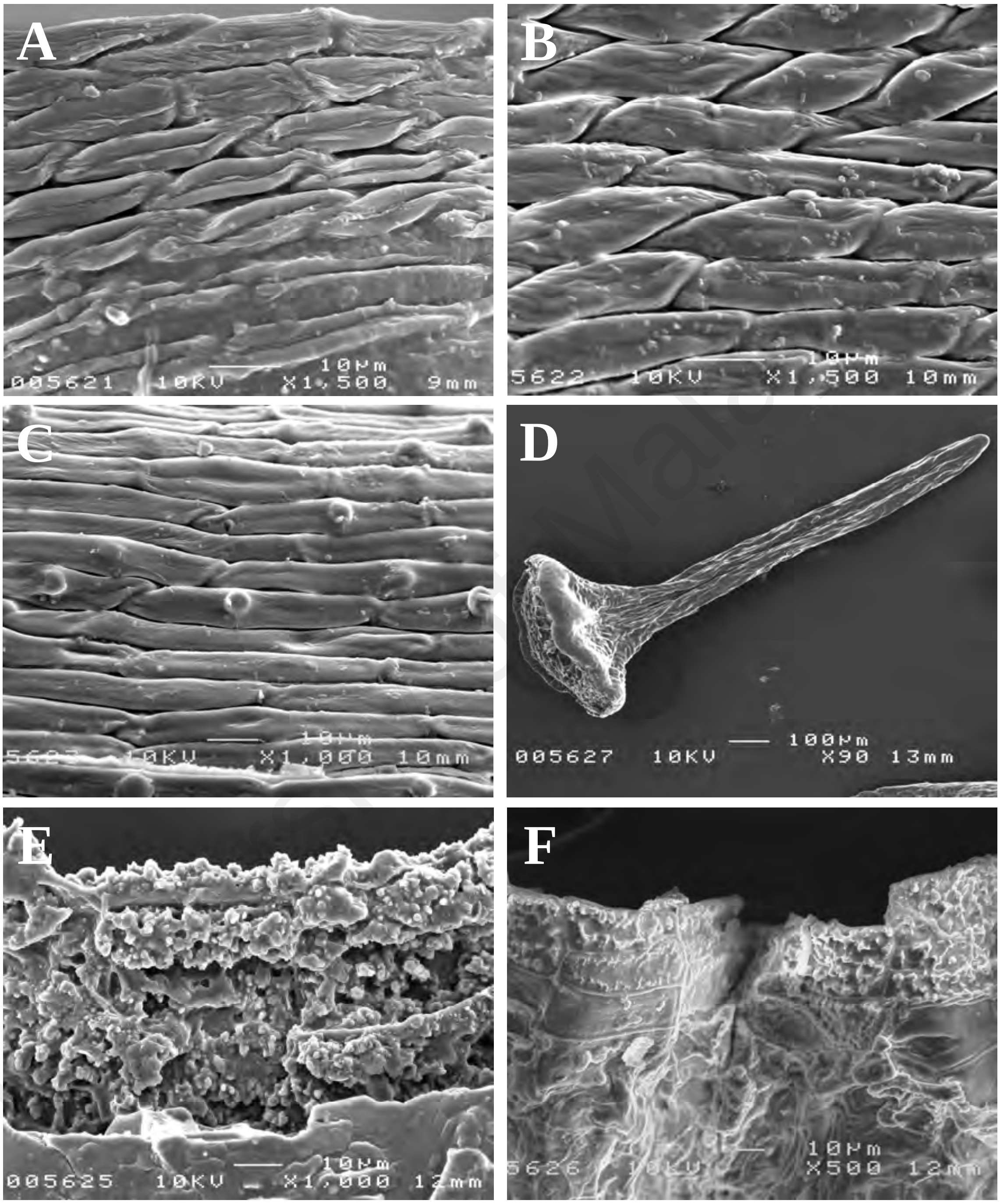

Figure 5.40. SEM images of *Macromitrium macrosporum* Broth. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** operculum; **E,** dorsal view of unsplit peristome teeth; **F,** ventral view of unsplit peristome teeth. [All from *Sinclair et al. 9149* (SING)]

M. *morobense* Bartram, Bryologist 48: 117 (1945). TYPE: Papua New Guinea, Morobe, Rawlinson Range, 7000–12000 ft [=2134–3658 m], *Clemens 12448* (holotype FH! isotypes F, NY) — fide Vitt et al. (1995).

M. *kinabaluense* J. Froehl., Rev. Bryol. Lichénol. 31: 92 (1962), ***syn*. *nov***. TYPE: North Borneo, Kinabalu, summit region, 10000–13000 ft [=3048–3962 m], 9.III.1961, *Meijer s.n*. (holotype S!).

M. *hamatum* Bartram, Bryologist 48: 117 (1945), *nom*. *illeg*., non Dixon (1937).

Plant robust, cushions-forming; young shoots olive-green, gradually turning to brownish and reddish-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches tall, 2.5–4.0 cm tall and 6–8 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender, triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, densely arranged, leaves erect-flexuose with curved to irregular-twisted apices (when dry), erecto-patent to erect-spreading (when moist); branch leaves 3.6–4.8(–5.5) × 0.7–0.8 mm, length-width ratio 5–7:1, slender lanceolate to ligulate-lanceolate, lamina straight to gently bent, plane; apex firm, long, slender-acuminate; margin subentire to crenulate, plane at distal part but deflexed at base; costa percurrent or filing the acumen. Upper laminal cells 10–18 × 8–10 µm, length-width ratio 1–2:1, oblate to rhombic, evenly thick-walled, not pitted, strongly bulging to conical-papillose; middle laminal cells 20–38 × 8–12 µm, grading from narrow-rhombic to gradually long-rectangular toward the basal lamina, incrassate, not pitted, with linear lumina, cells strongly bulging to conical-papillose, clear; basal laminal cells 42–70(–80) × 8–14 µm, length-width ratio 5–8:1, long-rectangular, incrassate, walls more or less evenly thickened, lumina 2–3 µm wide, linear, pitted only near juxtacostal region and insertion, cells flat, unipapillose or sometime smooth, especially at juxtacostal region and toward leaf margin, papillae generally low.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, much smaller than the branch leaves, 3.5–3.8 × 0.6–0.7 mm, broad-lanceolate, upper lamina long and narrow, expanding abruptly toward mid-leaf to form a long-oblong base, leaf base often with a few long-plications; apex slender, long-acuminate, apiculate to cuspidate; margin subentire, plane; costa shortly excurrent, ending in a cusp; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 1.6–1.8 mm long; paraphyses abundant, densely covering the vaginula, 0.8–0.9 mm long, made of 10–14 short- or long-rectangular cells. Seta 20–25 mm long, smooth, sinistrorse-twisted. Capsule urns 1.8–2.0 × 0.8–1.0 mm, ellipsoid to oblong, smooth, rim rounded or sulcate into eight angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.9–1.2 mm. Peristome single. Exostome teeth fused into a continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal side of teeth strongly papillose, papillae simple to compound, irregularly on “coralloid” wall thickenings; ventral side of teeth variously reticulate-papillose, sometime weak, with relatively small papillae; remnants of original cell-wall obscure on dorsal side, hidden by the “coralloid” wall thickenings, but distinct on ventral side, marked by low trabeculae. Endostome absent. Spores anisomorphic, larger spores 32–40 µm in diameter, smaller spores 16–24 µm in diameter. Calyptra mitrate, plicate, naked, calyptra base fringed and lacerated.

Other descriptions and illustrations: Bartram (1939) p. 183, pl. 14, fig. 228, as *M. goniostomum*; Vitt et al. (1995) p. 42–45, figs. 18, 39; Eddy (1996) p. 68, fig. 376 as *M. macrosporum*, p. 68–70, fig. 377 as *M. aspericuspis*, p. 70, fig. 378 as *M. goniostomum*.

Distribution: As. 2: China; As. 3: Thailand (Northern, Southeastern); As. 4: Indonesia (New Guinea, Sulawesi, Sumatra), Malaysia (Borneo), Papua New Guinea, Philippines (Luzon, Mindanao).

Habitat and ecology: Epiphytic on tree trunks and branches in rather open sites, often in subalpine scrub. In Malesia, the species is usually found above 3000 m, in the upper montane and subalpine zones; it has been collected as low as 2400 m in the Philippines (*Tan et al. 82-211*, TNS).

Notes:

1. In Malaysia, *M. macrosporum* is apparently rare; it has only been collected a few times on Mount Kinabalu. The species shares the habit of *M. angustifolium*. However, unlike the latter, *M. macrosporum* has conic-papillate upper laminal cells and tuberculate basal laminal cells. Outside Malaysia, the plant might be confused with *M. yuleanum* Broth. & Geh., a species common only to Western Melanesia (New Guinea and the Solomon Islands). *Macromitrium macrosporum* can be distinguished from the latter species by its erecto-patent to erect-spreading branch leaves (when moist) and almost entire leaf margins. *Macromitrium yuleanum*, however, has squarrose-recurved leaves with typically papillose-denticulate margins.

2. Material from Mount Kinabalu matches the isotype of *M. macrosporum* (*Giulianetti s.n.*, BM), except in its more robust plants which fit the description of *M. aspericuspis* (synonym of *M. macrosporum*, type from Sumatra). As noted by Vitt et al. (1995) and Eddy (1996), *M. macrosporum* is actually a very polymorphic species that can be variable in plant size and leaf cell ornamentation. Therefore, a broad concept of the species is preferred here.

3. *Macromitrium macrosporum* has been described as autoicous in the original publication, but only female plants were documented in a later publication by Vitt et al. (1995). The present study has found that the species is actually phyllodioicous, with

infrequent presence of dwarf male plants.

4. I have examined the type materials of *M. kinabaluense* and could not detect any morphological differences from *M. macrosporum*, so that name is reduced to synonymy.

Specimens examined:

MALAYSIA. Sabah: Ranau, Kinabalu Park, Mt. Kinabalu, 10700 ft [=3261 m], 13.VI.1957, *Sinclair et al*. *9149* [*c.fr*.] (SING!); *ibidem*, 10000–13000 ft [=3048–3962 m], 9.III.1961, *Meijer s.n*. [*c.fr*.] (holotype of *M*. *kinabaluense*: S!); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Panar Laban to Paka Cave, 3090 m, 10.V.2005, *Yong 6327* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, Panar Laban to Sayat-Sayat Checkpoint, 3330 m, 11.V.2005, *Yong 6362* (KLU!); *ibidem*, 3380 m, 11.V.2005, *Yong 6373* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, route from Panar Laban to summit of Mt. Kinabalu, 3450 m, 16.I.1997, *Akiyama et al*. *183* (HYO, BORH!). **PAPUA NEW GUINEA. Central:** Mt. Albert Edward, 3680 m, V–VII.1933, *Brass 4440* [*c.fr*.] (NY!); Owen Stanley Range, Mt. Scratchley, 12200 ft [=3719 m], *s.date*, *Giulianetti s.n*. [*c.fr*.] (isolectotype of *M*. *macrosporum*: BM!). **Eastern Highlands:** Mt. Wilhelm, 3500 m, 1.III.1965, *Eddy 2589 pp* [*c.fr*.] (BM!). **Morobe:** Mt. Sarawaket Southern Range, Sankwep River, 3500–3570 m, 9.VII.1981, *Koponen 32657* [*c.fr*.] (H, HSC, NY!). **West Sepik:** Star Mts., Mt. Auriga, Silil'katibin, 3450 m, 26.IV.1975, *Touw 16777* [*c.fr*.] (NY!); Star Mts., Mt. Capella, 3450 m, 14.IV.1975, *Touw 16240* [*c.fr*.] (NY!); *ibidem*, 5.V.1975, *Touw 17205* (NY! TNS!); *ibidem*, 3600 m, 17.IV.1975, *Touw 16376* [*c.fr*.] (NY!); *ibidem*, 3650 m, 8.V.1975, *Touw 17312* [*c.fr*.] (NY!); *ibidem*, 3900 m, 19.IV.1975, *Touw 16420* [*c.fr*.] (NY!); *ibidem*, 8.V.1975, *Touw 17369* [*c.fr*.] (NY!). **PHILIPPINES. Luzon:** Benguet, Bokod, Mt. Pulog, 2400 m, 13.V.1982, *Tan et al*. *82-211* [*c.fr*.] (TNS!).

14. ***Macromitrium nepalense*** **(Hook. & Grev.) Schwägr.** (Figs. 5.41 & 5.42)

Sp. Musc. Frond., Suppl. 2, 2 (2): 134, tab. 192 (1827). *Orthotrichum nepalense* Hook. & Grev. Edinb. J. Sci. 1: 117, tab. 4. (1824). *Leiotheca nepalensis* (Hook. & Grev.) Brid., Bryol. Univ. 1: 732 (1826). TYPE: Dhoopabasah and Beahico in Nepaul, *Wallich s.n.* (holotype BM).

Plant medium-sized, forming cushions or mats; young shoots yellowish-green, gradually turning olive-green or rusty-brown when mature, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches, short to fairly tall, 1.5–2(–3) cm tall and 3–4 mm wide, tightly arranged, rarely branched. Stem leaves inconspicuous, small, covered by rhizoids, lanceolate on young shoots, ligulate-lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, leaves twisted-contorted, with individual leaves irregularly inrolled, apices incurved or hidden by the strongly involute laminae (when dry), erect-spreading to wide-spreading with inflexed lamina (when moist); branch leaves 1.6–2.4 × 0.4–0.6 mm, length-width ratio 4–5:1, long, ligulate-lanceolate with an oblong base, lamina straight to gently bend inward, plane; apex firm, broadly acute to mucronate; margin subentire to crenulate, plane at distal part but reflexed at base; costa short-excurrent with 1–2 cells extending beyond the tip. Upper and middle laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, rounded to oblate, moderately thick-walled, walls not pitted, cells bulging, densely pluri-papillose, cells opaque; basal laminal cells 18–35 × 8–10 µm, length-width ratio 3.5–4.5:1, long-rectangular, incrassate, walls evenly thickened, lumina 2–4 µm wide, linear, pitted only near juxtacostal region and insertion, cells flat, unipapillose to tuberculate.

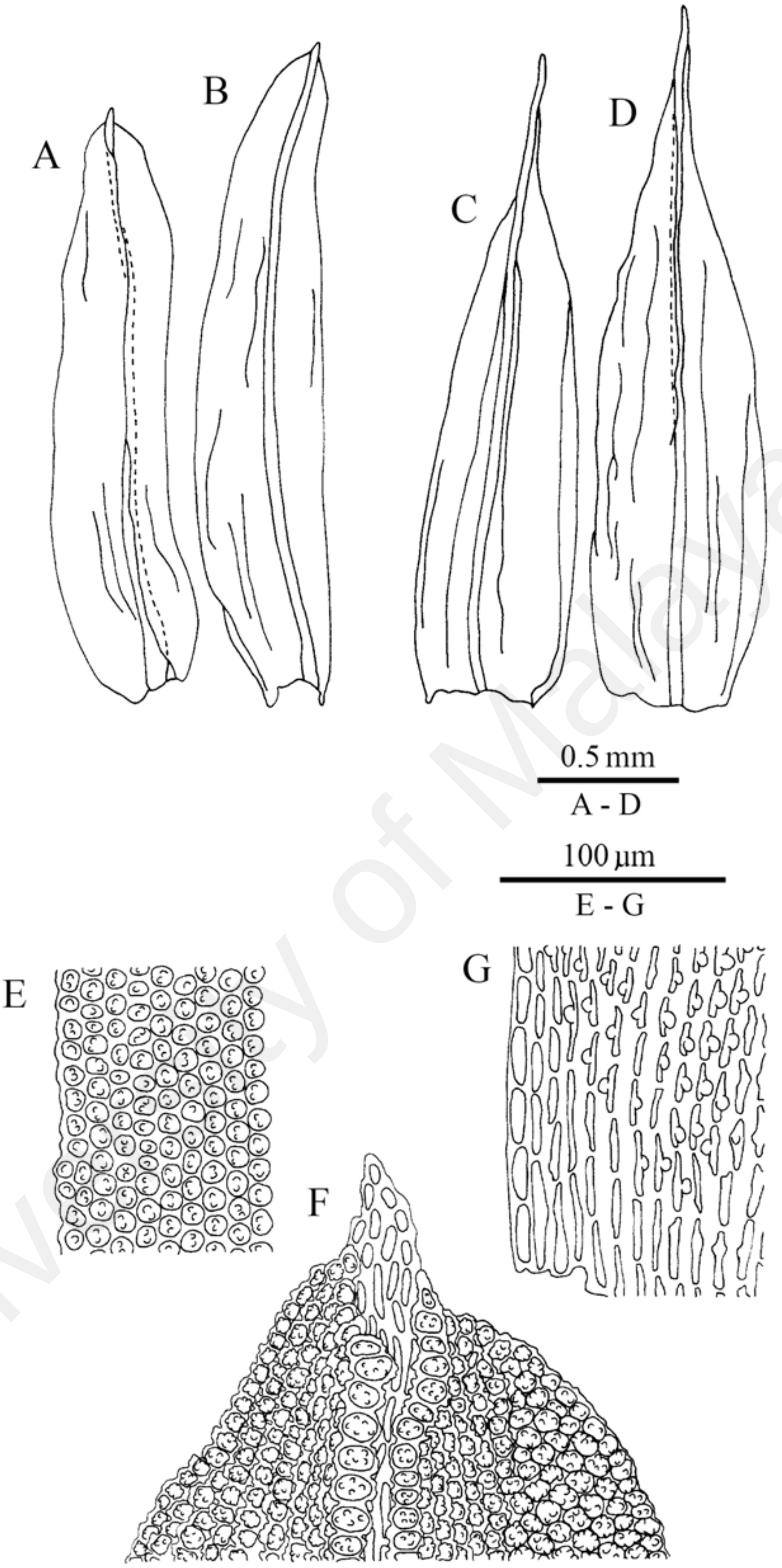

Figure 5.41. Illustrations of *Macromitrium nepalense* (Hook. & Grev.) Schwägr. — A-B, branch leaves; **C-D,** perichaetial leaves; **E,** mid-leaf cells; **F,** leaf apex;**G,** basal laminal cells. [All from *Damanhuri s.n.* (UKMB)]

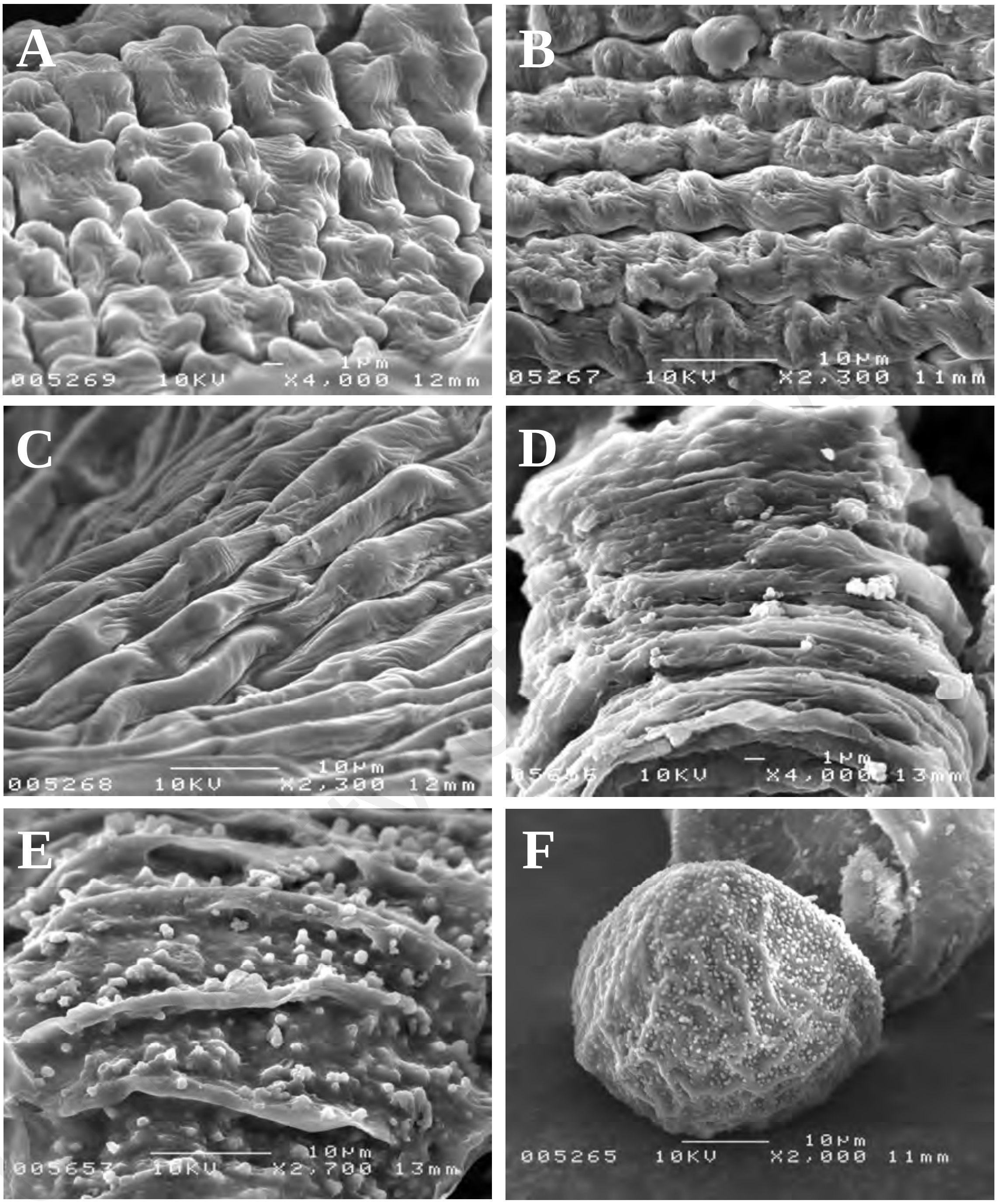

Figure 5.42. SEM images of *Macromitrium nepalense* (Hook. & Grev.) Schwägr. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** dorsal view of peristome teeth; **E,** ventral view of peristome teeth; **F,** detail of a macrospore. [All from *Damanhuri s.n.* (UKMB)]

Pseudoautoicous, dwarf male plants bud-like, small, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, usually much larger than branch leaves, 2.3–2.6 × 0.5–0.6 mm, more or less subulate-lanceolate, upper lamina narrow, expanding abruptly below apex to form a long-oblong base, leaf base often with a few long-plications; apex slender, long-acuminate, occasionally apiculate; margin subentire to entire, plane; costa percurrent or short-excurrent ending in an apiculus; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginulae 1.0–1.4 mm long; paraphyses abundant, densely covering the vaginula, 0.35–0.5 mm long, made of 8–10 short to long-rectangular cells. Setae 7–10 mm long, smooth, dextrorse or sinistrorse-twisted. Capsule urns 2.5–3.0 × 1.0–1.5 mm, long-ellipsoid to broad-cylindric, smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, phaneroporous; operculum rostrate, beak 0.9–1.0 mm. Peristome single. Exostome of 16 teeth that are separated above but connected at their base as a low membrane, erect to slightly incurved at top in both dry and wet conditions; dorsal side of teeth vertically striolate-papillose, dense, papillae wart-like to simple, scattered on coarse horizontal ridges; ventral side of teeth densely, reticulate-papillose with simple to compound papillae; remnants of original cell-wall obscure on dorsal side, hidden by horizontal ridges, but distinct on ventral side, marked by low and thick trabeculae. Endostome absent. Spores anisomorphic, larger spores 38–46 µm in diameter, smaller spores 12–22 µm in diameter. Calyptra mitrate, plicate, densely hairy, hairs long, stiff erect and mostly arise from the calyptra base, calyptra base fringed or lacerated.

Other descriptions and illustrations: Bartram (1939) p.175, pl. 13, fig. 216; Gangulee (1976) p. 1183–1184, fig. 575; Eddy (1996) p. 42, fig. 354.

Distribution: As. 2: China (Hong Kong, Yunnan); As. 3: Bangladesh, Cambodia, India (Arunachal, Assam, Kerala, Madras, Naga Hills, Sikkim, Western Ghats), Laos, Myanmar, Nepal, Pakistan, Sri Lanka, Thailand (Northern, Northeastern, Peninsula), Vietnam; As. 4: Indonesia (Sulawesi), Malaysia (Malay Peninsula), Philippines (Luzon)

Habitat and ecology: Epiphytic on tree trunks and branches, also common on rocks. The species is more common in open areas (e.g., savannah, disturbed forest) rather than in primary forest. The plant has a wide altitudinal range, from sea level to 2000 m.

Notes:

1. *Macromitrium nepalense* is common in the Indian subcontinent and Indochinese region, but sporadic in Malesia. The species resembles a large version of *M. falcatulum* and can only be distinguished from the latter by its larger plant and leaf sizes, longer seta, and longer hairs on the calyptra. In addition, the leaf base of *M. nepalense* mostly has long-rectangular cells that are at least three times longer than the upper laminal cells, whereas the leaf base of *M. falcatulum* has mostly short cells, with longer cells forming the last few rows before leaf insertion.

2. The species is characterized by its unique perichaetial leaves, which are lanceolate and end in a subulate apex, always much larger than the vegetative leaves, and erect and sheathing the seta base. These are good characters for distinguishing the species from its congeners.

3. Dixon (1926) first recorded the species for Peninsular Malaysia based on scanty material collected from Singapore (*Ridley 806*, SING), and his identification is hereby confirmed. The species was not documented again until Damanhuri (2000) reported it from the Belum Forest Reserve, Perak. However, that collection, *Damanhuri 99-478* (UKMB), is actually a plant of *M. falcatulum*.

Specimens examined:

CHINA. Fujian: Wuyishan, 19.VII.1980, *Lin 144a* [*c.fr.*] (NY!). **Hainan:** Ka-en, Mt.

Chim Fung, 2–31.I.1935, *Lau 5374* [*c.fr*.] (NY!). **Hong Kong:** *s.loc*., *s.date*, *s.coll*. *6* [*c.fr*.] (NY!). **BANGLADESH:** Khasia, *s.date*, *Griffith 44* [*c.fr*.] (NY!); Mt. Khasia, *s.date*, *s.coll*. [*c.fr*.] (NY!). **INDIA:** *s.loc*., *s.date*, *Griffith 38* [*c.fr*.] (NY!); *s.loc*., IX.1852, *Falconer s.n*. [*c.fr*.] (NY!). **Assam:** *s.loc*., *s.date*, *Burkill 36485* (SING!); *s.loc*., 16.XII.1911, *Burkill 37185* (SING!); *s.loc*., 19.XII.1911, *Burkill 37255* (SING!); *s.loc*., 900 m, 7.I.1912, *Burkill 37723* (SING!). **Kerala:** Nilgiri Mts., *s.date*, *Beddome 38* [*c.fr*.] (NY 2 sheets!). **Madras:** Madura, Palni Hill, Kodaikanal, *s.date*, *Foreau 1923*, *1925* [*c.fr*.] (TNS! NY). **Sikkim:** *s.loc*., 2000 m, *s.date*, *s.coll*. *214* [*c.fr*.] (NY!); Himalaya, 5000–8000 ft [=1524–2438 m], *Hooker 218* [*c.fr*.] (NY 2 sheets!). **Western Ghats:** Coorg [Kodagu], Mercara, XII.1897, *Walker 46* [*c.fr*.] (NY!). **INDONESIA**. **Sulawesi:** Kulawi, Lindu Lake, 900–1150 m, 11.III.2005, *Ariyanti s.n*. (SING!). **MALAYSIA. Pahang**: Cameron Highlands, Kampung Boh, 22.XI.1990, *Damanhuri s.n*. (UKMB!); *ibidem*, *Damanhuri s.n*. [*c.fr*.] (KLU! UKMB!); Cameron Highlands, Tanah Rata, Heritage Hotel, 1450 m, 2.XI.2004, *Yong 6060* (KLU!). **NEPAL:** *s.loc*., *s.date*, *Wallich s.n*. [*c.fr*.] (NY!). **PAKISTAN:** Bholan, Oongar Temple, 7000 ft [=2134 m], *s.date*, *Griffith 158* [*c.fr*.] (NY!). **PHILIPPINES. Luzon:** Bontoc, Mt. Masapilid, III.1920, *Ramos & Edano 38241* [*c.fr*.] (NY!). **SINGAPORE:** ?Bukit Timah, *s.date*, *Ridley 806* (SING!). **SRI LANKA:** *s.loc*., *s.date*, *Thwaites 38* [*c.fr*.] (NY!); *s.loc*., *s.date*, *Thwaites 41-1* [*c.fr*.] (NY!). **THAILAND. Payap:** Chiengmai, Mt. Suthep, 1650–1685 m, 29.XI.1965, *Touw 8708* [*c.fr*.] (NY!); near Karen Village of Sop Aep, 780–820 m, 15.XII.1965, *Touw 9473* [*c.fr*.] (NY!). **Rachaburi:** Nourthern Bo Luang, 1.VII.1968, *Larsen et al*. *1925* [*c.fr*.] (NY!).

15. *Macromitrium ochraceiodes* Dixon (Figs. 5.43 & 5.44)

J. Linn. Soc., Bot. 50: 89, fig. 17 (1935). TYPE: North Borneo, between Kamborangah and Pakka, Kinabalu, 2200–3100 m, 13.XI.1931, *Holttum 25481* (holotype NY! isotype SING!).

Plant robust, forming cushions; young shoots yellowish-green, gradually turning to olive-green and reddish-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short to tall, 2–4 cm tall and 6–9 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, triangular-lanceolate on young shoots, becoming more slender lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, densely arranged, leaves loosely erect, flexuose-twisted to curled-twisted, with apices variously curved or involute (when dry), wide-spreading to recurved-spreading, with recurved apices (when moist); branch leaves 3.3–5.3 × 0.8–1.0 mm, length-width ratio 3–5:1, long, slender- to broad-lanceolate with an oblong base, lamina mostly recurved, plane; apex firm, long, narrow-acuminate, cuspidate to piliferous; margin denticulate to serrulate, plane at distal part but reflexed at base; costa long-excurrent, ending in a 0.8–1.2 mm long cusp or hyaline arista. Upper laminal cells 8–11 × 8–10 µm, length-width ratio 1:1, oblate to short-rectangular, evenly incrassate, walls not pitted, intercellular spaces conspicuous, cells flat or low-bulging, smooth or occasionally pluri-papillose, papillae low and obscure, cell outline clearly seen; middle laminal cells 10–14 × 8–10 µm, grading from oblate or short-rectangular to gradually elongate toward the basal lamina, incrassate, with curved to more-or-less straight lumina, cells bulging to unipapillose, clear; basal laminal cells 40–75 × 8–12 µm, length-width ratio 5–7:1, long-rectangular, cells elongate toward

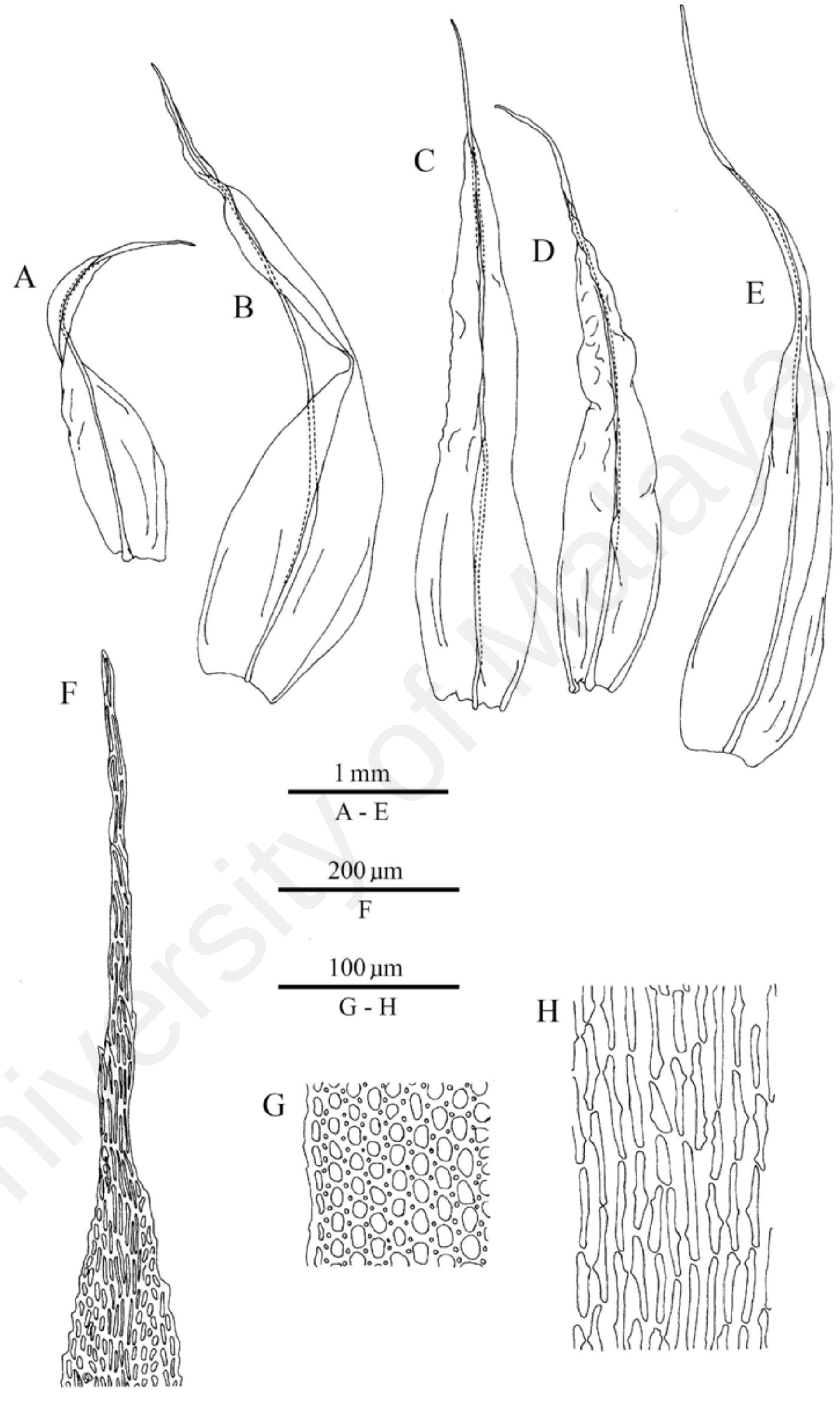

Figure 5.43. Illustrations of *Macromitrium ochraceoides* Dixon — A-D, branch leaves; **E,** perichaetial leaf; **F,** leaf apex; **G,** mid-leaf cells; **H,** basal laminal cells. [**A** from *Yong 6279* (KLU); **B** from *Damanhuri s.n.* (UKMB); **C, F-H** from *Yong 6280* (KLU); **D-E** from *Yong 6322* (KLU)]

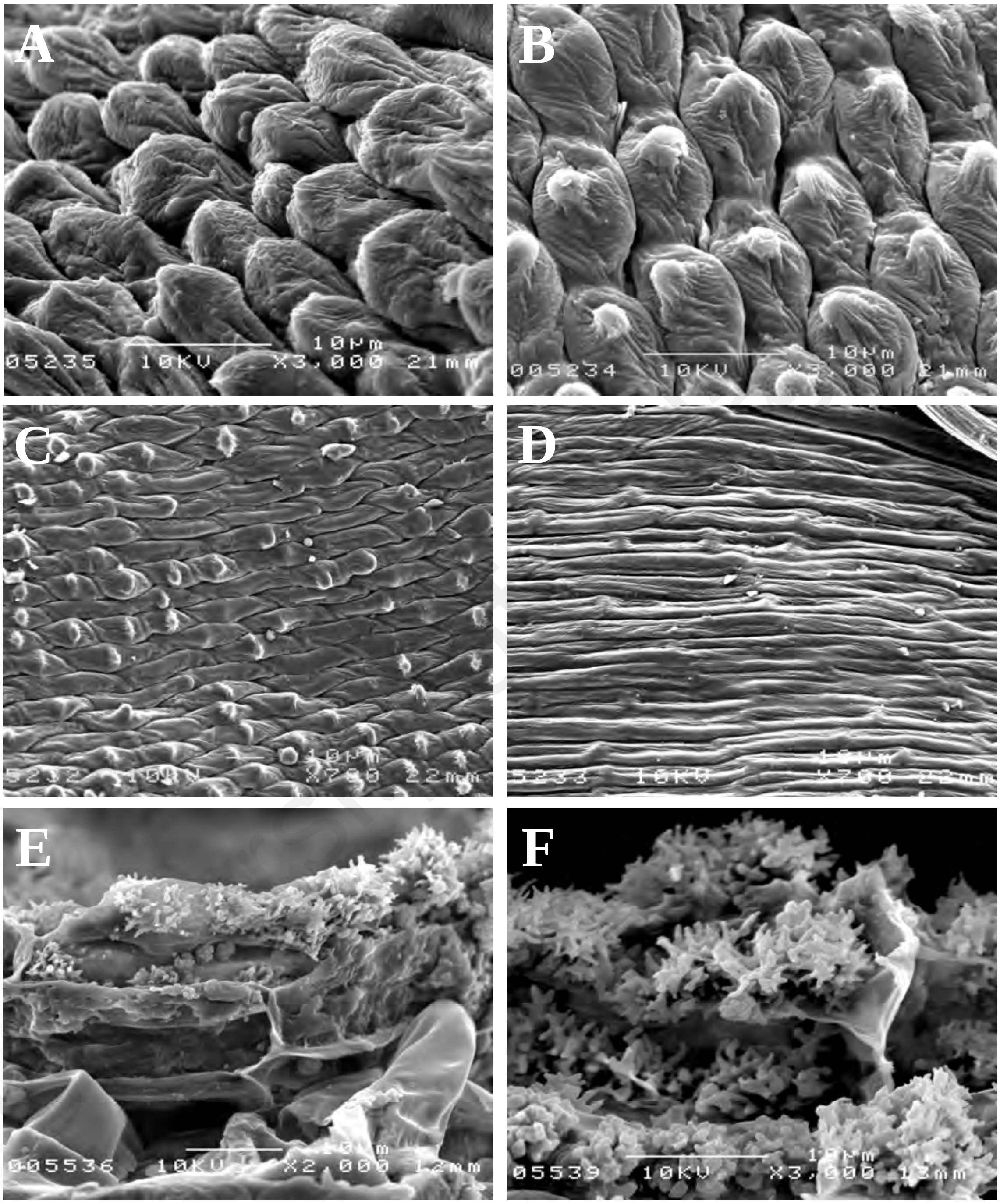

Figure 5.44. SEM images of *Macromitrium ochraceoides* Dixon — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells at upper half of leaf base; **D,** basal laminal cells at lower half of leaf base; **E,** dorsal view of unsplit peristome teeth; **F,** ventral view of unsplit peristome teeth. [All from *Yong 6322* (KLU)]

juxtacostal region, incrassate, walls more or less evenly thickened, lumina 2–3 µm wide, linear, pitted only near juxtacostal region and insertion, cells flat, mostly smooth with occasional unipapillose cells found at upper half of basal lamina.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves conspicuously erect, sheathing the seta, usually much larger than branch leaves, 5.8–6.3 × 1.1–1.2 mm, long, triangular-lanceolate to slender lanceolate, upper lamina long and slender, gradually expanding at mid-leaf to form a long oblong leaf base, leaf base often with a few long-plications; apex slender acuminate, cuspidate to piliferous; margin denticulate to serrulate to mid-leaf, entire below, plane; costa excurrent, ending in a long awn; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 2.2–2.5 mm long; paraphyses scarce, scattered on vaginula, 1.2–1.8 mm long, made of 28–40 quadrate to short-rectangular cells. Seta 10–12 mm long, papillose, sinistrorse-twisted. Capsule urns 2.2–2.5 × 1.5–1.8 mm, ellipsoid, smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 2–4, cryptoporous; operculum rostrate, beak 0.9–1.2 mm. Peristome single. Exostome teeth fused into a continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal and ventral side of teeth strongly papillose, papillae coronate, highly branched, sparsely distributed on teeth, denser on ventral side; vertical and horizontal cell-wall visible on both side of teeth, marked by tall and filmy trabeculae. Endostome absent. Spores anisomorphic, larger spores 45–50 µm in diameter, smaller spores 26–35 µm in diameter. Calyptra mitrate, plicate, densely hairy, hairs long and stiff, variously pointed and mostly arise near to the calyptra base, calyptra base fringed or lacerated.

Other descriptions and illustrations: Eddy (1996) p. 72, fig. 379, as *M. ochraceum*.

Distribution: Endemic to Borneo, Malaysia (As. 4), only known in the state of Sabah.

Habitat and ecology: Epiphytic on tree trunks and branches, also common on rocks and boulders in rather open areas. The species is very abundant above 2800 m on Mount Kinabalu, in the upper montane and subalpine zones, although it is also known from lower elevations on other mountains.

Notes:

Macromitrium ochraceiodes is closely allied to *M. ochraceum* and has been considered a form of the latter by Eddy (1996). However, the present study has found that both species are distinct by the following characters: a) long-piliferous costa of *M. ochraceoides* not found in *M. ochraceum*; and b) smooth laminal cells in the basal lamina of *M. ochraceoides*, at least in the lower half, but such smooth regions lacking in *M. ochraceum*. In addition, *M. ochraceoides* is often more robust in size compared to *M. ochraceum*.

Specimens examined:

MALAYSIA. Sabah: Ranau, Kinabalu Park, Mt. Kinabalu, *Damanhuri s.n.* (UKMB!); Ranau, Kinabalu Park, Mt. Kinabalu, below Pakka, 10200 ft [=3109 m], 15.XI.1931, *Holttum 25663* [*c.fr.*] (SING!); Ranau, Kinabalu Park, Mt. Kinabalu, Kamborangah-Pakka, 7200–10200 ft [=2195–3109 m], 13.XI.1931, *Holttum 25481* [*c.fr.*] (holotype of M. ochraceoides: NY; isotype of M. ochraceoides: SING!); Ranau, Kinabalu Park, Mt. Kinabalu, Paka Cave, 3100 m, 17.I.1997, *H. Akiyama et al. 659* (BORH! T. Yamaguchi); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Panar Laban to Paka Cave, 3050 m, 10.V.2005, *Yong 6326* [*c.fr.*] (KLU!); *ibidem*, 3070 m, 10.V.2005, *Yong 6328* [*c.fr.*] (KLU!); *ibidem*, 3080 m, 10.V.2005, *Yong 6308* (KLU!); *ibidem*, 3130 m, 10.V.2005, *Yong 6329* [*c.fr.*] (KLU!); *ibidem*, 3135 m, 10.V.2005, *Yong 6335*, *6336* [*c.fr.*] (KLU!); *ibidem*, 3145 m, 10.V.2005, *Yong 6322* [*c.fr.*] (KLU!); *ibidem*, 3175 m, 10.V.2005, *Yong 6319* [*c.fr.*] (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Panar Laban to Sayat-Sayat Checkpoint, 3330 m, 11.V.2005, *Yong 6369* [*c.fr.*] (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Timpohon Gate to Panar Laban, 2760 m, 9.V.2005, *Yong 6289* (KLU!); *ibidem*, 2900 m, 9.V.2005, *Yong 6280* (KLU!); *ibidem*, 2950 m, 9.V.2005, *Yong 6281* [*c.fr*.] (KLU!); *ibidem*, 2960 m, 9.V.2005, *Yong 6279* [*c.fr*.], *6284* (KLU!); Ranau, Kinabalu Park, Mt. Tambuyukon, Musang Camp (km 10) to the summit, 2230 m, 14.VIII.2008, *Suleiman 3741* [*c.fr*.], *3742* [*c.fr*.], *3743* (BORH, KLU! SNP); Tambunan, Mt. Trus Madi, 2230 m, 25.IX.1996, *Suleiman 225* [*c.fr*.] (BORH! MANCH); *ibidem*, 2260 m, 25.IX.1996, *Suleiman 216* [*c.fr*.] (BORH! MANCH).

16. *Macromitrium ochraceum* (Dozy & Molk.) Müll. Hal. (Figs. 5.45 & 5.46)

Bot. Zeit. 3: 544 (1845). *Schlotheimia ochracea* Dozy & Molk., Ann. Sci. Nat. Bot., sér. 3 (2): 314 (1844). LECTOTYPE (Vitt et al., 1995): Java, in alterioribus montosis in monte Megamendong, Sallak et Gédé vulgaris; fruget mense Dezembri-Februario, *Zippelius s.n*. (L; isolectotype BM!).

M. mindanaense Broth., Philipp. J. Sci. 3: 15 (1908). TYPE: Mindanao, Province of Misamis, Mount Malindang, on trees, V.1906, *Mearns & Hutchinson 4794* (holotype BM! isotype NY!) — fide Bartram (1939).

M. hallieri Fleisch. *ex* Broth., Nat. Pflanzenfam. 11: 35 (1925). TYPE: Borneo, Goenoeng Konopai, 1893/94, *Hallier s.n*. (holotype H-BR) — fide Vitt et al. (1995).

M. rubricuspis Broth., Mitt. Inst. Allg. Bot. Hamburg 7 (2): 123 (1928). TYPE: West-Borneo, Bukit Raja um 1100 m, *Winkler 3146* (holotype H-BR) — fide Dixon (1935).

M. clemensiae E.B. Bartram, Philipp. J. Sci. 61: 242 (1936), ***syn. nov*.,** non Noguchi (1953). TYPE: Borneo, Mt Kinabalu, Penibukan, jungle ridge above canopy tree, 4500 ft [=1372 m], 11.XI.1933, *Clemens 50305a* (holotype BM!).

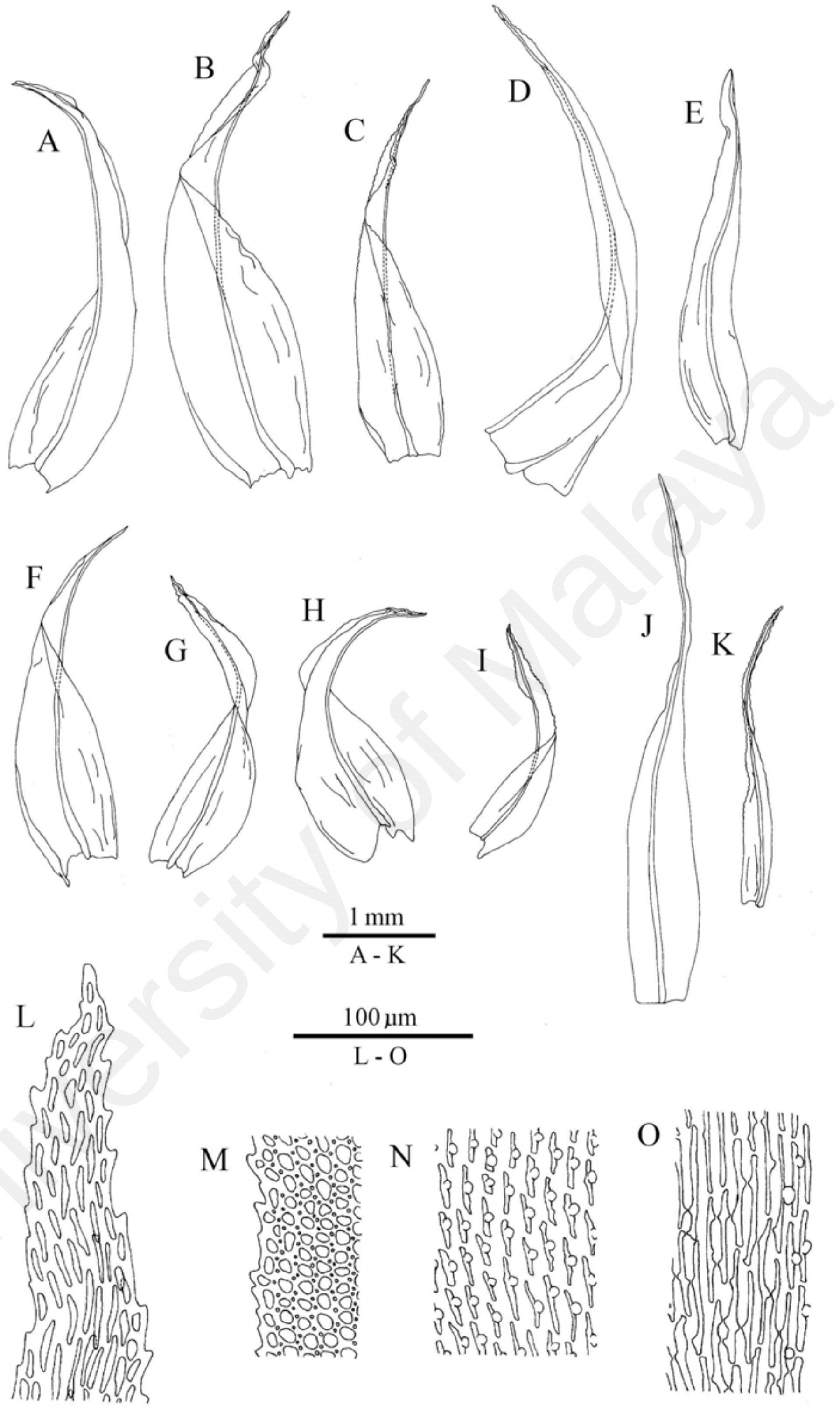

Figure 5.45. Illustrations of *Macromitrium ochraceum* (Dozy & Molk.) Müll. Hal. — **A-I,** branch leaves; **J-K,** perichaetial leaves; **L,** leaf apex; **M,** mid-leaf cells; **N,** basal laminal cells; **O,** cells near insertion. [**A, J** from *Guna 131d* (KLU); **B** from *Akin MB133* (BORH); **C** from *Mohamed & Yong 6804* (KLU); **D** from *Yong 2133* (KLU); **E** from *Manuel 2716* (KLU); **F** from *Keng 908* (SING); **G** from *Suleiman 1354* (BORH); **H, L-O** from *Holttum 25623* (SING); **I, K** from *Mohamed & Yong 6810* (KLU)]

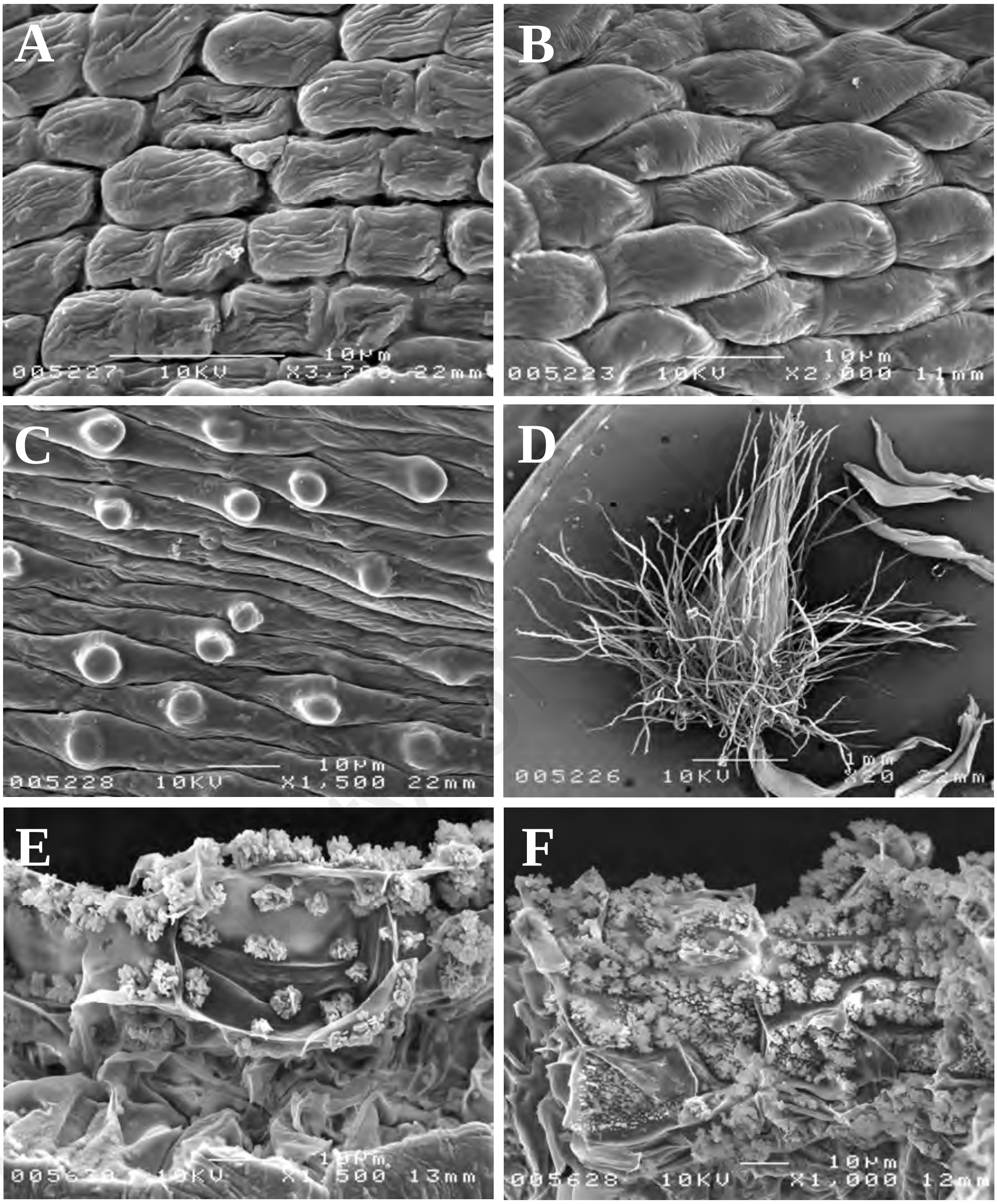

Figure 5.46. SEM images of *Macromitrium ochraceum* (Dozy & Molk.) Müll. Hal. — **A,** upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** calyptra; **E,** dorsal view of unsplit peristome teeth; **F,** ventral view of unsplit peristome teeth. [All from *Mohamed 4577* (KLU)]

M. norrisianum Vitt, Acta Bot. Fenn. 154: 53, fig. 2c, 24a–k (1995), ***syn. nov***. TYPE: Papua New Guinea, Southern Highlands Province, Lama Sawmill, 6 km SE of Ialibu, on *Elaeocarpus* trunk in grassland on gentle slope, 1860 m, 11.XII.1982, *Streimann 26580* (holotype H; isotypes ALTA, CBG, LAE, NY!).

Plant medium-sized to fairly large, forming cushions or mats; young shoots yellowish-green, gradually turning to olive-green and reddish-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short to tall, 2–5(–6) cm tall and 4–8 mm wide, loose or tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, triangular-lanceolate on young shoots, becoming more slender lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, lax to densely arranged, leaves loosely erect, erect-twisted to flexuose-twisted, with apices variously curved (when dry), wide-spreading to recurved-spreading, with recurved apices (when moist); branch leaves (2.1–)3.2–4.0(–4.8) × 1.0–1.2 mm, length-width ratio 3–4:1, long, slender- to broad-lanceolate with an oblong base, lamina mostly recurved, plane; apex firm, slender, long, acuminate; margin denticulate to serrulate, plane at distal part but reflexed at base; costa ending in the apex or percurrent. Upper laminal cells 8–11 × 8–10 µm, length-width ratio 1:1, oblate to short-rectangular, evenly incrassate, walls not pitted, intercellular spaces conspicuous, cells flat or low-bulging, smooth or occasionally pluri-papillose, papillae low and obscure, cell outline clearly seen; middle laminal cells 10–14 × 8–10 µm, grading from oblate or short-rectangular to gradually elongate toward the basal lamina, incrassate, with curved to more-or-less straight lumina, cells bulging to unipapillose, clear; basal laminal cells 20–48(–64) × 8–12 µm, length-width ratio 3–5:1, long-rectangular, cells elongate toward leaf insertion, incrassate, walls more or less evenly thickened, lumina 2–3 µm wide, linear, pitted only near juxtacostal region and insertion, cells flat, unipapillose to tuberculate, papillae weakened or smooth toward juxtacostal region.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves conspicuously erect, sheathing the seta, usually much larger than branch leaves, 4.1–4.7 × 0.7–0.9 mm, long, triangular-lanceolate to slender lanceolate, upper lamina long and slender, gradually expanding at mid-leaf to form a long oblong leaf base, leaf base often with a few long-plications; apex slender acuminate to sometimes cuspidate; margin denticulate to serrulate to mid-leaf, entire below, plane; costa percurrent or occasionally short-excurrent, extending beyond leaf tip as a cusp; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 1.7–2.1 mm long; paraphyses scarce, scattered on vaginula, 0.7–1.0 mm long, made of 12–16 short- or long-rectangular cells. Seta 7–10 mm long, papillose, sinistrorse-twisted. Capsule urns 2.0–2.1 × 1.0–1.3 mm, ellipsoid, smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, cryptoporous; operculum rostrate, beak 0.9–1.2 mm. Peristome single. Exostome teeth fused into a continuous membrane, erect to recurved at top in both dry and wet conditions; dorsal and ventral side of teeth strongly papillose, papillae coronate, highly branched, sparsely distributed on teeth, denser on ventral side; remnants of original cell-wall visible on both side of teeth, marked by tall and filmy trabeculae. Endostome absent. Spores anisomorphic, larger spores 34–40 µm in diameter, smaller spores 16–22 µm in diameter. Calyptra mitrate, plicate, densely hairy, hairs long and stiff, variously pointed and mostly arise from calyptra base, calyptra base fringed or lacerated.

<u>Other descriptions and illustrations</u>: Müller (1849) p. 732; Dozy & Molkenboer (1861)

p. 118, tab. 95; Fleischer (1904) p. 414–416; Bartram (1939) p. 181–182, pl.13, fig. 226; Vitt et al. (1995) p. 56–58, fig. 25; Eddy (1996) p. 45–46, fig. 357 as *M. clemensiae* and p. 70-72, fig. 380 as *M. ochraceum*.

Distribution: As. 4: Indonesia (Borneo, Java, New Guinea, Sulawesi, Sumatra), Malaysia (Malay Peninsula, Borneo), Papua New Guinea, Philippines (Mindanao, Negros).

Habitat and ecology: Epiphytic on tree trunks and branches, occasionally on rocks and boulders in rather open areas. The species is very common in highland heath forest, where the trees are generally slender with small crowns that allow ample sunlight to reach the ground. In Malaysia, the plant occurs from 1100 m upwards, in the lower montane and upper montane zones.

Notes:

1. *Macromitrium ochraceum* can be easily recognized by the following characters: a) robust plant size; b) smooth to bulging upper laminal cells and distinctly tuberculate basal laminal cells; c) apically serrulate leaf margin; d) strongly papillose seta; and e) densely hairy calyptra. Very often, the leaf laminae and costae of *M. ocharaceum* turn reddish when mature, giving living plants a characteristic reddish-brown colour.

2. From examination of a wide range of specimens, the species is now understood to be very variable in leaf dimensions and basal laminal cell characters. The branch leaf is generally lanceolate in *M. ochraceum*; nevertheless shape can be variable. On the other hand, the occasional presence of smooth cells at the leaf base, either at the leaf marginal or juxtacostal regions, gives the impression that the tuberculate leaf base is bordered by smooth regions or that the leaf base is partially smooth. Based on such a character, Vitt et al. (1995) erected *M. norrisianum*, which is here placed in the synonymy of *M. ochraceum*.

3. *Macromitrium megalocladon* Fleisch., a species known only in New Guinea,

resembles a robust form of *M. ochraceum*. That species is characterized by having its branch leaves more-or-less neatly arranged in five longitudinal ranks on branches. Apart from this, there is no other clear-cut distinction between the two, as noted by Vitt et al. (1995). Further studies may indicate that *M. megalocladon* should be recognized as a distinct infraspecific taxon within *M. ochraceum*.

4. I have examined the type materials of *M. clemensiae* and could not detect any morphological differences from *M. ochraceum*, so that name is reduced to synonymy.

<u>Specimens examined</u>:

INDONESIA. Java: *s.loc.*, *s.date*, *s.coll.* [*c.fr.*] (BM!); *s.loc.*, *s.date*, *Zollinger s.n. ex Hb. Dozy & Molk.* [*c.fr.*] (NY!); Gedeh, Tjiburrum, 1100 m, 1.V.1913, *Fleischer 583* [*c.fr.*] (BM!); *ibidem*, 1700 m, III.1902, *Fleischer 218* [*c.fr.*] (BM! NY!); *ibidem*, 1800 m, 28.V.1902, *Fleischer s.n.* [*c.fr.*] (BM! NY 2 sheets!); Megamendong, Salak & Gedeh, *s.date*, *Zippelius s.n.* (isolectotype of *M. ochraceum*: BM!). **Kalimantan:** Mt. Rumput, VIII.1912, *Henderson 185* (SING!). **Sumatra:** *s.loc.*, *s.date*, *Pictet s.n. ex Hb. Dozy & Molk.* [*c.fr.*] (NY!); Kerinchi-Seblat Nasional Park, Mt. Lumut, *Ho 05-169*, *05-170* (SING!). **MALAYSIA. Malaya**: 6.VII.1964, *Clear 1134* [*c.fr.*] (KLU!). **Kedah**: Jitra, Mt. Jerai (Kedah Peak), 1.IV.1925, *Holttum 14871* [*c.fr.*] (KLU! SING!); *ibidem*, 1110 m, 26.VIII.1988, *Sadiah et al. 91a*, *97a*, *7315* (KLU!). **Pahang**: Cameron Highlands, *s.date*, *Mohamed 26b* (KLU!); Cameron Highlands, Batu Mentiggi, Trail 13/14, 19.VI.1988, *Damanhuri s.n.* (UKMB!); Cameron Highlands, Brinchang, Rose Garden, 1540 m, 12.IV.1999, *Mohamed et al. 9178* (KLU!); Cameron Highlands, Golf Course, 7.VII.1964, *IDC 1279* [*c.fr.*] (KLU! UKMB!); *ibidem*, 7.VII.1964, *IDC 1294* [*c.fr.*] (KLU! UKMB!); Cameron Highlands, Mt. Brinchang, 23.XI.1990, *Damanhuri s.n.* (UKMB!); Cameron Highlands, Mt. Perdah, trail 12, 18.VI.1988, *Damanhuri s.n.* [*c.fr.*] (UKMB!); Cameron Highlands, Mt. Jasar, 5000 ft [=1524 m], *s.date*, *Spare 3511* (BM!); *ibidem*, jungle path no. 11, 1470 m, 21.VII.1999, *Tan et al. 24* (UKMB!); Cameron

Highlands, Robinson Waterfall, 1120m, *Damanhuri 9178* (KLU!); *ibidem*, jungle path no. 9, 1500 m, 9.X.2003, *Yong et al*. *4684* (KLU!); Cameron Highlands, Sungai Burong, 5000 ft [=1524 m], 20.V.1936, *Holttum 31364* (SING 2 sheets!); Cameron Highlands, Tanah Rata, jungle path no. 10, 1500 m, 13.III.2004, *Yong et al.4908*, *4909* (KLU!); Cameron Highlands, Tanah Rata, Parit Waterfall, jungle path no. 4, 1365–1400 m, 26.VI.2006, *Yong 6699* (KLU!); *ibidem*, 1400 m, 9.X.1999, *Gunaseelan & Ponniah 543* (KLU!); *ibidem*, 1420 m, 7.X.2003, *Yong et al*. *4640* (KLU!); Cameron Highlands, Tanah Rata, garden of Pelangi Apartment, 1375m, 5.XII.2004, *Yong & Goh 6123* (KLU!); Cameron Highlands, trail from Sg Palas Tea Estate to Mt. Brinchang, 1850 m, 4.IX.1999, *Gunaseelan & Ponniah 204* (KLU!); Cameron Highlands, Tanah Rata Town, 19.VI.1988, *Damanhuri s.n*. [*c.fr*.] (UKMB!); *ibidem*, 1450 m, 24.IV.1999, *Gunaseelan & Mohamed 131d* [*c.fr*.] (KLU!); Genting Highlands, 23.VI.1989, *Mohamed s.n*. (KLU!); Genting Highlands, Mt. Ulu Kali, 5000 ft [=1524 m], 30.VII.1978, *Manuel 2716* (KLU!); *ibidem*, 1730 m, 13.IX.1983, *Damanhuri 3104* (UKMB!); *ibidem*, 1750 m, 17.XI.1983, *Damanhuri 2667* (UKMB!); *ibidem*, 1760 m, 11.I.1984, *Damanhuri 3841* (UKMB!); Taman Negara, Mt. Tahan, 5000 ft [=1524 m], 20.VIII.1928, *Holttum 20867* (SING!); *ibidem*, 6000 ft [=1829 m], 1.IX.1928, *Holttum 20898* [*c.fr*.] (SING!); Taman Negara, Merapoh, Mt. Tahan, 1700 m, 14.VI.1999, *Yong 1094* (UKMB!); *ibidem*, 1800 m, 15–19.VI.1995, *Ibrahim 297* (KLU!); 1850 m, 17.IX.1999, *Yong 2133* (KLU! UKMB!). **Sabah**: Long Miao, 1238 m, 24.III.1999, *Ibrahim AI 436* [*c.fr*.], *AI 437* [*c.fr*.] (SING!); Long Pasia, Rekong Waterfall, 1461 m, 8.XI.2003, *Suleiman 1379* [*c.fr*.], *1380* (BORH! SAN); Long Pasia, Rimau Hill, 1125 m, 7.XI.2003, *Suleiman 1347* (BORH! SAN); *ibidem*, 1182 m, 7.XI.2003, *Suleiman 1354* [*c.fr*.] (BORH! SAN); Ranau, Kinabalu Park, Mt. Kinabalu, *Damanhuri s.n*. (UKMB!); *ibidem*, 8.VIII.1933, *Clemens 34368a* [*c.fr*.] (NY!); Ranau, Kinabalu Park, Mt. Kinabalu, Keebambang River, 4000 ft [=1219 m], 8.VIII.1933, *Clemens 34368* [*c.fr*.] (BM!); Ranau, Kinabalu Park, Mt. Kinabalu, Penibukau, 4500 ft [=1372 m], 11.XI.1933, *Clemens 50305a* [*c.fr*.] (holotype of *M. clemensiae*: BM!); Ranau, Kinabalu Park, Mt. Kinabalu, Maraiparai ridge, 5000 ft [=1524 m], 24.XI.1931, *Holttum 25623* (SING!); Ranau, Kinabalu Park, Mt. Kinabalu, multipurpose hall near to the park headquarter, 1500 m, 8.V.2005, *Yong 6233* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, Sayap, Sg Wariu trail to Gua Melayu, 900 m, 4.VI.1992, *Mohamed 4577* [*c.fr*.], *4592* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Timpohon Gate to Panar Laban, 2700 m, 9.V.2005, *Yong 6273* [*c.fr*.] (KLU!); *ibidem*, 2760 m, 9.V.2005, *Yong 6278* [*c.fr*.] (KLU!); *ibidem*, 2900 m, 9.V.2005, *Yong 6271* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Mt. Tambuyukon, Musang Camp (km 10) to the summit, 1450 m, 14.VIII.2008, *Suleiman 3641* (BORH, KLU! SNP); Sipitang, Mt. Lumaku, 1550 m, 29.VII.2008, *Suleiman 3370* (BORH, KLU!); *ibidem*, 1600 m, 29.VII.2008 *Suleiman 3380* (BORH, KLU!); *ibidem*, 1650 m, 29.VII.2008, *Suleiman 3388, 3422* (BORH, KLU!); Tambunan, Crocker Range Park, Mt. Alab, 1800 m, 8.IX.2008, *Suleiman & Masundang 3784* (BORH!); Tambunan, Mahua, Mt. Minduk Sirung, 1600 m, 3.IV.2008, *Suleiman & Masundang 2691* (BORH!); *ibidem*, 1620 m, 1.IV.2008, *Suleiman & Masundang 2587* (BORH!); Tawau, Maliau Basin, *Eucalyptus* Camp, 980–1100 m, 16–24.VI.2006, *Mohamed & Yong 6803* [*c.fr*.], *6804* [*c.fr*.], *6805* [*c.fr*.], *6807*, *6808* [*c.fr*.], *6809* [*c.fr*.], *6810* [*c.fr*.], *6811*, *6812* [*c.fr*.], *6900* [*c.fr*.], *6901* [*c.fr*.], *6902*, *6903*, *6904* [*c.fr*.], *6905*, *6907* [*c.fr*.], *6908*, *6909* [*c.fr*.], *6911* [*c.fr*.], *6912*, *6913* [*c.fr*.], *6958*, *7086* [*c.fr*.], *7189*, *7190* [*c.fr*.], *7191* [*c.fr*.], *7192* [*c.fr*.], *7195* [*c.fr*.], *7196* [*c.fr*.], *7197* [*c.fr*.], *7330* [*c.fr*.], *7333* [*c.fr*.], *7334*, *7335* (KLU!); Tawau, Maliau Basin, Jalan Babi, 800–1100 m, 12–25.V.1996, *Akin MB41*, *MB45* (BORH! SAN); Tawau, Maliau Basin, trail to Tibaw Camp, 800–1100 m, 12–25.V.1996, *Akin MB133* (BORH! SAN). **Sarawak:** Mt. Dulit, 1932, *Oxford Expedition 2000b*, *2000c* [*c.fr*.] (BM!); *ibidem*, 17.IX.1932, *Richards M1905* [*c.fr*.] (SING!); *ibidem*, 1230 m, 24.IX.1932, *Richards M2055* [*c.fr*.] (SING!);

Mt. Mulu, 3500–4100 ft [=1067–1250 m], 29.VI.1964, *Keng 908* (SING!). **Selangor:** Genting Highlands, Gohtong Jaya, road to Batang Kali, 950m, 11.X.2003, *Yong et al. 4719* [*c.fr*.] (KLU!); Genting Highlands, water reservoir near Genting Resort, 1240 m, 16.XII.1983, *Damanhuri 3562* (UKMB!). **PAPUA NEW GUINEA. Morobe:** Aseki, Aseki-Bulolo Road, 1580 m, 5.XII.1982, *Streimann 26143* [*c.fr*.] (H, NICH, NY!); Bulolo, Gumi Divide, 1700 m, 13.X.1982, *Streimann 25151* [*c.fr*.] (H, LAE, NICH, NY!). **Southern Highlands:** Lalibu, Lama Sawmill, 1860 m, 11.XII.1982, *Streimann 26580* (H, LAE, NY 2 sheets!). **West Sepik:** Star Mts., Sibil-valley, 1200–1300 m, 15.VIII.1959, *Zanten 863* [*c.fr*.] (NY!). **PHILIPPINES, Mindanao:** Bukidnon, Mt. Kalatungan, Pangantucan, 12–14.V.1999, *Lubos K221* (SING!); Misamis, Barangay Lunutan, Mt. Lumot, 1680 m, 24.VIII.1999, *Schumm & Schwarz 4132* (SING!); Misamis, Mt. Malindang, V.1906, *Mearns & Hutchinson 4794* [*c.fr*.] (holotype of *M. mindanaense*: BM! isotype: NY!). **Negros:** Negros Oriental, Dumaguete (Cuernos Mts.), IV.1908, *s.coll. 9592* [*c.fr*.] (BM! NY 2 sheets!); Negros Oriental, Mt. Mandalangan, ILCO logging area, 800 m, VII.1964, *Hale & Banaag 26698* [*c.fr*.] (NY! TNS!).

17. *Macromitrium orthostichum* Nees ex Schwägr. (Figs. 5.47 & 5.48)

Sp. Musc. Frond., Suppl. 4: 316, tab. 316a, tabs. 1–10 (1842). LECTOTYPE (Vitt & Ramsay, 1985): In Java a Blumio lectum misit *Nees ab Esenbeck s.n.* (G; isolectotypes G, NY!).

M. angulatum Mitt., J. Linn. Soc., Bot. 10: 167 (1868). LECTOTYPE (Vitt & Ramsay, 1985): Samoa, Tutuila, on *Hibiscus* tree, 1000 ft [=305 m], *Powell 67* (NY!) — fide Eddy (1996).

M. appressifolium Mitt., J. Linn. Soc., Bot. 13: 302 (1873). *M. orthostichum* subsp. *appressifolium* (Mitt.) Fleisch., Musci Buitenzorg 2: 413 (1904). LECTOTYPE (Vitt et al., 1995): Java, *s. coll. ex Hb. Dozy & Molk.* (NY) — fide Vitt et al. (1995).

M. minutum Mitt., J. Linn. Soc., Bot. 13: 303 (1873), ***syn. nov***. LECTOTYPE (***hic designatus***): Java, in Mount Megamendong, 4–6000 ft [=1220–1829 m], *Motley s.n.* (NY! isolectotypes NY! BM!).

M. seminudum Thwait. & Mitt., J. Linn. Soc., Bot. 13: 303 (1873). *M. orthostichum* subsp. *seminudum* (Thwait. & Mitt.) Fleisch., Musci Buitenzorg 2: 412 (1904). TYPE: Ins. Ceylon, *Thwaites s.n.* (holotype NY; isotype G) —fide Vitt et al. (1995).

M. scleropodium Bescherelle, Ann. Sci. Nat., Bot., sér. 6, 9: 357 (1880). TYPE: Réunion, *L'Isle 289* (holotype BM; isotype BM-K) —fide Wilbraham (2007).

M. papuanum Dixon in Forbes, J. Bot. 61, Suppl.: 63 (1923). TYPE: Papua New Guinea, Sogere, 2000 ft, *Forbes 515b* (holotype BM!) — fide Eddy (1996).

M. fragilifolium Dixon, Ann. Bryol. 5: 28 (1932), non Lindb. (1876). TYPE: Ad Eugeniam vivam, Fort de Kock, Sumatra, XII.1929, *Jacobson s.n.* (*R. 264hb. Verd.*) (holotype BM) — fide Eddy (1996).

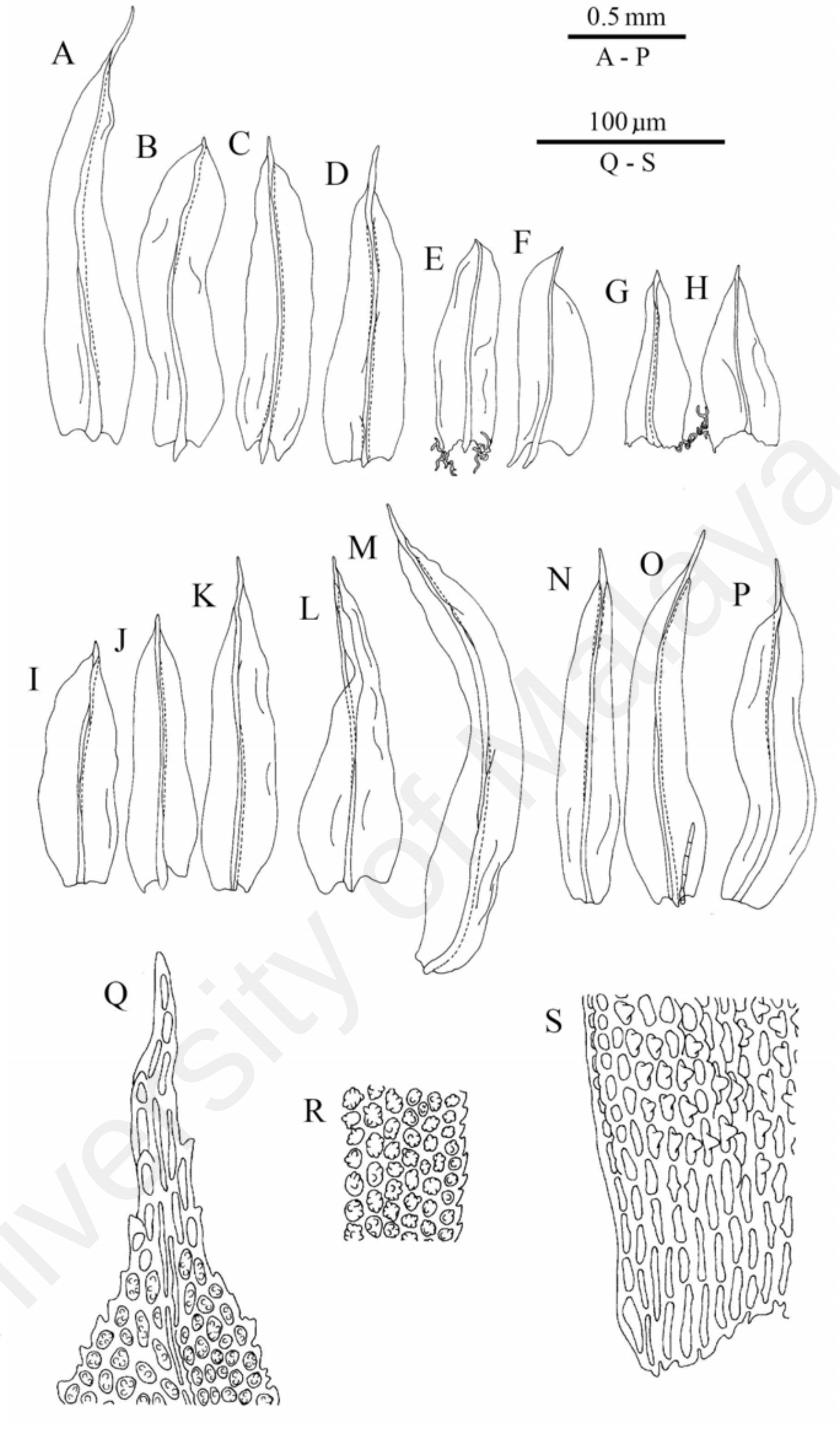

Figure 5.47. Illustrations of *Macromitrium orthostichum* Nees ex Schwägr. — A-L, branch leaves; **M-P,** perichaetial leaves (left to right arranged from outer to inermost position); **Q,** leaf apex; **R,** mid-leaf cells; **S,** basal laminal cells. [**A** from *Yong 6211* (KLU); **B** from *Yong 6250* (KLU); **C** from *Guna & Mohamed 154b* (KLU); **D** from *Mohamed 9093* (KLU); **E** from *Yong & Sabda 2598* (KLU); **F** from *Yong 6057* (KLU); **G-H** from *Mohamed & Yong 4793* (KLU); **I-K, M-O, Q-S** from *Yong et al. 4641* (KLU); **L, P** from *Yong 6443* (KLU)]

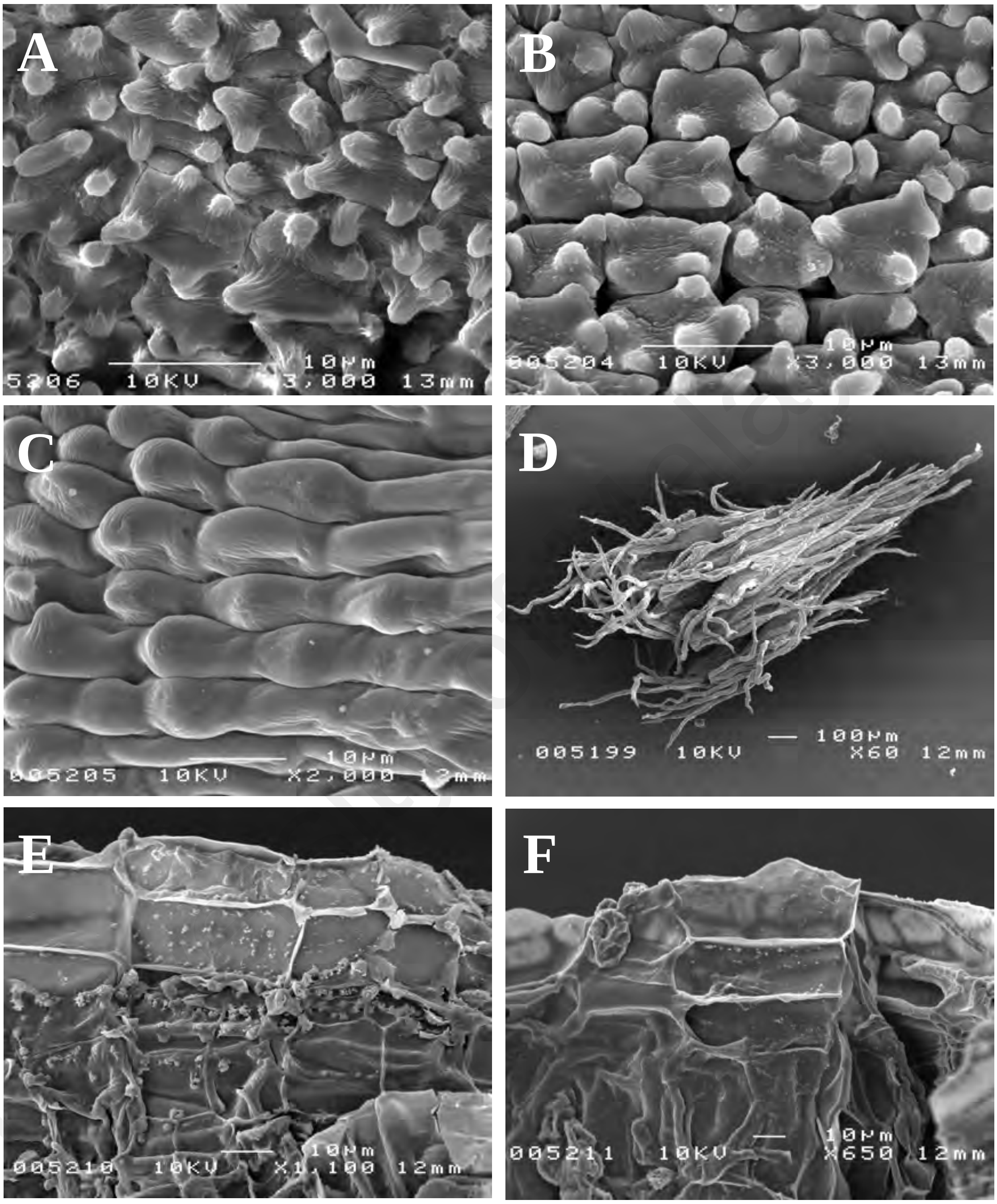

Figure 5.48. SEM images of *Macromitrium orthostichum* Nees ex Schwägr. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** calyptra; **E,** dorsal view of unsplit peristome teeth; **F,** ventral view of unsplit peristome teeth. [All from *Yong & Goh 6116* (KLU)]

M. *wellingtonianum* Vitt, J. Hattori Bot. Lab. 54: 61 (1983), ***syn*. *nov***. TYPE: New Zealand, North Island, Tararua Range, 60 km North of Wellington, 800 m, *Balázs NJ-S/I/J* (holotype ALTA; isotype EGR).

M. *pilosum* Broth., Gard. Bull. Straits Settlem. 4: 18 (1926), *nom*. *nud*.

Plant small, forming cushions; young shoots yellowish-green, gradually turning to olive-green and dark green at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 1–2 cm tall and 1–2 mm wide, tightly arranged, frequently branched, into two secondary branches that are almost equal in length. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate to triangular-lanceolate on young shoots, becoming more slender lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, in five distinctive ranks, leaves erect to erect-flexuose, loosely appressed on branches with leaf apices variously curved or twisted (when dry), wide-spreading to recurved-spreading (when moist); branch leaves 0.8–1.4 × 0.2–0.4 mm, length-width ratio 2–4:1, slender or broad, ovate-lanceolate to oblong-lanceolate with an long-oblong base, lamina straight, plane; apex firm, broad or slender, short, acute to acuminate, mucronate to cuspidate; margin denticulate to serrulate at upper lamina but entire below, plane at distal part but reflexed at base; costa short-excurrent, extending beyond leaf tip as a mucro, or occasionally in cusp that achieved 0.4 mm long. Upper and middle laminal cells 8–12 × 8–10 µm, length-width ratio 1:1, oblate to short-rectangular, moderately thick-walled, walls not pitted, cells bulging, pluri-papillose, cells sometime obscure due to the dense papillae; basal laminal cells 12–18 × 10–12 µm, length-width ratio 1–2:1, cells grading from oblate or short-rectangular to gradually elongate only near extreme leaf base, evenly incrassate, lumina broad, short- to long-rectangular, pitted only near juxtacostal region and insertion, cells bulging or flat, unipapillose to tuberculate, rhizoids often developed from a few cells found near to the leaf alar region.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.2–0.3 mm long, ovate to ovate-lanceolate. Perichaetial leaves conspicuous, erect to erect-spreading, loosely sheathing the seta, much larger than branch leaves, 0.7–1.5 × 0.3–0.4 mm, with its longest length in outer perichaetial leaf, oblong-lanceolate to slender lanceolate, upper lamina broad, with margins almost parallel to leaf base; apex slender acuminate to cuspidate; margin denticulate to serrulate to mid-leaf, entire below, plane; costa short-excurrent, extending beyond leaf tip as a cusp; laminal cells grading from short-rectangular and pluripaillose at leaf apex, gradually elongated and becoming smooth at leaf base, evenly incrassate, straight and linear lumen only found at extreme leaf base, rarely pitted. Vaginula 0.7–1.2(–1.6) mm long; paraphyses abundant, scattered on vaginula, 0.2–0.4 mm long, made of 5–8 short- or long-rectangular cells. Seta 2–4 mm long, papillose, sinistrorse-twisted. Capsule urns 0.9–1.2 × 0.7–1.0 mm, short-ovoid to ellipsoid, smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–5, phaneroporous; operculum rostrate, beak 0.4–0.5 mm. Peristome single. Exostome teeth fused into a tall, continuous membrane, erect in both dry and wet conditions; dorsal and ventral side of teeth smooth or weakly ornamented, irregular papillose, papillae simple and low, sparsely distributed on teeth; remnants of original cell-wall visible on both side of teeth, marked by tall and filmy trabeculae. Endostome absent. Spores anisomorphic, larger spores 38–46 µm in diameter, smaller spores 22–28 µm in diameter. Calyptra mitrate, plicate, densely hairy, hairs stiff and long, variously pointed, mostly found near to the calyptra base, calyptra base deeply lobed.

Other descriptions and illustrations: Müller (1849) p. 745–746; Dozy & Molkenboer

(1861) p. 129–130, tab. 107; Fleischer (1904) p. 407–409 as *M. minutum*, p. 410–412 as *M. orthostichum*, p. 412–413 as *M. seminudum*, p. 413–414 as *M. appressifolium*; Brotherus (1925) p. 29, figs. 443A–B, 446; Bartram (1939) p. 172–173, pl. 13, fig. 211; Vitt et al. (1995) p. 13–16, figs. 6, 39 as *M. angulatum*; Vitt et al. (1995) p. 58–60, figs. 2d, 26, 40 as *M. orthostichum*; Eddy (1996) p. 34–37, figs. 346, 348 as *M. orthostichum*, p. 37, fig. 349 as *M. minutum*; Wilbraham (2007) p. 57, fig. 2.

Distribution: Paleotropic. Afr 2: Cameroon, Gabon, Uganda, Zaire; Afr 3: Mascarene (Réunion); As 3: Sri Lanka, Thailand (Peninsula); As 4: Indonesia (Bali, Flores, Java, Lombok, Seram, Sulawesi, Sumatra, Sumbawa, Ternate, West Irian), Philippine (Camiguin, Leyte, Luzon, Mindanao, Mindoro), Papua New Guinea; OC: Samoa, Solomon Islands, Tahiti; Austr. 2: New Zealand.

Habitat and ecology: Epiphytic on tree trunks and lower branches, occasionally on rocks. In Malaysia, the species is very common at 1000 m and above; mostly found in the lower montane zone. It has been collected frequently from roadside trees and trees growing in gardens on mountains.

Notes:

1. *Macromitrium orthostichum* is the smallest member of the genus known in Malesia. Its diagnostic features are: a) monopodial branches frequently branched, mostly appearing forked; b) branch leaves neatly arranged in five longitudinal ranks; c) laminal cells mostly oblate to quadrate, with evenly thick walls throughout the lamina; d) seta papillose; e) calyptra densely hairy. The species is very polymorphic with two extreme leaf forms observed: a) short, oblong with broad acute apex; and b) elongate, oblong-lanceolate with sharp acuminate apex. However, the distinction between these is not consistent.

2. The species has been much confused in the past, as many names have been erected based on observed variants. Mitten (1873) created Section *Cometium* to accommodate

M. orthostichum and alike taxa that are small in plant dimensions, with branches often forked, branch leaves serially arranged and rounded laminal cells. In the same publication, Mitten also erected four new species for Section *Cometium*, which were merely forms of *M. orthostichum* as we now understand it. Fleischer (1904) had also sought to further refine Mitten's concept by treating *M. orthostichum* and related taxa under Subsection *Micro-cometium*. From a different perspective, Brotherus (1925) acquired Mitten's concept but raised the Section *Cometium* to a subgeneric position, subsequently listing 12 names under the newly erected Subgenus *Cometium*.

3. Members of this group were distinguished based primarily on the relative length of perichaetial leaves and the vaginulae (Mitten, 1873; Brotherus, 1925). This is not a reliable character to use because outer perichaetial leaves and inner perichaetial leaves have not been properly distinguished by these past authors. In fact, outer perichaetial leaves are as long as or longer than the vaginulae; whereas inner perichaetial leaves are always shorter than the vaginulae (and therefore always shorter than the outer perichaetial leaves). Thus, when only outer perichaetial leaves are considered, such as when inner perichaetial leaves are occasionally (variably) reduced or absent, the vaginulae may be mistakenly described as being "shorter than the perichaetial leaves". Conversely, when the inner perichaetial leaves are specially considered, the vaginulae then appeared to be "longer than the perichaetial leaves". Hence, many of the earlier *Cometium* taxa recognized by Mitten, Fleischer and Brotherus were placed in the synonymy of *M. orthostichum* by later workers (Vitt et al., 1995; Eddy, 1996). By the same considerations, *Macromitrium minutum*, traditionally recognized by having "perichaetial leaves longer than its vaginula" is here placed in the synonym of *M. orthostichum*.

4. Vitt et al. (1995) had distinguished *M. angulatum* from related taxa by the bulging and often non-papillate upper laminal cells. In fact, leaf cells in the lectotype of *M.*

angulatum (*Powell 67*, NY) are commonly papillate and less often smooth. Also, cell ornamentation is variable in *M. orthostichum*, which has smooth or pluripapillose upper laminal cells. *M. angulatum* is justifiably synonymized under *M. orthostichum*.

Specimens examined:

INDONESIA. Bali: *s.loc.*, VI.1938, *Jaeg 3* (BM!). **Java:** *s.loc.*, *s.date*, *s.coll*. [*c.fr*.] (NY 2 sheets!); *s.loc.*, 1861, *Wichura s.n.* [*c.fr*.] (BM!); Gedehgebirge, Tjibodas, 1450 m, IV.1900, *Fleischer 361* [*c.fr*.] (NY!); Mt. Megamendong, *s.date*, *s.coll*. [*c.fr*.] (NY!); *ibidem*, 4–6000 ft [=1219–1829 m], *Motley s.n.* (lectotype of M. minutum: NY! isolectotype: NY! BM!); Mt. Pangerango, *s.date*, *s.coll*. [*c.fr*.] (NY!); Mt. Pangerango, 860 m, 6.IV.1894, *Schiffner 3894* [*c.fr*.] (BM! NY 2 sheets! TNS!); Mt. Pangerango, Tjibodas, 1420 m, 1894, *Schiffner 11718* [*c.fr*.] (NY!); Mt. Salak, bei Buitenzorg, 26.VII.1938, *Jaeg 1* [*c.fr*.] (BM!); Preanger, Telaga bodas, 1200–1650 m, 15.II.1894, *Schiffner 11734* [*c.fr*.] (NY!); Sindanglaya, 1050 m, XI.1901, *Fleischer 217* [*c.fr*.] (BM 2 sheets! NY 2 sheets!); Tjibodas, *s.date*, *Ernst 5* [*c.fr*.] (BM!); Tjibodas, 1450 m, III.1900, *Fleischer 127* [*c.fr*.] (BM! NY 3 sheets!); *ibidem*, 1500 m, 29.IX.2001, *Tan s.n.* (KLU!); Tjinjirocan, *s.date*, *Ernst 6* [*c.fr*.] (BM!); Tjipannas, 1000 m, III.1902, *Fleischer s.n.* [*c.fr*.] (NY!). **Sulawesi:** Latimojong Mts., Mt. Rantemario, 2000 m, 22.XI.1969, *Eddy 5516 pp* [*c.fr*.] (BM!). **Sumatra:** Padang Pandjang, 800 m, XI.1929, *Jacobson 62b* [*c.fr*.], *62f* (BM!). **MALAYSIA. Johore**: Endau-Rompin, Mt. Tiong, 480 m, 25.VII.2002, *Yong & Sabda 2598, 2601* (KLU!). **Kelantan**: Lojing Highlands, Mt. Warpu, 1450 m, 29.V.2008, *Suleiman 3094* [*c.fr*.] (BORH! KLU!); Taman Negara, Kuala Koh, trail from Kem Aring to Kem ATM, 350 m, 12.IX.1999, *Yong 1793c* (KLU!). **Pahang**: Cameron Highlands, 6.VII.1964, *Clear 1132*, *1136* [*c.fr*.], *1137*, *1212* (KLU!); *ibidem*, 4800 ft [=1463 m], 1.IV.1930, *Holttum 23304* [*c.fr*.] (BM! SING!); *ibidem*, 1560 m, 10.III.1989, *Mohamed 9093* (KLU!); Cameron Highlands, Brinchang, jungle path no. 1, 1550 m, 10.VII.2004, *Yong 6017* [*c.fr*.], *6019, 6020* (KLU!); Cameron

Highlands, Brinchang, Kampung Teria, 1700 m, 6.XII.2004, *Yong & Goh 6133* [*c.fr*.] (KLU!); Cameron Highlands, Brinchang, Mt. Brinchang, 1.I.1989, *Damanhuri 3998* (UKMB!); *ibidem*, 23.XI.1990, *Damanhuri s.n.* (UKMB!); *ibidem*, 1950–1980 m, 3.VIII.1988, *Mohamed & Damanhuri 1030f*, *5011* (KLU!); *ibidem*, 2000 m, 12.IV.1987, *Mohamed et al*. *9164* [*c.fr*.] (KLU!); Cameron Highlands, Brinchang, Mt. Brinchang, Sg. Palas, 1930 m, 12.IV.1987, *Mohamed et al*. *9230c* [*c.fr*.] (KLU!); Cameron Highlands, Brinchang, Rose Garden, 1540 m, 12.IV.1987, *Mohamed 9181* [*c.fr*.] (KLU!); Cameron Highlands, Fairlei Estate to Sg. Mensun, 1280 m, 8.XI.1989, *Sadiah & Zamzuri 1299* (KLU!); Cameron Highlands, Jumper Rest House, 26.X.1987, *Mohamed & Zamzuri 1072a*, *1072b* (KLU!); Cameron Highlands, Mt. Beremban, 2.VI.1988, *Damanhuri s.n.* (UKMB!); Cameron Highlands, Mt. Jasar, 31.XII.1988, *Damanhuri s.n.* [*c.fr*.] (UKMB!); Cameron Highlands, jungle path no. 3, 1500 m, 5.IX.1999, *Gunaseelan & Ponniah 255* (KLU!); Cameron Highlands, Ringlet, Boh Tea Plantation, 1460 m, 28.X.1987, *Mohamed & Zamzuri 1120* [*c.fr*.], *1121a* [*c.fr*.] (KLU!); Cameron Highlands, Ringlet, Boh Tea Plantation Estate to Kampung Orang Dalam, 940 m, 11.XI.1989, *Sadiah & Zamzuri 1499* (KLU!); Cameron Highlands, Robinson Waterfall, 5000 ft [=1524 m], 6.III.1980, *Manuel 3320* (KLU!); *ibidem*, 1260 m, 11.VII.2004, *Yong 6052*, *6053* [*c.fr*.] (KLU!); *ibidem*, 1430 m, 9.X.2003, *Yong et al*. *4677*, *4683*, *4685* (KLU!); Cameron Highlands, Strawberry Park Hotel, 1500 m, 2.VIII.1988, *H Mohamed & Damanhuri 1094*, *1099a*, *1101* (KLU!); Cameron Highlands, Tanah Rata Town, 1450 m, 24–25.IV.1999, *Gunaseelan & Mohamed 124* [*c.fr*.], *150a*, *154b* (KLU!); *ibidem*, 5200 ft [=1585 m], 3.IX.1965, *Inoue 10568* [*c.fr*.] (TNS!); Cameron Highlands, Tanah Rata, *Camellia* Garden, 1500 m, 1.XI.2004, *Yong 6057* (KLU!); Cameron Highlands, Tanah Rata, Cool Point Hotel, 1450 m, 22.V.2006, *Yong 6691*, *6692* [*c.fr*.] (KLU!); Cameron Highlands, Tanah Rata, Government Rest House, 1440 m, 26.X.1987, *Mohamed & Zamzuri 1171a*, *1171c* (KLU!); Cameron

Highlands, Tanah Rata, Heritage Hotel, 1450 m, 2.XI.2004, *Yong 6064* (KLU!); Cameron Highlands, Tanah Rata, jungle path no. 10, 1500 m, 13.III.2004, *Yong et al*. *4906a*, *4906b* (KLU!); Cameron Highlands, Tanah Rata, Kem Slim, 1450 m, 5.IX.1999, *Gunaseelan & Ponniah 328b* (KLU!); Cameron Highlands, Tanah Rata, MARDI Research Station, 1440 m, 22.III.1989, *Bakar 346* (KLU!); *ibidem*, 1370 m, VIII.1994, *Seki 36* (KLU!); Cameron Highlands, Tanah Rata, Parit Waterfall, 1365–1400 m, 26.VI.2006, *Yong 6698* (KLU!); *ibidem*, 1420 m, 7.X.2003, *Yong et al*. *4611*, *4615*, *4616*, *4637* [*c.fr*.], *4641* [*c.fr*.] (KLU!); *ibidem*, 1365–1400 m, 22.V.2006, *Yong 6696*, *6697*, *6700* (KLU!); *ibidem*, 1400 m, 29.VII.2007, *Yong 7437* (KLU!); Cameron Highlands, Tanah Rata, Pelangi Apartment, 1375m, 5.XII.2004, *Yong & Goh 6116* [*c.fr*.] (KLU!); Cameron Highlands, Ulu Bertam Forest Reserve, 1465 m, 7.X.2003, *Yong et al*. *4659* [*c.fr*.], *4661* [*c.fr*.] (KLU!); *ibidem*, 9.X.2003, *Yong et al*. *4685* (KLU!); Fraser's Hill, *Damanhuri s.n*. (UKMB!); Fraser's Hill, Bukit Jeriau, 1053 m, 21.VII.2003, *Lok 53* (SING!); Fraser's Hill, Jelai Tower, 1160 m, 11.III.2000, *Damanhuri et al*. *2000-149* (UKMB!); *ibidem*,1170 m, 11.III.2000, *Damanhuri et al*. *2000-150* (UKMB!); Fraser's Hill, RHB bungalow, 1100 m, 10.III.2000, *Damanhuri et al*. *2000-101* (UKMB!); Fraser's Hill, Temerloh Bungalow, 1180 m, 10.III.2000, *Damanhuri et al*. *2000-23*, *2000-32* (UKMB!); Fraser's Hill, The Quest, 1120 m, 11.III.2000, *Damanhuri et al*. *2000-137* (UKMB!). **Perak**: Mt. Batu Puteh, 3400 ft [=1036 m], *Wray 929* [*c.fr*.] (BM 2 sheets! SING!), 976 (SING!); Taiping, Taiping Hill (Maxwell Hill), below Caunfield Hill, 1000–1200 m, 9.VI.1983, *Mohamed et al*. *8148* [*c.fr*.] (KLU!); *ibidem*, 1100–1400 m, 11.III.2004, *Mohamed & Yong 4876* (KLU!); *ibidem*, 1120–1200 m, 8.III.2004, *Mohamed & Yong 4769*, *4793* [*c.fr*.], *Yong 4809* [*c.fr*.] (KLU!); Taiping, Taiping Hill (Maxwell Hill), Gunung Hijau Rest House, 1120 m, 7.III.2004, *Mohamed* & *Yong 4743* (KLU!); *ibidem*, 1180 m, 6.VI.1983, *Mohamed et al*. *8001* [*c.fr*.] (KLU!). **Sabah**: Ranau, Kinabalu Park, Bukit Tupai Trail, 1455 m, 13.V.2005, *Yong 6442*, *6445* [*c.fr*.] (KLU!);

Ranau, Kinabalu Park, multipurpose hall, 1500 m, 8.V.2005, *Yong 6237* [*c.fr*.], *6238*, *6246*, *6250* (KLU!); Ranau, Kinabalu Park, below Timpohan Gate, 1490 m, 8.V.2005, *Yong 6211* (KLU!); Ranau, Mt. Kinabalu, Kiau, 3000 ft [=914 m], 21.XI.1931, *Holttum 25695 pp* [*c.fr*.] (BM!); Ranau, Mt. Kinabalu, Tenompok, 4700 ft [=1433 m], 11.XI.1931, *Holttum 25692b* [*c.fr*.] (BM!), *25693* [*c.fr*.] (SING!); Sipitang, Mt. Lumaku, Muaya Waterfall, 750 m, 7.III.2009, *Suleiman 4145* (BORH, KLU!); Tambunan, Bolotikon Village to Melungung Camp, 800 m, 25.IX.2008, *Suleiman & Masundang 4093* (BORH!); Tambunan, mile 32 to Longkogungan Village, 650 m, 22.IX.2008, *Suleiman & Masundang 3992* (BORH!); Tawau, Maliau Basin, *Eucalyptus* Camp, 980–1100 m, 16–24.VI.2006, *Mohamed & Yong 6953*, *6958*, *7193* [*c.fr*.] (KLU!). **Selangor:** Genting Highland, Awana cable car station, 1000 m, 4.X.2003, *Yong 4527*, *4531b* (KLU!); *ibidem*, 1030 m, 22.V.2006, *Yong 6666*, *6667* (KLU!); Genting Highland, Mt. Bunga Buah, 1100 m, 25.III.2006, *Yong 6661* (KLU!); Genting Highland, water reservoir near Genting Resort, 1240 m, 16.X.1983, *Damanhuri s.n.* (KLU!); *ibidem*, 16.XII.1983, *Damanhuri 3494* (UKMB!); *ibidem*, 1420 m, 14.XII.1983, *Damanhuri 3224*, *3282* (UKMB!). **PAPUA NEW GUINEA. Central:** Boridi, 4700 ft [=1433 m], 22.IX.1935, *Carr 13318* [*c.fr*.] (BM 2 sheets! NY!); Boridi, The Gap, 7000 ft [=2134 m], 30.I.1936, *Carr 73* [*c.fr*.] (BM!); Sogere Region, 2000 ft [=610 m], 14.I.1886, *Forbes 515b* [*c.fr*.] (holotype of *M. papuanum*: BM!); **Eastern Highlands:** Goroka, 4000 ft [=1219 m], 22.VI.1968, *Weber & McVean 34045* (NY!). **Gulf:** Kaintiba, Hepataewa, 1200 m, 26.I.1983, *Streimann 33855* [*c.fr*.] (ALTA, NY!). **Madang:** Finisterre Range, Budemu, 1250 m, *Eddy 464 pp* (BM!); Finisterre Range, Moro, 1500 m, 31.X.1964, *Eddy 823 pp* (BM!); *ibidem*, 1650 m, 1.XI.1964, *Eddy 833 pp* (BM!). **Milne Bay:** Agun, 3500 ft [=1067 m], 28.V.1954, *Cruttwell 464* [*c.fr*.], *471* [*c.fr*.] (BM!); Raba Raba, Goepon, 2515 m, 14.VII.1972, *Steven & Veldkamp 55557* [*c.fr*.] (BM!). **Morobe:** *s.loc*., 6.IV.1940, *Clemens 41124* [*c.fr*.] (NY!); Aseki, Koke Village, 1500 m, 20.I.1981, *Streimann & Tamba 11776* (NY!); Aseki, Pouyu Village, 1500 m, 24.I.1981, *Streimann & Tamba 12579*, *12653* [*c.fr*.], *12757* (NY!); Aseki, Windowi Village, 1350 m, 6.XII.1982, *Streimann & Mundua 26217* [*c.fr*.] (ALTA, H, NICH! NY!); Bulolo, Logging area, 1500 m, 27.I.1981, *Streimann & Bellamy 13231* [*c.fr*.] (H, LAE, NY!); Bulolo, Manki Trig., Bulolo-Watut Divide, 1500 m, 27.IV.1982, *Streimann 18911* (NY!); *ibidem*, 1530 m, 26.I.1981, *Streimann & Bellamy 12829*, *12929*, *12937*, *13079* [*c.fr*.] (H, NY!); Bulolo, Nauti Village, Upper Watut River, 880 m, 28.I.1981, *Streimann 13440*, *13441* (H, LAE, NY!); Bulolo, Slate Creek and Gumi Creek Divide, 2100 m, 30.I.1981, *Streimann 13848*, *13852* (LAE, NY!); Menyamya, Yakwoi River, 1300 m, 1.V.1982, *Streimann 19310* (NY!); Menyamya, Yinimba, 1900 m, 30.IV.1982, Streimann 19441 (NY!); Wago, Herzog Mts., 1500 m, 21.I.1965, *Eddy 1866 pp* [*c.fr*.] (BM!); Wantoat, Wantoap River, 1500–1700 m, 29.V.1981, *Norris 60382* (H, HSC, NY!). **Simbu Province:** Mt. Wilhelm, Kegsugl Forest, 7500 ft [=2286 m], 4.VIII.1994, *Tan 94-4820b* (SING!). **Southern Highlands:** Ialibu, Iaro River, Onim, 2230 m, 11.IX.1982, *Streimann 23878* [*c.fr*.] (ALTA, LAE, NICH, NY!). **West Sepik:** Star Mts., Busilmin, 1450 m, 28.III.1975, *Touw 15084* [*c.fr*.] (NY!); Star Mts., Folongonom, 2300 m, 11.V.1975, *Touw 17619* [*c.fr*.] (NY!). **PHILIPPINES. Luzon:** Bontoc, Caraga, Mt. Caua, III.1920, *Ramos & Edano 38225* [*c.fr*.], *38228* [*c.fr*.] (BM! NY!); Mt. Mavireles, 400 m, VII.1904, *Leiberg 1215b* [*c.fr*.] (NY!). **Mindanao:** *s.loc*., II.1905, *Williams 3144* [*c.fr*.] (NY!); *s.loc*., III–IV.1912, *Ramos 14890* [*c.fr*.] (NY!); Misamis Oriental, Mt. Lumot, Barangay Lunutan, 1110 m, 24.VIII.1999, *Schumm & Schwarz 4131* [*c.fr*.] (SING!). **Negros:** Negros Oriental, Dumaguete (Cuernos Mts.), VI.1908, *s.coll*. *10238* (NY!).

18. ***Macromitrium papillisetum*** **Dixon** (Figs. 5.49 & 5.50)

J. Linn. Soc., Bot. 50: 89. 1935. TYPE: Borneo, Bettotan, near Sandakan, 23.VII.1927, *Kloss 18742* (holotype BM; isotype SING!).

Plant small, forming short-cushions or mats; shoot olive-green to rusty-brown, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5 cm tall and 1–2 mm wide, compactly arranged, rarely branched. Stem leaves inconspicuous, small, covered by rhizoids, triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, densely arranged with indistinct funiculate, leaves flexuose-twisted with incurved apices (when dry), erect-spreading to wide-spreading (when moist); branch leaves 1.1–1.3 × 0.3–0.4 mm, length-width ratio 2–3:1, slender lanceolate to lingulate with an oblong base, lamina straight, plane; apex firm, obtuse to mucronate; margin subentire to crenulate, plane at distal part but reflexed at base; costa shortly excurrent with 1–2 cells extending beyond the tip. Upper and middle laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, rounded to oblate, moderately thick-walled, walls not pitted, cells bulging, densely pluri-papillose, cells opaque; basal laminal cells 15–20 × 8–10 µm, length-width ratio 2:1, short to long-rectangular, gradually elongate toward leaf insertion, incrassate, walls evenly thickened, lumina 3–5 µm wide, pitted only near juxtacostal region and insertion, cells flat, unipapillose to tuberculate.

Pseudoautoicous, dwarf male plants bud-like, small, perigonial leaves 0.2–0.3 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, usually much larger than branch leaves, 1.5–1.6 × 0.5–0.6 mm, broad-lanceolate, upper lamina narrow, expanding abruptly below apex to form a long-

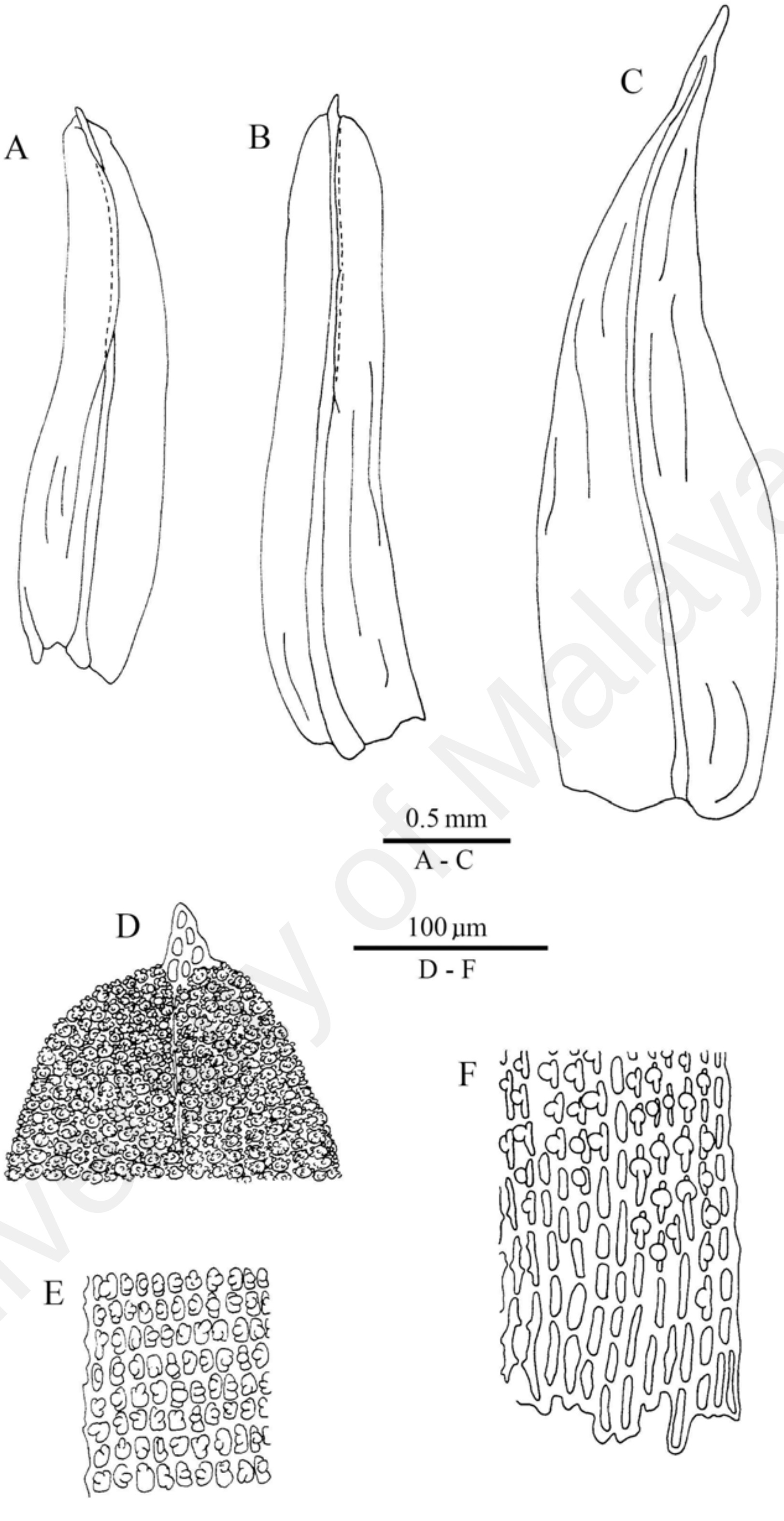

Figure 5.49. Illustrations of *Macromitrium papillisetum* Dixon — A-B, branch leaves; **C,** perichaetial leaf; **D,** leaf apex; **E,** mid-leaf cells; **F,** basal laminal cells. [All from *Kloss 18742* (SING, isotype)]

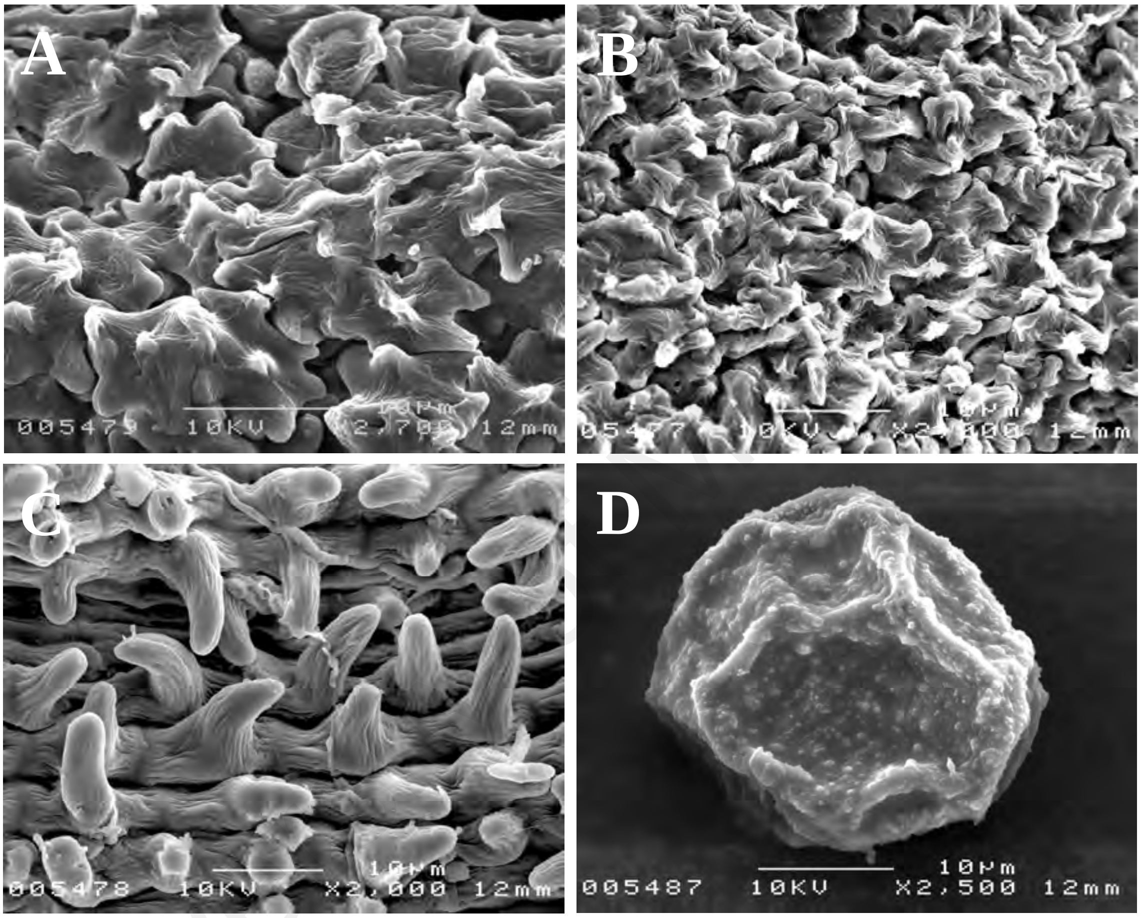

Figure 5.50. SEM images of *Macromitrium papillisetum* Dixon — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** macrospore. [All from *Kloss 18742* (SING, isotype)]

oblong base, leaf base often with a few long-plications; apex slender, long-acuminate, apiculate; margin subentire to entire, plane; costa percurrent or short-excurrent ending in a stout-apiculus; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 0.9–1.0 mm long; paraphyses abundant, densely covering the vaginula, 0.3–0.4 mm long, made of 6–8 short to long-rectangular cells. Seta 3–5 mm long, papillose, sinistrorse-twisted. Capsule urns 1.1–1.2 × 1.0 mm, globose to ellipsoid, smooth, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 2–4, cryptoporous; operculum rostrate, beak 0.4–0.5 mm. Peristome absent. Spores anisomorphic, larger spores 30–35 µm in diameter, smaller spores 15–20 µm in diameter. Calyptra mitrate, plicate, densely haired, hairs short, stiff erect and freely distributed on calyptra, hairs twisted only near calyptra base, base fringed or lacerated.

Other descriptions and illustrations: Eddy (1996) p. 42–43, fig. 356.

Distribution: Endemic to Malaysia (Borneo) (As. 4).

Habitat and ecology: Lowland epiphyte.

Notes:

1. *Macromitrium papillisetum* is a peculiar species that is only known from the type collection. The species is distinctive by its a) small plant size; b) compactly arranged, short monopodial branches; c) densely pluripapillate upper laminal cells and tuberculate basal laminal cells; and d) papillose seta and densely hairy calyptra. In Malaysia, *M. papillisetum* has some resemblance to *M. orthostichum* in its small size, and also to *M. blumei* in its oblong-lingulate leaves. However, the densely spirally inserted branch leaves and strongly pluripapillose upper lamina cells in *M. papillisetum* clearly separate it from *M. orthostichum* (branch leaves in five longitudinal ranks on branches) and *M. blumei* (upper laminal cells either smooth or bulging).

2. Eddy (1996) suspected that the absence of peristome teeth in this species, as reported

in the original publication (Dixon, 1935), may have been due to a lack of mature capsules. Nevertheless, present observation of mature capsules found in the isotype packet has confirmed that *M. papillisetum* is gymnostomous.

Specimens examined:

MALAYSIA. Sabah: Bettotan, near Sandakan, 23.VII.1927, *Kloss 18742* [*c.fr*.] (isotype of *M. papillisetum*: SING!).

19. *Macromitrium parvifolium* Dixon (Figs. 5.51 & 5.52)

J. Bot. 80: 6 (1942). TYPE: Papua New Guinea, Alola, on tree, 1800 m, 11.I.1936, *Carr 15049* (holotype BM! isotype NY!).

M. daymannianum Bartram, Brittonia 9: 43 (1957). TYPE: Papua New Guinea, Milne Bay, Mt. Dayman, north slopes, 2230 m, on branches of a tall *Araucaria, Brass 22306* (holotype FH!) — fide Vitt et al. (1995).

M. brevirameum Bartram, Contr. U.S. National Herb. 37: 54 (1965). TYPE: Papua New Guinea, Eastern Highlands, Mt. Otto, south slopes, high epiphyte in *Castanopsis* forest, 2000 m, *Brass 31117* (isotype L) — fide Vitt et al. (1995).

M. brevirameum Bartram, Rev. Bryol. Lich. 30: 195 (1962), *nom. nud*.

Plant small to medium-sized, forming short-cushion or mats; young shoots yellowish-green, gradually turning olive-green to brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches short, 0.5–1 cm tall and 2–3 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, slender, triangular-lanceolate on young shoots, becoming longer at older portions, apex acuminate with percurrent costa.

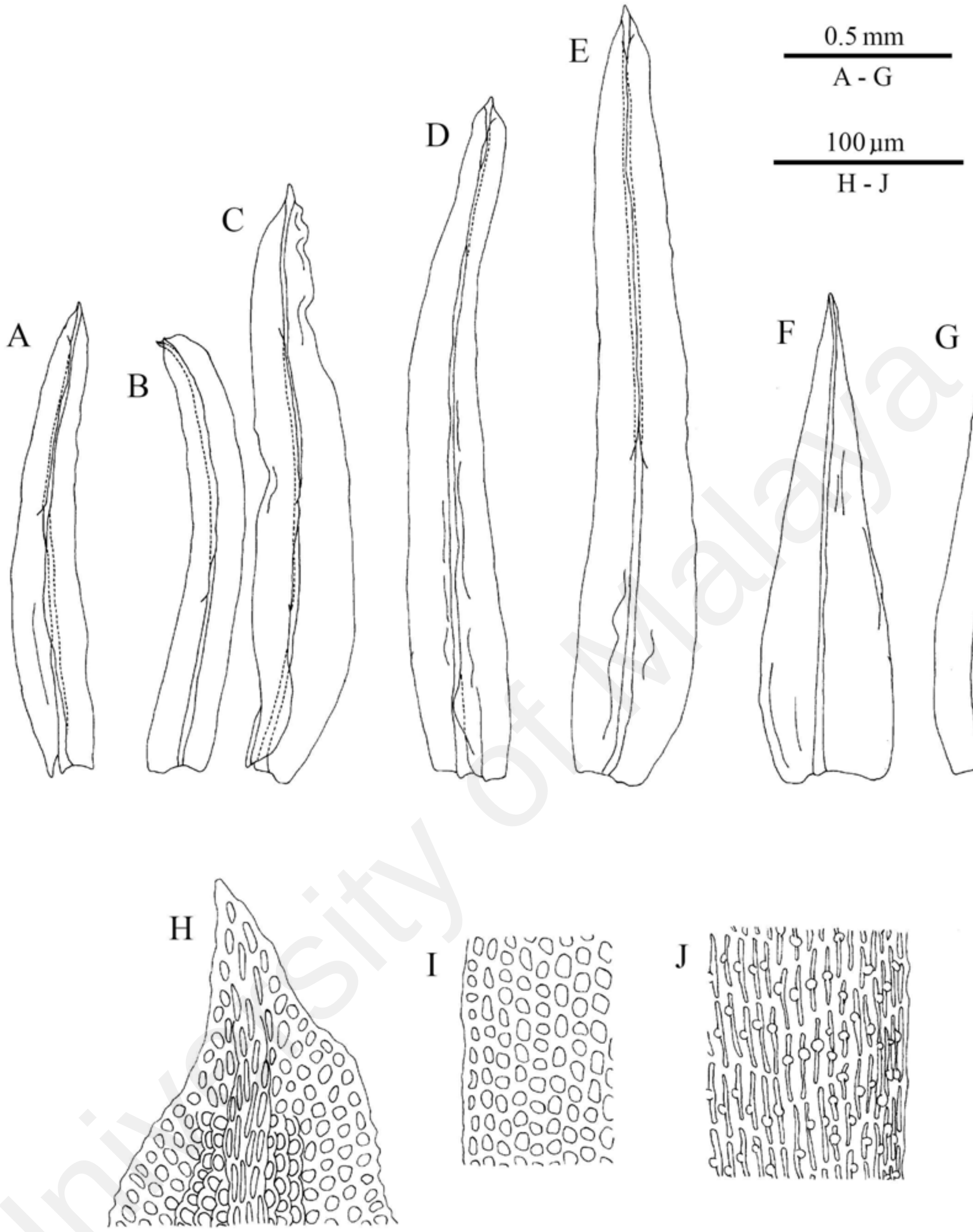

Figure 5.51. Illustrations of *Macromitrium parvifolium* Dixon — A-E, branch leaves; **F-G,** perichaetial leaves; **H,** leaf apex; **I,** mid-leaf cells; **J,** basal laminal cells. [**A, F** from *Menzel et al. 4950* (NY); **B-C, G** from *Carr 15049* (NY, isotype); **D** from *Suleiman 207* (BORH); **E, H-J** from *Yong 6437* (KLU)]

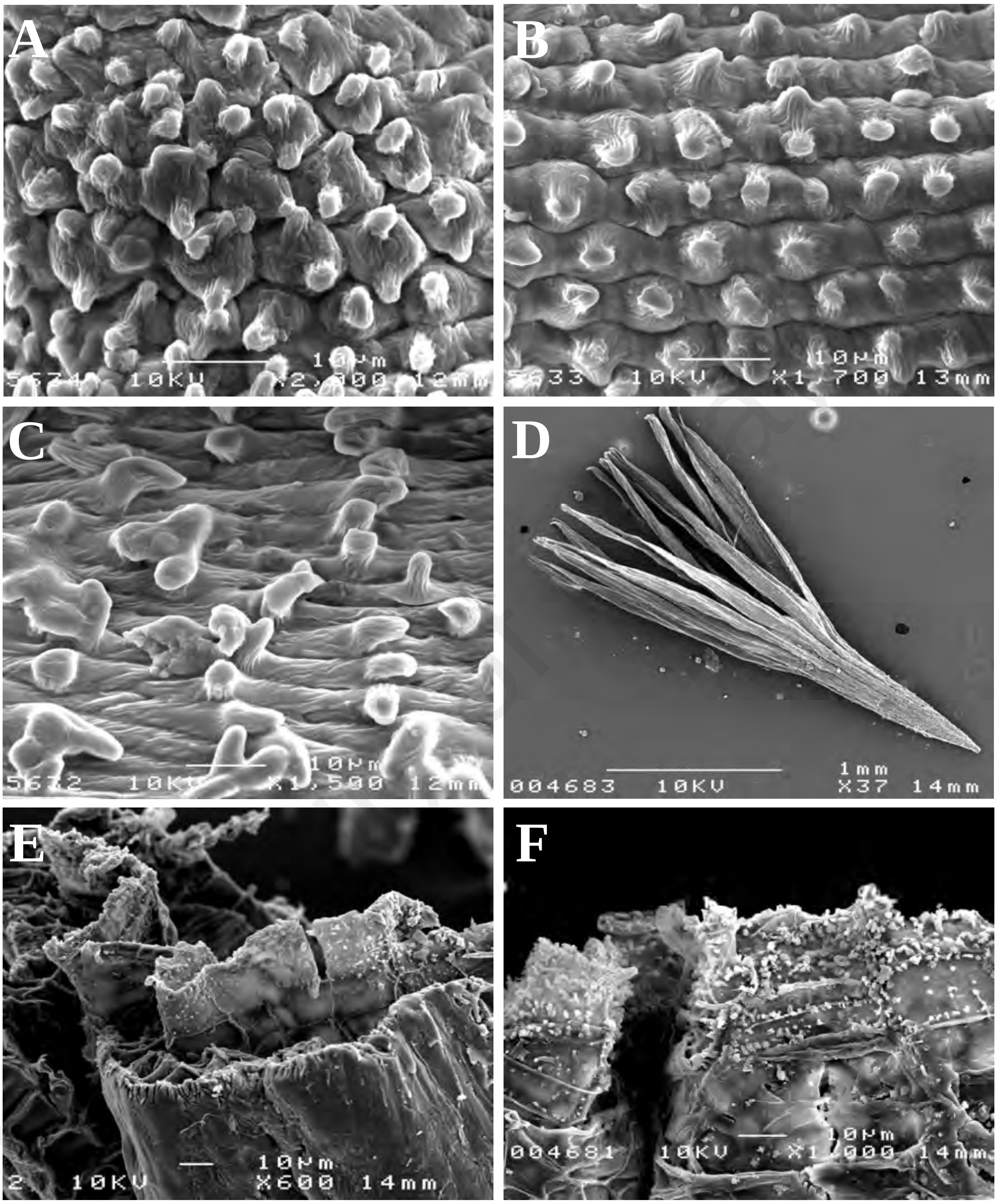

Figure 5.52. SEM images of *Macromitrium parvifolium* Dixon — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** calyptra; **E,** dorsal view of unsplit peristome teeth; **F,** ventral view of unsplit peristome teeth. [All from *Mohamed & Yong 6964* (KLU)]

Branch leaves spirally inserted on branch, densely arranged, indistinctly funiculate with leaves more or less spirally wound around branch, each leaf flexuose-twisted (when dry), wide-spreading to recurved-spreading (when moist); branch leaves 1.7–2.2(–2.5) × 0.3–0.4 mm, length-width ratio 5–7:1, slender lanceolate to ligulate-lanceolate, with margins parallel from apex to leaf base, lamina bent to recurved, plane; apex firm, broadly acute; margin crenulate, plane at distal part but deflexed at base; costa percurrent or filing the acument. Upper laminal cells 10–12 × 10–12 µm, length-width ratio 1:1, oblate to short-rectangular, evenly incrassate, not pitted, strongly bulging with 1–2 conical-papillae, lumina oval; middle laminal cells 10–16 × 10–12 µm, grading from short-rectangular to gradually elongate toward the basal lamina, incrassate, not pitted, with square to rectangular lumina, cells strongly bulging, conical-papillose, clear; basal laminal cells 24–42 × 8–10 µm, length-width ratio 3–4:1, long-rectangular, incrassate, walls evenly thickened, lumina 2–4 µm wide, linear, not pitted, cells strongly bulging, unipapillose to tuberculate.

Pseudoautoicous, if dwarf male plants present, bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, smaller than the branch leaves, 1.5–1.7 × 0.2–0.3 mm, slender, triangular-lanceolate, upper lamina narrow, expanding gradually toward mid-leaf to form an oblong base, leaf base without distinct plications; apex acuminate; margin subentire, plane; costa percurrent; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 0.7–1.0 mm long; paraphyses scarce, scattered on vaginula, 0.4–0.6 mm long, made of 6–10 short- or long-rectangular cells. Seta 10–12 mm long, smooth, dextrorse or sinistrorse-twisted. Capsule urns 1.2–1.3 × 0.6–0.7 mm, short-ovoid to ellipsoid, smooth, rim rounded or sulcate into eight angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 4–5, cryptoporous; operculum rostrate, beak 0.8–1.0 mm. Peristome single. Exostome teeth fused into a continuous membrane, erect in both dry and wet conditions; dorsal and ventral side of teeth smooth or weakly ornamented, irregular papillose, papillae simple and low, sparsely distributed on teeth; remnants of original cell-wall visible on both side of teeth, marked by low and filmy trabeculae. Endostome absent. Spores anisomorphic, larger spores 30–38 µm in diameter, smaller spores 16–20 µm in diameter. Calyptra mitrate, plicate, naked, base deeply lobed into 4–8 wide-spreading strips.

Other descriptions and illustrations: Vitt et al. (1995) p. 60–63, fig. 27

Distribution: As. 4: Malaysia (Borneo), Papua New Guinea.

Habitat and ecology: Epiphytic on tree trunks and lower branches in primary forest. In Malaysia, the species occurs at 1500–2000 m, in the lower montane zone, although elsewhere it has been reported up to 2500 m (Vitt et al., 1995).

Notes:

1. This plant is characterized by: a) slender-lanceolate to lingulate-lanceolate branch leaves that are often whorled and appear rope-like; b) almost parallel leaf margins; c) acute apex with percurrent costa; d) smooth upper laminal cells that are strongly bulging to conic-papillose, but unipapillose to tuberculate basal laminal cells; and f) naked calyptra. The species has been mistakenly placed in the synonymy of *M. zollingeri* (Eddy, 1996), now a variety of *M. blumei*. However, *M. parvifolium* can always be distinguished from both *M. blumei* var. *zollingeri* and *M. blumei* var. *blumei* by its much longer and slender vegetative leaf blade (oblong-lanceolate in *M. blumei*), and percurrent costa (excurrent in *M. blumei*). In addition, *M. parvifolium* has weakly papillose to almost smooth peristome teeth, whereas the peristome teeth of the other taxa mentioned are always strongly papillose.

2. In the absence of fertile material, this species can be confused with *M. falcatulum* as they share similar leaf shape and cell characters. However, the branch leaves of *M.*

falcatulum are generally wider, especially at leaf base, and its tuberculate basal laminal cells gradually grade into smooth cells in the last few rows before the leaf insertion. In contrast, *M. parvifolium* has a narrower leaf base with smooth basal laminal cells. In addition, *M. parvifolium* would not be mistaken for *M. falcatulum* because the calyptra of *M. parvifolium* is glabrous, whereas that of *M. falcatulum* is always densely hairy.

3. This curious species was formerly thought to be restricted to New Guinea (Vitt et al., 1995). Its discovery in Borneo (Sabah) marks its western extent, although it is infrequently collected there. Thus, the plant is now known to have a curious disjunctive distribution, on different sides of the Wallace's Line.

Specimens examined:

MALAYSIA. Sabah: Ranau, Kinabalu Park, Bukit Tupai Trail, 1470 m, 13.V.2005, *Yong 6437* [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Silau-Silau Trail, 1500 m, 24.VIII.1986, *Menzel et al. 4950* [*c.fr*.] (KLU!); Tambunan, Mt. Trus Madi, 1980 m, 24.IX.1996, *Suleiman 207* (BORH! SING); Tawau, Maliau Basin, *Eucalyptus* Camp, 980–1100 m, 16–24.VI.2006, *Mohamed & Yong 6906* [*c.fr*.], *6910*, *6964* [*c.fr*.] (KLU!). **PAPUA NEW GUINEA. Central:** Alola, 6000 ft [=1829 m], 11.I.1936, Carr 15049 (holotype of *M. parvifolium*: BM! isotype NY!).

20. *Macromitrium salakanum* Müll. Hal. (Figs. 5.53, 5.54 & 5.55)

Syn. Musc. Frond. 2: 646 (1851). LECTOTYPE (Vitt et al., 1995): Java, ad arbores montis Salak, *Zollinger 1426* (L; isolectotype BM).

M. humile Bosch & Sande Lac., Bryol. Jav. 1: 128, tab. CVI (1860). LECTOTYPE (Vitt et al., 1995): Java, Salak et Gedé, groeiende tussen *Macromitrium goniorrhynchum* en eene *Pottia*, *Teysmann s.n.* (L) — fide Vitt et al. (1995).

M. pungens Mitt. *ex* Bosch & Sande Lac., Bryol. Jav. 1: 122, tab. XCIX (1860). TYPE: Java, *Teysmann s.n.* (holotype L) — fide Vitt et al. (1995).

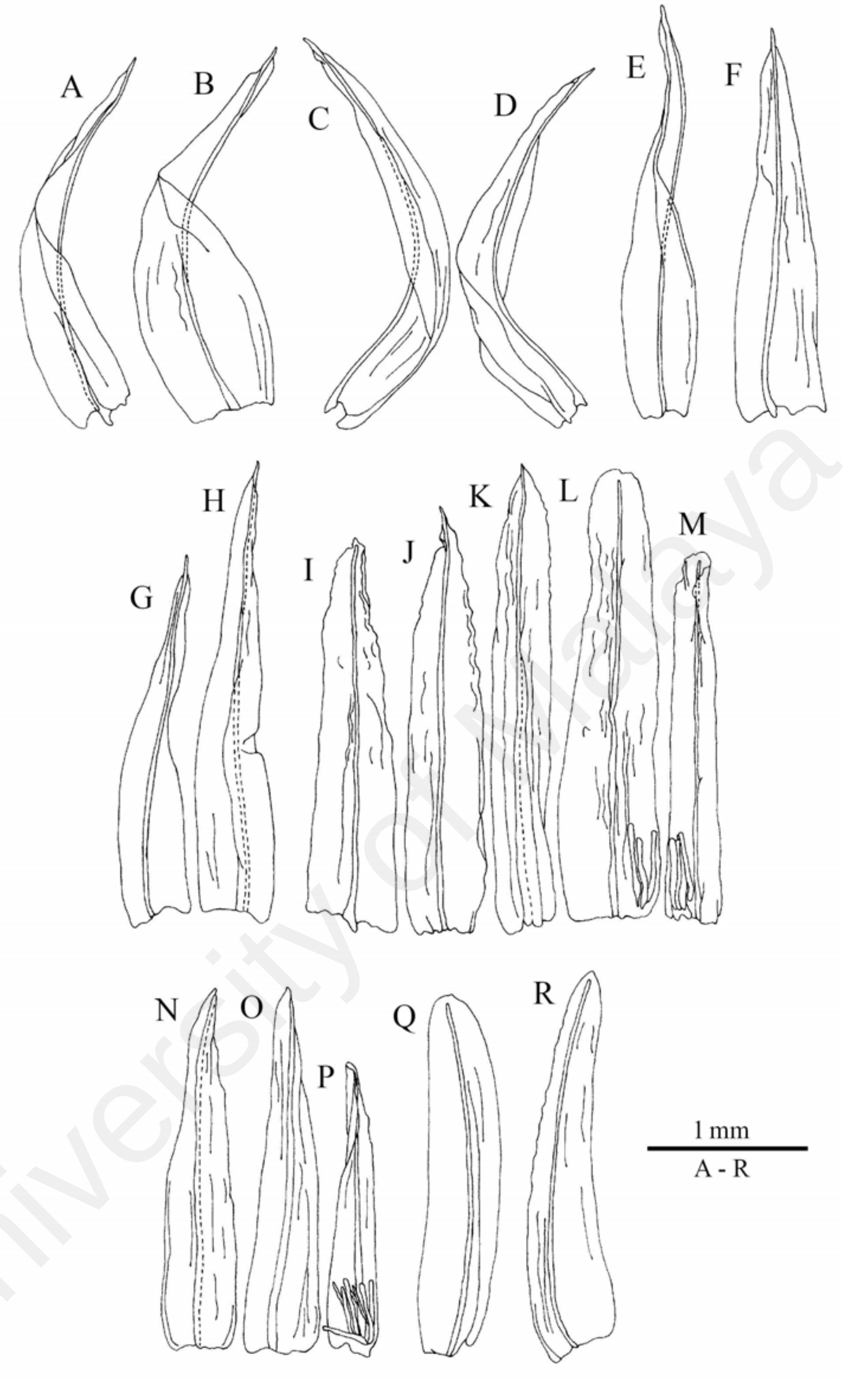

Figure 5.53. Illustrations of *Macromitrium salakanum* Müll. Hal. — A-H, branch leaves; **I-R,** perichaetial leaves (arranged from left to right, outer to inner most position). [**A** from *Mohamed & Yong 4769* (KLU); **B** from *Damanhuri 2000-122* (UKMB); **C, I-M** from *Mohamed & Zamzuri 1121a* (KLU); **E, N-P** from *Halimatul et al. s.n.* (KLU); **F, Q** from *Damanhuri 2000-138* (UKMB); **G-H, R** from *Damanhuri 2000-13* (UKMB)]

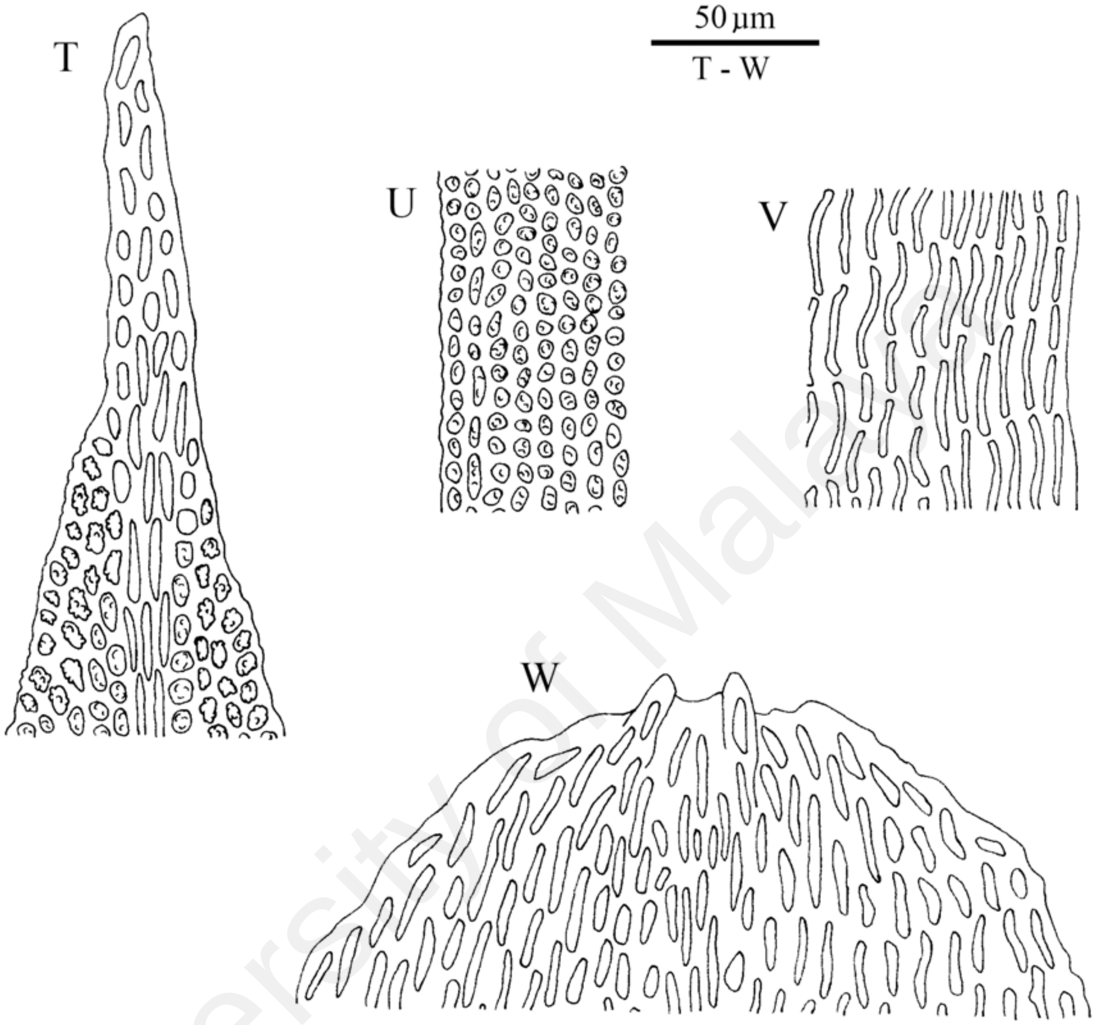

Figure 5.54. Illustrations of *Macromitrium salakanum* Müll. Hal. — S, leaf apex; **T,** mid-leaf cells; **U,** basal laminal cells; **V,** perichaetial leaf apex. [**S-V** from *Mohamed & Yong 4769* (KLU)]

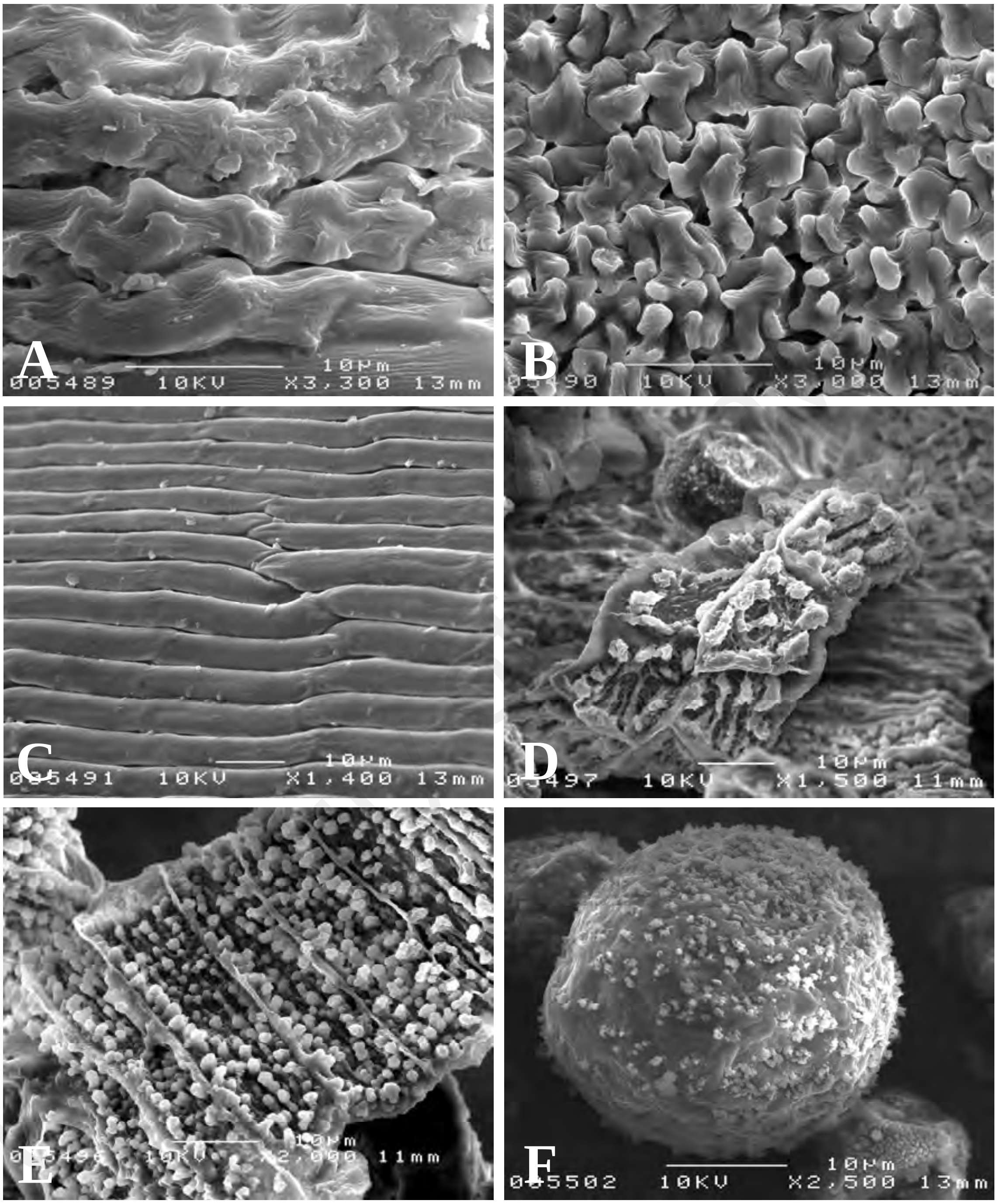

Figure 5.55. SEM images of *Macromitrium salakanum* Müll. Hal. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** dorsal view of peristome teeth; **E,** ventral view of peristome teeth; **F,** macrospore. [All from *Yong et al. 4910* (KLU)]

M. *reflexifolium* Sande Lac., Natuurk. Verh. K. Ak. Wet. Amsterdam 13: 8, tab. 5C (1872), *nom*. *illeg*., non Mitt. (1869). *M*. *celebense* Paris, Ind. Bryol. 773 (1897). *M*. *salakanum* var. *reflexifolium* Bartram, Philipp. J. Sci. 8: 179 (1939). LECTOTYPE (Vitt et al., 1995): Celebes in Menado, *de Vriese s.n*. (L) — fide Vitt et al. (1995).

M. *benguetense* R.S. Williams, Bull. New York Bot. Gard. 8 (31): 343 (1914), ***syn*. *nov***. TYPE: Philippines, Northern Luzon, Benguet, Baguio, on tree, 1570 m, X.1904, *Williams 830* (holotype NY! isotype NY!).

M. *nova-guinense* Broth. *ex* Fleisch., Musci Buitenzorg 2: 447 (1904), *nom*. *nud*.

Plant medium-sized, forming cushions or mats; young shoots yellowish-green, gradually turning to olive-green and brownish at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches generally short, 1–2(–3) cm tall and 2–4 mm wide, tightly arranged, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, triangular-lanceolate on young shoots, becoming more lanceolate at older portions, apex acuminate with percurrent costa.

Branch leaves spirally inserted on branch, lax or densely arranged, indistinctly funiculate with leaves irregularly twisted, flexuose-contorted, with incurved to deflexed-twisted apices (when dry), erect-spreading, wide-spreading to occasionally squarrose-recurved (when moist); branch leaves 1.8–2.5(–2.8) × 0.5–0.8(–1.0) mm, length-width ratio 3–4:1, slender lanceolate to lanceolate with an oblong base, lamina often recurved, plane; apex firm, long-slender, acuminate with apiculate point; margin subentire to crenulate, plane at distal part but reflexed at base; costa shortly excurrent, ending in an apiculus. Upper laminal cells 5–6 × 5–6 µm, length-width ratio 1:1, rounded, oblate to short- or wide-rectangular, evenly incrassate, walls not pitted, cells flat to low-bulging, pluri-papillose, papillae sometime weak; middle laminal cells 8–12 × 6–8 µm, grading from oblate or short-rectangular to gradually elongate toward the basal lamina, cells not uniform in length, incrassate, with curved to more-or-less straight lumina, cells flat, weakly papillose to smooth, clear; basal laminal cells 28–38(–42) × 8–12 µm, length-width ratio 3–4:1, long-rectangular, incrassate, walls unevenly thickened, lumina 2–3 µm wide, strongly curved to sigmoid in appearance, pitted only near juxtacostal region and insertion, cells flat, smooth.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.5–0.8 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, about the size or larger than branch leaves, 2.5–2.8 × 0.5–0.8 mm, lingulate to oblong-laceolate, upper lamina broad, margins almost parallel below apex to the long-oblong leaf base, leaf base often with a few long-plications; apex broadly acute to more commonly obtuse or retuse; margin subentire to entire, plane; costa usually ending below leaf apex; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, rarely pitted. Vaginula 0.9–1.0 mm long; paraphyses abundant, densely covering the vaginula, 0.5–0.8 mm long, made of 6–15 short to long-rectangular cells. Seta 4–6 mm long, smooth, dextrorse-twisted. Capsule urns 1.2–1.5 × 0.9–1.2 mm, short-ovoid to ellipsoid, lightly 8-plicate to smooth, rim rounded or sulcate into four angles when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 3–6, cryptoporous; operculum rostrate, beak 0.9–1.1 mm. Peristome single. Exostome of 16 teeth that are separated above but connected at their base as a low membrane, erect to slightly incurved at top in both dry and wet conditions; dorsal side of teeth vertically striolate-papillose with simple wart-like or relatively large, compound papillae, irregularly distributed on coarse vertical ridges; ventral side of teeth horizontally striolate-papillose with simple or relatively large, compound papillae, either on irregular reticula or vaguely raised, thin horizontal ridges; remnants of original cell-wall obscure on dorsal side, hidden by papillae, but marked by tall and filmy trabeculae on the ventral. Endostome absent. Spores anisomorphic, larger spores 24–28 µm in diameter, smaller spores 14–18 µm in diameter. Calyptra mitrate, plicate, sparsely hairy, with a few stiff erect hairs mostly on ridges near to the calyptra base, base fringed or lacerated.

Other descriptions and illustrations: Dozy & Molkenboer (1861) p. 121–122, tab. 98; Fleischer (1904) p. 440–441 as *M. humile*, p.442–444, fig. 82 as *M. salakanum*, p. 445–446 as *M. pungens*, p. 446–447 as *M. celebense*; Bartram (1939) p. 174, pl.13, fig. 214, as *M. benguetense*, p. 179, pl. 13, fig. 223, as *M. salakanum*; Vitt et al. (1995) p. 65–68, fig. 29; Eddy (1996) p. 52, fig. 362.

Distribution: As. 3: Cambodia; As. 4: Indonesia (Bali, Flores, Java, Lombok, Sulawesi, Sumatra, West Irian), Malaysia (Malay Peninsula, Borneo), Papua New Guinea, Philippines (Camiguin, Luzon, Leyte, Mindanao, Palawan); Oc.: New Caledonia, Solomon Islands.

Habitat and ecology: Epiphytic on tree trunks and branches, rarely near to the ground but occasionally on rocks and concrete structures. A very common species in Malaysia, especially at elevations between 1000–1600 m in the lower montane zone, sometimes lower. The plant is known to tolerate rather exposed sites on mountains rather well, such as on trees along roadsides and in gardens.

Notes:

1. *Macromitrium salakanum* is recognized by its long-lingulate perichaetial leaves which end in a blunt or obtuse apex. On the branch leaves, the upper laminal cells are always short and pluripapillate, while the lower laminal cells are long and smooth, with irregularly thickened walls. This species can be easily confused with *M. angustifolium* and *M. fuscescens* and the distinction from these species is discussed thereunder.

2. The identity of *M. benguetense* has been much questioned, including by Bartram

(1939) and Eddy (1996). Later, Guo et al. (2007) placed *M. bengeutense* in the synonymy of *M. schmidii* Müll. Hal., a gymnostomous species mostly found in India and Indochina. In the original publication, *M. benguetense* was mistakenly described as having "narrowly lanceolate-pointed" perichaetial leaves and branch leaves with "highly mamillose upper laminal cells"; its peristome condition was not mentioned. In fact, as found in the type material (*Williams 830*, NY), both perichaetial leaf and leaf cell characters match those of *M. salakanum*, and furthermore, remnants of peristome teeth were clearly present. Here, *M. benguetense* is placed as a synonym of *M. salakanum*.

<u>Specimens examined</u>:

INDONESIA. Java: *s.loc.*, *s.date*, *s.coll.* [*c.fr.*] (NY!); *s.loc.*, *s.date*, *s.coll. ex Hb. Besch.* [*c.fr.*] (BM 2 sheets!); *s.loc.*, *s.date*, *s.coll. ex Hb. Besch. ex. Dozy & Molk.* [*c.fr.*] (BM!); *s.loc.*, *s.date*, *s.coll. ex Hb. Hampe ex Lacoste* [*c.fr.*] (BM!); Java: *s.loc.*, *s.date*, *s.coll. ex Hb. Hooker* [*c.fr.*] (BM!); *s.loc.*, *s.date*, *Junghuhn s.n.* [*c.fr.*] (BM-Hampe!); *s.loc.*, VII–X.1854, *Motley s.n.* [*c.fr.*] (NY!); *s.loc.*, I.1919, *Wintz s.n.* [*c.fr.*] (NY!); Mt. Halimun National Park, Kantor TNGHS, 700 m, 9.IX.2005, *Yong 6613* [*c.fr.*], *6614*, *6615*, *6618* (KLU!); Mt. Halimun National Park, Mt. Kendang, 990 m, 10.IX.2005, *Yong 6621* (KLU!); Mt. Megamendong, Tugu, 1100–1310 m, 5.I.1894, *Schiffner 11759* (NY!); Mt. Pangerango, *s.date*, *Kurz 481* [*c.fr.*], *906* [*c.fr.*] (BM-Hampe!); *ibidem*, 800–900 m, IV.1894, *Schiffner 11774* [*c.fr.*] (NY!); Soerabaya, I.1889, *Wintz s.n.* [*c.fr.*] (NY!); Tjibodas, 1400 m, 8.V.1894, *Schiffner 3895* [*c.fr.*] (NY 2 sheets!); *ibidem*, 1450 m, II.1900, *Fleischer 130* [*c.fr.*] (BM 2 sheets!); *ibidem*, 1450 m, III.1900, *Fleischer 128* [*c.fr.*] (NY 2 sheets!), *129* [*c.fr.*] (BM!); *ibidem*, 1450 m, VII.1898, *Fleischer 39* [*c.fr.*] (NY!); *ibidem*, 1500 m, 29.IX.2001, *Tan s.n.* (KLU!); Tjibodas, Garten, 3.II.1893, *Moller s.n.* [*c.fr.*] (NY!); Tjibodas am Gedeh, 1450 m, II.1898, *Fleischer 164* [*c.fr.*] (NY!); Tjibodas, Mt. Gedeh, 23.XI.1921, *Overeom 4244* [*c.fr.*] (NY!); *ibidem*, 4500 ft

[= 1372 m], 19.V.1922, *Burkill 8165* [*c.fr.*] (BM! SING!); Tjibodas, Urwald, 7.VI.1893, *Moller s.n.* (NY!). **Sumatra:** *s.loc.*, *s.date*, *Teysmann s.n. ex Hb. Dozy & Molk.* (NY!); Jaloe, IV.1917, *Bunnemeijer 2195* (*81*) [*c.fr.*] (BM!); Mt. Singalang, 550 m, 21.VII.1894, *Schiffner 11795* (NY!); *ibidem*, 1600 m, 16.VI.1999, *Zakaria 28* [*c.fr.*] (KLU!); Padang Pandjang, 800 m, 1929, *Jacobson 30* [*c.fr.*], *62c* [*c.fr.*] (BM!); Pajakumbuh, Mt. Sago, P. Mengatas, 750 m, 19.X.1955, *Meijer 6383* [*c.fr.*] (NY!). **MALAYSIA. Malaya:** *s.loc.*, *s.date*, *Razali RJ2618* [*c.fr.*] (UKMB!). **Johore**: Endau-Rompin, Mt. Tiong, 700 m, 26.VII.2002, *Yong & Sabda 2756*, *2757*, *2758* (KLU!). **Kedah**: Jitra, Mt. Jerai, 2.VIII.1988, *Sadiah et al. 170* (KLU!); Langkawi Islands, Mt. Raya Forest Reserve, 670 m, 16.IV.2003, *Mohamed & Yong 3484* (KLU!). **Pahang**: Cameron Highlands, Boh Tea Estate, 1400m, 8.XI.1960, *Poore 685*, *690* [*c.fr.*] (KLU!); Cameron Highlands, Brinchang, Rose Garden, 1540 m, 12.IV.1987, *Mohamed et al. 9181d* (KLU!); Cameron Highlands, Brinchang, below Mt. Brinchang, 1500 m, 29.VII.2007, *Yong 7439* [*c.fr.*] (KLU!); Cameron Highlands, Brinchang, Mt. Brinchang, 1950–1980 m, 3.VIII.1988, *Mohamed & Damanhuri 1030d* (KLU!); Cameron Highlands, Fairlei Estate to Sg. Mensun, 1100 m, 8.XI.1989, *Sadiah & Zamzuri 1322* [*c.fr.*] (KLU!); Cameron Highlands, jungle path no. 10, 1500 m, 13.III.2004, *Yong et al. 4910* [*c.fr.*] (KLU!); Cameron Highlands, Jumper Rest House, 26.X.1987, *Mohamed & Zamzuri 1072g* (KLU!); Cameron Highlands, Ringlet, Boh Tea Plantation Estate to Kampung Orang Dalam, 960m, 11.XI.1989, *Sadiah & Zamzuri 1483* [*c.fr.*] (KLU!); Cameron Highlands, road to Kampung Raja, 1220 m, 10.X.1999, *Gunaseelan & Ponniah 520* (KLU!); Cameron Highlands, Robinson Waterfall, jungle path no. 9, 1430 m, 7.X.2003, *Yong et al. 4678*, *4682* (KLU!); Cameron Highlands, Tanah Rata Town, 1450 m, 24–25.IV.1999, *Gunaseelan & Mohamed 140a* (KLU!); Cameron Highlands, Tanah Rata, jungle path no. 3, 1450 m, 9.X.1999, *Gunaseelan & Ponniah 451* [*c.fr.*] (KLU!); Cameron Highlands, Tanah Rata, Heritage Hotel, 1450 m, 2.XI.2004, *Yong*

6066 (KLU!); Cameron Highlands, Tanah Rata, Osmaniah Mosque, 22.III.1989, *Bakar 362* (KLU!); Cameron Highlands, Tanah Rata, Parit Waterfall, 1400 m, 29.VII.2007, *Yong 7436* [*c.fr*.] (KLU!); *ibidem*,1420 m, 7.X.2003, *Yong et al*. *4642* (KLU!); Cameron Highlands, Tanah Rata, Pelangi Apartment, 1375m, 5.XII.2004, *Yong & Goh 6120*, *6121* [*c.fr*.], *6125* [*c.fr*.] (KLU!); Fraser's Hill, 22.I.1988, *Damanhuri s.n*. (UKMB!); Fraser's Hill, Allan's Water, 1180 m, 3.I.2008, *Yong 7465* (KLU!); *ibidem*, 1200 m, 10.III.2000, *Damanhuri et al*. *2000-12* (UKMB!); Fraser's Hill, Bishop trail, 1200 m, 26.V.2006, *Yong 7459* (KLU!); Fraser's Hill, golf course, 1300 m, 17.III.1994, *Mohamed 8705* [*c.fr*.] (KLU!); Fraser's Hill, Jelai Tower, 1100, 11.III.2000, *Damanhuri et al*. *2000-143* [*c.fr*.] (UKMB!); Fraser's Hill, Jeriau Waterfalll, 860 m, 10.III.2000, *Damanhuri et al*. *2000-53*, *2000-60*, *2000-61* (UKMB!); Fraser's Hill, RHB Bank Bungalow, 1100 m, 10.III.2000, *Damanhuri et al*. *2000-99* [*c.fr*.] (UKMB!); Fraser's Hill, Temerloh Bungalow, 1180 m, 10.III.2000, *Damanhuri et al*. *2000-21* [*c.fr*.], *2000-24* [*c.fr*.], *2000-25* [*c.fr*.], *2000-26* [*c.fr*.], *2000-31* [*c.fr*.], *2000-38* [*c.fr*.], *2000-39* [*c.fr*.] (UKMB!); Fraser's Hill, The Quest, 1100 m, 11.III.2000, *Damanhuri et al*. *2000-13* [*c.fr*.], *2000-105* [*c.fr*.], *2000-110* [*c.fr*.], *2000-111* [*c.fr*.], *2000-112* [*c.fr*.], *2000-113*, *2000-114* [*c.fr*.], *2000-115* [*c.fr*.], *2000-116* [*c.fr*.], *2000-117* [*c.fr*.], *2000-119* [*c.fr*.], *2000-121*, *2000-122* [*c.fr*.], *2000-123*, *2000-126* [*c.fr*.], *2000-129* [*c.fr*.], *2000-134* [*c.fr*.] *2000-138* [*c.fr*.] (UKMB!); Fraser's Hill, Ye Old Smoke House, 1120 m, 10.III.2000, *Damanhuri et al*. *2000-79*, *2000-85*, *2000-86*, *2000-87*, *2000-88*, *2000-89*, *2000-95* [*c.fr*.] (UKMB!); Genting Highland, Mt. Ulu Kali, 5500 ft [=1676 m], 26.VII.1987, *Z.A.Wahab 18378* (UKMB!); *ibidem*, 1750 m, 11.X.2003, *Yong et al*. *4690* (KLU!); Genting Highland, water reservoir near Genting Resort, 1500 m, 28.IV.1982, *Mohamed 4737* [*c.fr*.] (KLU!). **Penang:** Penang Hill, 700 m, 14.IV.1971, *Tixier 5648* (SING!). **Perak**: Taiping, Taiping Hill (Maxwell Hill), 1400 m, 21.IX.1983, *Razali RJ1337* (UKMB!); *ibidem*, 3741 ft [=1402 m], 25.III.1967, *S.C.Quah 11* (KLU!); Taiping,

Taiping Hill (Maxwell Hill), below Caunfield Hill, 1120 m, 7.III.2004, *Mohamed & Yong 4752* (KLU!); *ibidem*, 1120–1200 m, 8.III.2004, *Mohamed & Yong 4762* [*c.fr*.], *4767*, *4768* [*c.fr*.], *4769*, *4788* (KLU!); Taiping, Taiping Hill (Maxwell Hill), Gunong Hijau Rest House, 1180 m, 6.VI.1983, *Mohamed et al*. *8001* [*c.fr*.], *8140* [*c.fr*.] (KLU!); Taiping, Taiping Hill (Maxwell Hill), trail to Mt. Hijau, 1180 m, 6.V.1983, *Mohamed 8003* [*c.fr*.] (KLU!); Taiping, Taiping Hill (Maxwell Hill), Tempinis Bungalow, 1120–1200 m, 9.III.2004, *Mohamed & Yong 4900* (KLU!). **Perlis**: Wang kelian, Wang Mu Forest Resrve, Bukit Pelarit, 220–553 m, 2.X.1999, *Damanhuri 99-221*, *99-254* (UKMB!). **Sabah:** Crocker Range Park, Papar, Between Ulu Kimanis Base camp and Celcom Tower, alt. 680 m, 31.VIII.2002, *Akiyama Crocker-147* (BORH! HYO); Crocker Range Park, Permanent plot at Crocker Nature Centre, Keningau, subplot C0, alt. 1145 m, 12.X.2005, *Kong 68* (BORH!); Crocker Range Park, Salt Trail, Kg. Tikolod to Kg. Kionop, 468 m, 25.VIII.2003, *Suleiman 1259* [*c.fr*.] (BORH! SNP); Crocker Range Park, Salt Trail, Kg. Tikolod to Kg. Kionop, 399 m, 25.VIII.2003, *Suleiman 1260* [*c.fr*.] (BORH! SNP); Crocker Range Park, Ulu Kimanis, Rinangisan Hill, 1381 m, 28.VIII.2002, *Suleiman 970* (BORH! SNP); Ranau, Kinabalu Park, Mt. Kinabalu, *Damanhuri s.n*. (UKMB!); Ranau, Kinabalu Park, Bukit Tupai Trail, 1455 m, 13.V.2005, *Yong 6441* [*c.fr*.] (KLU!); Sipitang, Mt. Lumaku, Muaya Waterfall, 750 m, 7.III.2009, *Suleiman 4147*, *4148* [*c.fr.*] (BORH, KLU!); *ibidem*, 1100 m, 5.VIII. 2009, *Suleiman 4211* [*c.fr.*] (BORH, KLU!). **Selangor**: Genting Highland, Awana cable car station, 1000 m, 4.X.2003, *Yong 4529*, *4530*, *4531a* [*c.fr*.] (KLU!); Genting Highland, Gohtong Jaya,1055 m, 9.IX.2003, *Yong et al*. *4741* (KLU!); *ibidem*, 1120 m, 9.IX.2003, *Yong et al*. *4738* (KLU!); Genting Highland, Gohtong Jaya, road to Batang Kali, 935 m, 11.X.2003, *Yong et al*. *4712* [*c.fr*.], *4716*, *4718a* [*c.fr*.] (KLU!); Genting Highland, Masjid Noah, 1110 m, 29.VIII.1991, *Mohamed 7666b* (KLU!); Genting Highland, Mt. Bunga Buah, 600 m, 26.III.1995, *Ellis GH9502* [*c.fr*.] (BM!); Genting Highland, road to

Genting-Sempah, 955 m, 22.V.2006, *Yong 6679*, *6681* (KLU!); *ibidem*, 1030 m, 22.V.2006, *Yong 6683*, *6685* (KLU!); Genting Highland, water reservoir near Genting Resort, 1420 m, 14.XII.1983, *Damanhuri s.n.* (UKMB!); Hulu Langat Forest Reserve, Mt. Nuang, 1020 m, 14.VII.1998, *Yong 321* (UKMB!); Kuala Kubu Baru, 2000 ft [=610 m], 23.VII.1979, *Hamzah 25* [*c.fr*.] (KLU!); Ulu Gombak Forest Reserve, Genting Sempah Road, 1700 ft [=518 m], 7.IX.1965, *Inoue 10741* (TNS!). **Terengganu**: Dungun, Mt. Mandi Angin, Pasir Raja Forest Reserve Compartment 5, 150 m, 6.VI.2004, *Yong 5760* (KLU!); Dungun, Mt. Mandi Angin, Pasir Raja Forest Reserve Compartment 16–18, 985 m, 7.VI.2004, *Yong 5830* (KLU!). **PAPUA NEW GUINEA. Eastern Highlands:** Kainantu, Kassam Pase, 1520 m, 5.IV.1982, *Streimann 17912* (NY!). **Morobe:** Aseki, Pouyu Village, 1500 m, 24.I.1981, *Streimann & Tamba 12580* [*c.fr*.] (NY!); Bulolo, Upper Watut River, 1750 m, 22.VIII.1982, *Streimann 23083* [*c.fr*.] (ALTA, LAE, NICH, NY!). **Southern Highlands:** Nogoti, Tagari River, Tari-Komo Road, 1250 m, 16.XII.1982, *Streimann 32565* [*c.fr*.] (ALTA, KRAM, LAE, NY! TBA). **PHILIPPINES. Leyte:** Baybay, Mt. Pangasungan, 400–650 m, 21.V.1984, *Tan et al. 84-263* [*c.fr*.] (TNS!). **Luzon:** Albay, Mt. Malinao, 2.II.1956, *Edano 37235* (SING!); Battan, Mt. Mariveles, *s.date*, *Whitford 433* [*c.fr*.] (NY!); *ibidem*, 16.VIII.1908, *Robinson 6213* [*c.fr*.] (NY!); Benguet, Baguio, 1570 m, X.1904, *Williams 830* [*c.fr*.] (holotype of *M. benguetense*: NY! isotype: NY!); Cagayan, Claveria, VIII.1909, *McGregor 10739* [*c.fr*.] (NY!); Laguna, San Antonio, IX–X.1912, *Ramos 16671* [*c.fr*.] (BM!); Mt. Santo Jonas, 1900 m, X.1904, *Williams 1758* [*c.fr*.] (NY!); Pampanga, Mt. Arayat, 1000 m, I.2004, *Linis 895-04* (SING!); Pampanga, Mt. Pinatubo, Camp Stotsenburg,V.1927, *Elmer 22265* (NICH!); Rizal, Mt. Lumutan, VII.1917, *Ramos & Edano 29822* (NY!); Sorsogon, Irosin, Mt. Bulusan, XI.1915, *Elmer 15101* [*c.fr*.] (BM!); upper Ramos River, 912 m, I.1904, *Williams 817* [*c.fr*.] (NY!). **Mindanao:** Bukidnon, Mt. Kalatungan, Pangantucan, 12–14.V.1999, *Lubos K192* (SING!); Caraga, Butuan, III–VII.1911, *Weber 1298* [*c.fr*.], *1314* [*c.fr*.] (NY!); Misamis Oriental, Mt. Lumot, Barangay Lunutan, 1150 m, 24.VIII.1999, *Bernabe et al*. *3986*, *4021* (SING!); South Cotabato, Mt. Matutum, 16–25.VII.1999, *Lubos M6* (SING!); Zamboanga, Sax River, 5.III.1905, *Williams 2381* [*c.fr*.] (NY!); *ibidem*, 550 m, II.1905, *Williams 3141* [*c.fr*.] (NY!).

5.3.4 *Schlotheimia* Brid.

Muscol. Recent. Suppl. 2: 16 (1812). *Macromitrium* sect. *Schlotheimia* (Brid.) Müll. Hal., Bot. Zeitung (Berlin) 3: 541 (1845). TYPE: *S*. *torquata* (Hedw.) Brid.

Plants cladocarpous, robust, usually cushion-forming. Stem (primary axis) branched sympodially, plagiotropic, creeping with numerous, erect, short, simple, monopodial branches (secondary axis). Monopodial branches branched sympodially, branched more or less regularly, with 1–2 subsequent branches formed almost immediate or short distance beneath perichaetium. Creeping stems tomentose, rhizoids never extended up to the erect branches. Stem leaves always smaller, resembling branch leaves in shape. Branch leaves more or less uniform in shape, oblong-lanceolate to lingulate-lanceolate, leaf base not decurrent, and leaf lamina unistratose thick. Leaf cells prosenchymatous, upper laminal cells short to long, oblate to long-rhombic, smooth, but basal laminal cells consistently long-rectangular, prorate; juxtacostal cells and marginal cells at basal lamina not distinctly differentiated. Plant phyllodioicous. Dwarf male bud-like. Perichaetial leaves conspicuous or not. Vaginula long, densely covered by long and filamentous paraphysis; paraphysis uniseriate, branched at their base. Seta moderately long, extended. Capsule exerted, urn narrowed to seta in short distance, exothecial cells incrassate; stomata phaneroporous, many, commonly found near urn base; operculum rostrate with a long beak that perpendicular to operculum base. Peristome double. Teeth 16, free, exostome alternate with endostome. Anisospory. Calyptra mitrate, completely covering the urn, smooth, naked and base shallowly dissected into several lobes.

Notes:

1. A genus with about 121 accepted species names (Crosby et al., 1999), mostly tropical in origin with a small number of species reported from subtropical to temperate regions (with the highest diversity in continental South America and Madagascar) (Vitt, 1989). In Malesia, five out of the six reported species are endemic. Among these, *S. rubiginosa* is endemic to Mt. Kinabalu, whereas *S. wallisii* has a wider distribution and is reported from Borneo and the Philippines to New Guinea. *Schlotheimia* is only known from higher elevations (1500 m to the tree line).

2. *Schlotheimia* spp. can be easily distinguished from other Orthotrichaceae by their cladocarpic habit, both exostome and endostome well-developed with separated teeth, and smooth calyptra with base dissected into trapezoid lobes. In addition, both *Schlotheimia* species in Borneo have prosenchymatous laminal cells that appear prorate under high magnification (the other Orthotrichaceae have consistenly parenchymatous laminal cells).

3. The branch leaves of both *Schlotheimia* species are often strongly coiled on the branch, giving a rope-like perspective, but this is not unique as the character also occurs in other Bornean mosses.

1. *Schlotheimia rubiginosa* C.H. Wright (Figs. 5.56 & 5.57)

Trans. Linn. Soc. London, Bot. 4: 257 (1894). TYPE: North Borneo, Mt. Kinabalu, 10500 ft [=3200 m], *Haviland 1418* (holotype NY; isotype BM!).

Plant robust, forming tall-cushions; young shoots yellowish-green, gradually turning to olive-green and reddish-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature

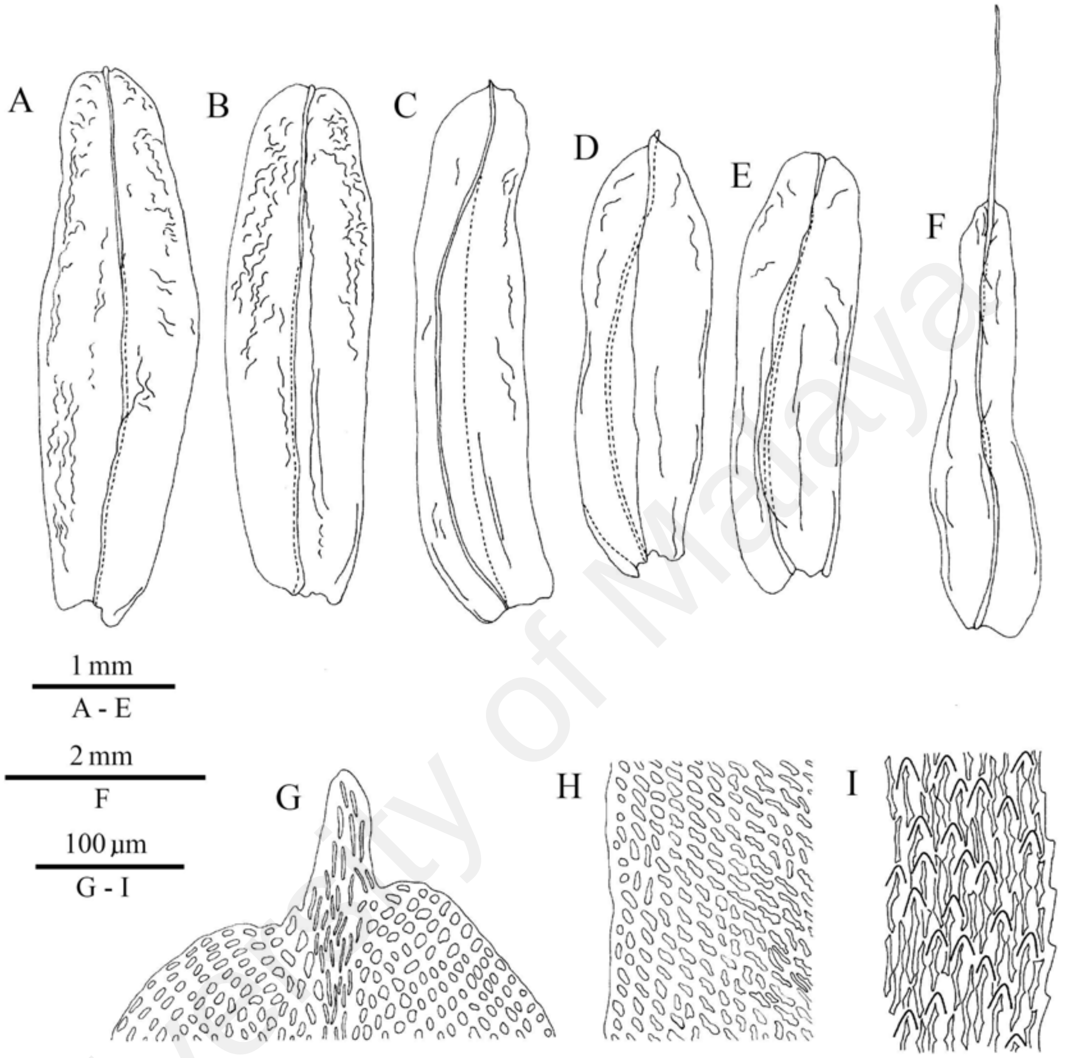

Figure 5.56. Illustrations of *Schlotheimia rubiginosa* C.H. Wright — A-E, branch leaves; **F,** perichaetial leaf; **G,** leaf apex; **H,** mid-leaf cells; **I,** basal laminal cells. [**A, G-I** from *Yong 6272* (KLU); **B** from *Yong 6291* (KLU); **C** from *Shea 3099* (SAN); **D** from *Meijer B11925* (TNS); **E-F** from *Holttum 25671* (SING)]

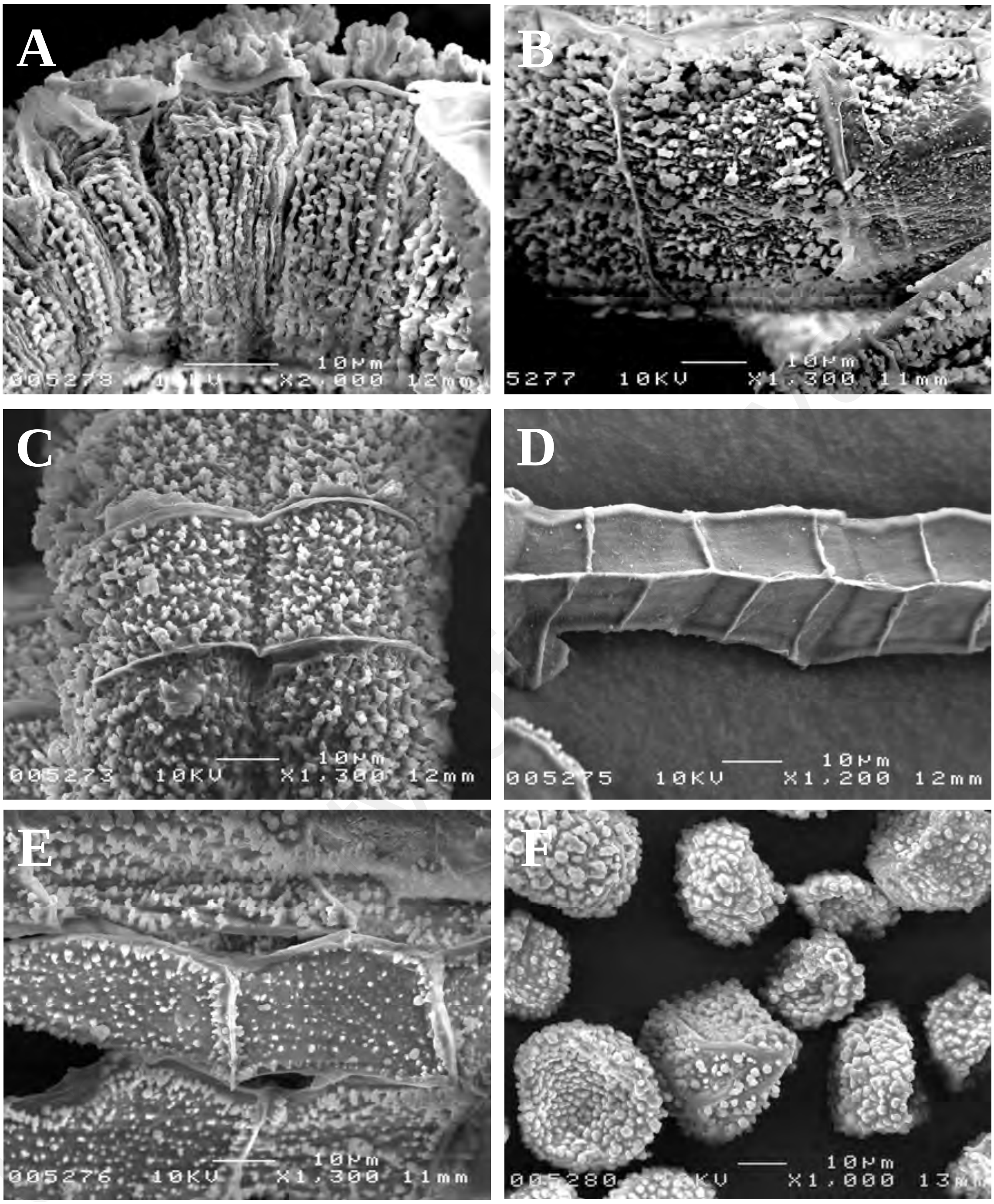

Figure 5.57. SEM images of *Schlotheimia rubiginosa* C.H. Wright — A, dorsal view of outer peristome teeth, lower portion; **B,** ventral view of outer peristome teeth, lower portion; **C,** ventral view of outer peristome teeth, upper portion; **D,** dorsal view of inner peristome teeth; **E,** ventral view of inner peristome teeth; **F,** spores. [All from *Yong 6287* (KLU)]

portions. Erect branches tall, 4–5 cm tall and 6–8 mm wide, tightly arranged, on short interval, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate on young shoots, elongate at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, densely arranged, more or less funiculate with leaves spirally wound on branch, flexuose-twisted, with curved apices (when dry), erect-spreading to wide-spreading with flexuose lamina (when moist); branch leaves 3.0–4.2 × 0.6–1.0 mm, length-width ratio 3–4:1, oblong-lanceolate, lingulate-lanceolate, lamina mostly straight, occasionally with deflexed apex, strongly rugose; apex firm, broad, retuse to obtuse, occasionally broad-acute to mucronate; margin crenulate to denticulate above but smooth below, plane at distal part but reflexed at leaf base; costa percurrent or short-excurrent with 1–2 cells extending beyond the tip. Upper laminal cells 10–25 × 8–10 µm, length-width ratio 1–2:1, oblate to rhombic, evenly incrassate, occasionally pitted, flat, smooth, lumen oval to long-rectangular; middle laminal cells 12–30 × 8–10 µm, grading from narrow-rhombic to gradually long-rectangular toward the basal lamina, incrassate, pitted, with slanted, long-rectangular lumina, cells smooth, clear; basal laminal cells 58–65 × 8–10 µm, length-width ratio 5–6:1, long-rectangular, incrassate, walls mostly evenly thickened, lumina 3–4 µm wide, linear, pitted, cells prorate on distal-end, rough.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, often longer than branch leaves, 3.5–4.1 × 0.8–1.0 mm, oblong-laceolate to lingulate, upper lamina broad, expanding gradually to a long-oblong base, leaf base often with a few long-plications; apex broadly acute, piliferous; costa long-excurrent, ending in a hyaline arista that reach 1.2–2.5 mm long; margin subentire, plane; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 1.0–1.4 mm long; paraphyses abundant, concentrated near the base of vaginula, 1.0–1.2 mm long, made of 20–30 short- or long-rectangular cells. Seta 5–12 mm long, smooth, dextrorse twisted. Capsule urns 2.3–3.5 × 0.9–1.0 mm, broad-cylindric, smooth, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 12–14, phaneroporous; operculum rostrate, beak 0.9–1.1 mm. Peristome double. Exostome of 16 long teeth that separated above but connected at their base as a low membrane, recurved at top when dry, but straight in wet condition, teeth with distinctive median furrow and articulated on dorsal face; dorsal side of teeth densely reticulate-papillose on top but horizontal striolate-papillose at below, papillae simple to compound; ventral side of teeth densely reticulate-papillose with simple to compound papillae; remnants of original cell-wall hidden on dorsal side, marked by horizontal furrows, but marked by tall and filmy trabeculae on the ventral. Endostome of 16 thin segments arise from a very low basal membrane, straight in both dry and wet conditions, segment keeled with a vertical divisural line on dorsal face; dorsal side of segment smooth, while ventral side of segment papillose, papillae simple to compound, scattered on segment; remnants of original cell wall marked by transverse lines on dorsal side but by low and filmy trabeculae on the ventral. Larger spores 40–45 µm in diameter, smaller spores 18–24 µm in diameter. Calyptra mitrate, smooth, naked, calyptra base shallowly dissected into 4–8 rectangular clefts when mature.

Distribution: Endemic to Mount Kinabalu, Sabah, Malaysia (As. 4).

Habitat and ecology: Epiphytic or growing on rock in rather open area. The plant is most common at upper montane forest to subalpine elevation (2700–3200 m), with a rare occasion collected from lower montane forest at 1720 m.

Notes:

1. *Schlotheimia rubiginosa* resembles the larger form of *S. wallisii* in most features,

except for the often retuse vegetative leaf apex in *S. rubiginosa*. Also, in *S. rubiginosa*, the costa is long-excurrent only in the perichaetial leaves, whereas in *S. wallisii*, both vegetative and perichaetial leaves end in long-excurrent costae (aristae).

2. SEM examination of peristome teeth further supports the distinction of these two species. In *S. rubiginosa*, the exostome teeth are dorsally papillose, whereas in *S. wallisii* papillae are absent. Further, the endostome teeth are dorsally smooth and ventrally papillose in *S. rubiginosa*, but dorsally papillose and ventrally striolate in *S. wallisii*. Such characters, although cryptic, clearly tell the two species apart.

3. It is possible that *S. rubiginosa* and *S. wallisii* are vicariant. The former is thus far only known on Mount Kinabalu, where it appears to have adapted to higher elevations (it is very abundant at 2700–3200 m) and a more open environment, and where *S. wallisii* is uncommon. The more widespread *S. wallisii* occupies a wider but lower elevational range, from lower montane to upper montane zone (1500–3000 m). Although there is as yet no molecular evidence for this, the restriction of a higher-elevation taxon surrounded by a more widespread, lower-elevation taxon that is morphologically very closely related suggests the vicariance (possible divergence) of a population derived from *S. wallisii*.

Specimens examined:

MALAYSIA. Sabah: Ranau, Kinabalu Park, Mt. Kinabalu, *s.date*, *Damanhuri s.n.* (UKMB); *ibidem*, 10500 ft [=3200 m], *Haviland 1418* [*c.fr.*] (isotype of *S. rubiginosa*: BM!); Ranau, Kinabalu Park, Mt. Kinabalu, Paka Cave, 9500 ft [=2896 m], 22.VII.1960, *Meijer B10407* [*c.fr.*] (L, NY!); *ibidem*, 10000 ft [=3048 m], 13.II.1963, *Meijer B11918* [*c.fr.*], *B11925* [*c.fr.*] (L, NY! TNS!); *ibidem*, 10200 ft [=3109 m], 15.XI.1931, *Holttum 25643* [*c.fr.*], *25671* [*c.fr.*] (SING!) (NY! SING!); Ranau, Kinabalu Park, Mt. Kinabalu, Paka Cave to Lobang, Mt. Kinabalu, 15.XI.1915, *Clemens 10740* [*c.fr.*] (NY!); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Laban Rata to Paka Cave, 3000 m, 10.V.2005, *Yong 6306*, [*c.fr*.] (KLU!); *ibidem*, 3025 m, 10.V.2005, *Yong 6333*, *6334* (KLU!); *ibidem*, 3040 m, 10.V.2005, *Yong 6321* (KLU!); *ibidem*, 3050 m, 10.V.2005, *Yong 6313* (KLU!); *ibidem*, 3095 m, 10.V.2005, *Yong 6323*, [*c.fr*.], *6324*, [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, trail from Timpohon Gate to Laban Rata, 2700 m, 9.V.2005, *Yong 6272*, [*c.fr*.] , *6274*, [*c.fr*.], *Yong 6275*, [*c.fr*.] (KLU!); 2900 m, 18.I.1997, *Akiyama et al*. *251* (HYO, BORH!); *ibidem*, 9.V.2005, *Yong 6287*, [*c.fr*.], 6288 (KLU!); *ibidem*, 12.V.2005, *Yong 6405*, *6406* (KLU!); *ibidem*, 3000 m, 9.V.2005, *Yong 6290*, [*c.fr*.], *6291*, [*c.fr*.] (KLU!); *ibidem*, 3050 m, 9.V.2005, *Yong 6285*, [*c.fr*.] (KLU!); *ibidem*, 10.V.2005, *Yong 6320*, [*c.fr*.] (KLU!); Ranau, Kinabalu Park, Mt. Tombuyukon, Musang Camp (km 10) to the summit, 1720 m, 14.VIII.2008, *Suleiman 3708*, [*c.fr*.] (BORH, KLU! SNP).

2. *Schlotheimia wallisii* Müll. Hal. (Figs. 5.58 & 5.59)

Linnaea 37: 173 (1872). LECTOTYPE (Vitt et al., 1993): Insulae Philippinae regione montosa, 1870, *Wallis s.n*. (NY).

S. *splendida* Mitt., Trans. Linn. Soc. London, Bot. 4: 256 (1894). SYNTYPES: North Borneo, Kinabalu, Maripari, 5000 ft [=1524 m], *Haviland 1419* (BM); *Low*, *Burbidge* (BM).

S. pilicalyx Broth. & Geh., Öfv. Finska Vet. Soc. Förh. 37: 163 (1895). LECTOTYPE (Vitt et al., 1993): Nova Guinea, in cacumine montium Owen Stanley Range, *MacGregor 10* (H-BR; isolectotype BM!) — fide Vitt et al. (1993).

S. *speciosissima* Broth., Philipp. J. Sci. 3: 17 (1908). TYPE: Mindanao, Prov. of Misamis, Mt. Malindang, *Mearns & Hutchinson For*. *Bur*. *4798* (holotype Manila Herb., destroyed; isotype US?).

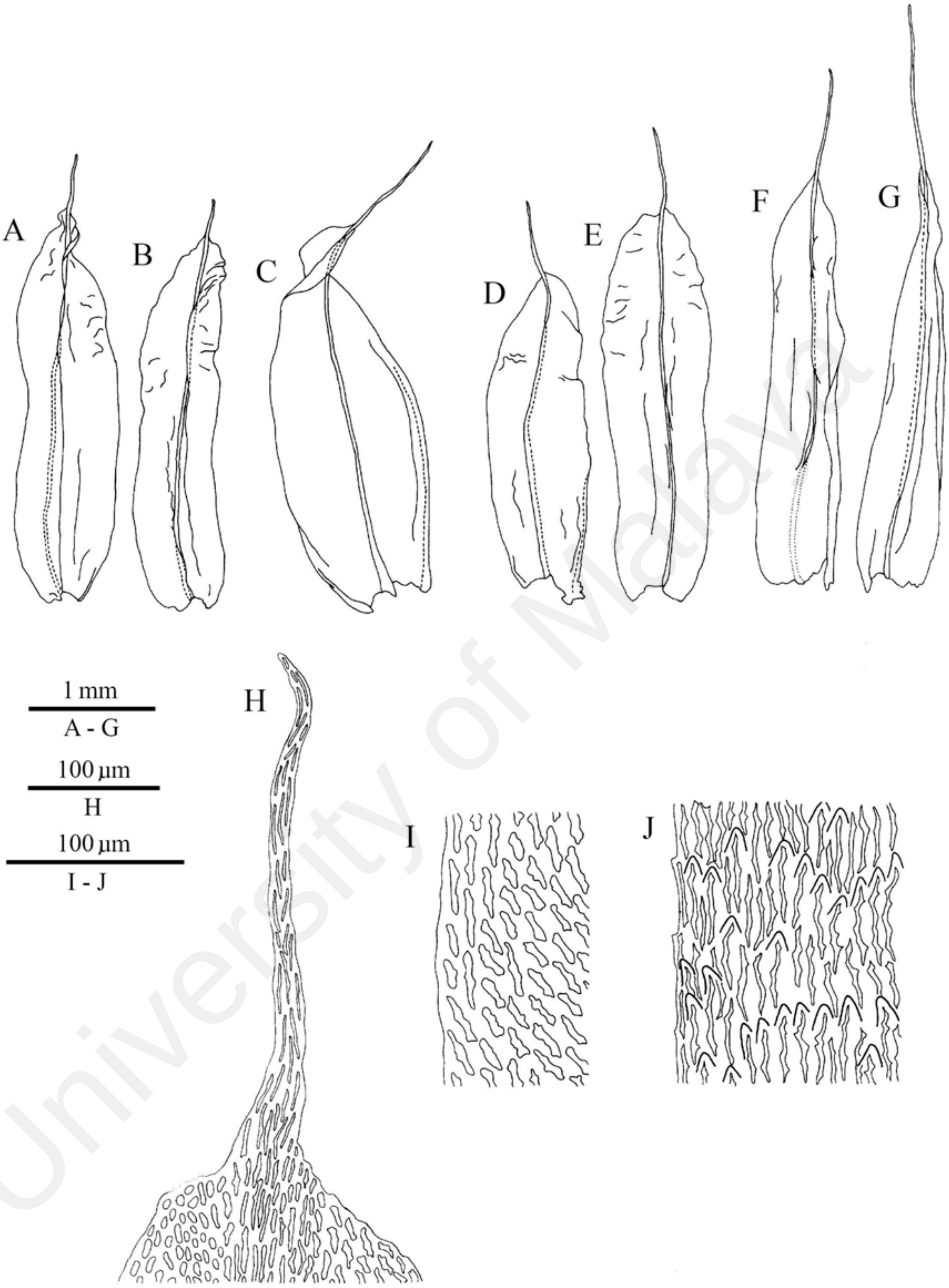

Figure 5.58. Illustrations of *Schlotheimia wallisii* Müll. Hal. — **A-E,** branch leaves; **F,** outer perichaetial leaf; **G,** inner perichaetial leaf; **H,** leaf apex; **I,** mid-leaf cells; **J,** basal laminal cells. [**A-B, H-J** from *Yong 6301* (KLU); **C** from *Koponen 30602* (TNS); **D-G** from *Tan et al. 82-209* (KLU)]

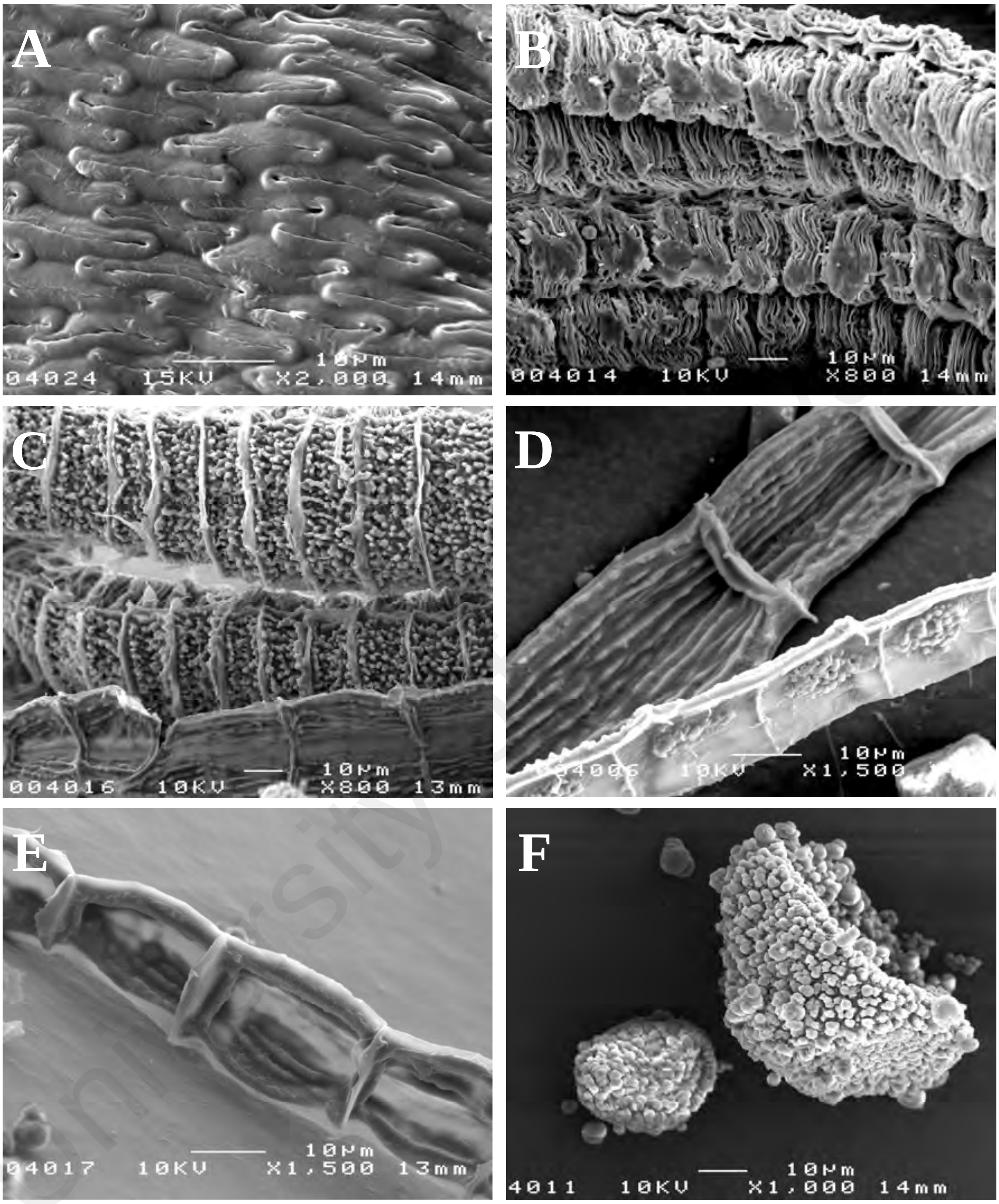

Figure 5.59. SEM images of *Schlotheimia wallisii* Müll. Hal. — A, basal laminal cells; **B,** dorsal view of outer peristome teeth; **C,** ventral view of outer peristome teeth; **D,** dorsal view of inner peristome teeth (top, in half row), ventral view of inner peristome teeth (bottom); **E,** ventral view of inner peristome teeth; **F,** spores. [All from *Eddy 1364* (BM)]

S. gigantea Fleisch., Hedwigia 50: 282 (1911). TYPE: Hollandisch-New-Guinea, Urwälder am Gipfel des Hellwiggebirges (Agathodämonsberg) an Baumästen bei ca. 2500 bis 3000 m Hohe, XI.1910, *Römer 1266* (holotype FH; isotypes L, NY!) — fide Vitt et al. (1993).

S. gigantea var. *pilosa* Fleisch., Nova Guinea 8: 745 (1912). *S. pilosa* (Fleisch.) Fleisch., Nova Guinea 12: 116 (1914). TYPE: Niederl. Neu-Guinea, Urwälder am Gipfel des Hellwig-Gebirges am Agathodämonsberg bei ca. 2500 bis 3000 m Hohe, XI.1910, *Römer 1307* (holotype FH) — fide Vitt et al. (1993).

S. koningsbergeri Fleisch., Nova Guinea 12: 117, taf. XXX1 (1914). LECTOTYPE (Vitt et al., 1993): Niederl.-Sudwest-Neu-Guinea, Am Goliath-Gebirge zwischen 1950–3000 m, auf der Erde, detex. *De Kock 26* (FH; syntypes FH, FH, L) — fide Vitt et al. (1993).

S. subrubiginosa Dixon, Farlowia 1: 32 (1943). TYPE: Indonesia, Paniai, Meerendal, 4000–4100 m, Mt. Carstensz, *Wissel 7* (*BZ3990*) (holotype BM; isotype L) — fide Vitt et al. (1993).

S. lamii Broth., Natuurk. Tijdschr. Ned.-Indië 88: 139 (1929), *nom. nud.*

Plant robust, forming short- to tall-cushions; young shoots yellowish-green, gradually turning to olive-green and reddish-brown at mature portions, brownish to darker below. Stems creeping, covered by rhizoidal tomentum, often denuded of stem leaves at mature portions. Erect branches generally tall, (1–)2–3 cm tall and 5–6 mm wide, tightly arranged, on short interval, occasionally branched. Stem leaves inconspicuous, small, covered by rhizoids, ovate-lanceolate on young shoots, elongate at older portions, apex acuminate with excurrent costa.

Branch leaves spirally inserted on branch, densely arranged, more or less funiculate with leaves spirally wound on branch, flexuose-twisted, with curved apices (when dry), erect-spreading to wide-spreading with flexuose lamina (when moist); branch leaves 2.5–3.2 × 0.6–0.9 mm, length-width ratio 3–4:1, oblong-lanceolate, lingulate to ligulate-lanceolate, lamina mostly straight, occasionally with deflexed apex, smooth or occasionally rugose; apex firm, broad, obtuse to broad-acute, piliferous; margin crenulate to denticulate above but smooth below, plane at distal part but reflexed at leaf base; costa long-excurrent, ending in a 0.6–1.0 mm long hyaline arista. Upper laminal cells 20–30 × 8–10 µm, length-width ratio 2–3:1, oblate to rhombic, evenly incrassate, occasionally pitted, flat, smooth, lumen oval to long-rectangular; middle laminal cells 30–55 × 8–10 µm, grading from narrow-rhombic to gradually long-rectangular toward the basal lamina, incrassate, pitted, with slanted, long-rectangular lumina, cells smooth, clear; basal laminal cells 68–84 × 10–12 µm, length-width ratio 6–8:1, long-rectangular, incrassate, walls mostly evenly thickened, lumina 3–4 µm wide, linear, pitted, cells prorate on distal-end, rough.

Pseudoautoicous, dwarf male plants bud-like, perigonial leaves 0.4–0.5 mm long, ovate to ovate-lanceolate. Perichaetial leaves erect to erecto-patent, loosely sheathing the seta, often longer than branch leaves, 4.0–4.2 × 0.9–1.2 mm, oblong-laceolate to lingulate, upper lamina broad, expanding gradually to a long-oblong base, leaf base often with a few long-plications; apex obtuse to broad-acute, piliferous; margin subentire, plane; costa long-excurrent, ending in a 1.6–2.2 mm long hyaline arista; laminal cells distinctively incrassate with straight and sigmoid-curved lumen continuing from leaf base into leaf apex, pitted. Vaginula 1.0–1.4 mm long; paraphyses abundant, concentrated near the base of vaginula, 1.0–1.1 mm long, made of 22–28 short- or long-rectangular cells. Seta 8–11 mm long, smooth, dextrorse twisted. Capsule urns 2.5–3.2 × 0.7–0.9 mm, broad-cylindric, smooth, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 10–14, phaneroporous; operculum rostrate, beak 0.9–1.1 mm. Peristome double. Exostome of 16 long teeth that separated above but connected at their base as a low membrane, recurved at top when dry, but straight in wet condition, teeth with distinctive median furrow and articulated on dorsal face; dorsal side of teeth densely transverse-striate, coarse but without papillae; ventral side of teeth densely reticulate-papillose with simple to compound papillae; remnants of original cell-wall obscure on dorsal side, marked by horizontal furrows, visible on the ventral, marked by tall and filmy trabeculae. Endostome of 16 thin segments arise from a very low basal membrane, straight in both dry and wet conditions, segment keeled with a vertical divisural line on dorsal face; dorsal side of segment papillose, while ventral side of segment longitudinal-striate, striate smooth or occasionally papillose, papillae wart-like; remnants of original cell wall marked by tranverse lines on dorsal side but by tall and filmy trabeculae on the ventral. Larger spores 42–46 µm in diameter, smaller spores 20–25 µm in diameter. Calyptra mitrate, smooth, naked, calyptra base shallowly dissected into 4–8 rectangular clefts when mature.

Other descriptions and illustrations: Fleischer (1912) p. 744, tab. CXXIIB [as *S. gigantea*]; Fleischer (1914) p. 116, tab. XXX [as *S. pilosa*]; p. 117, tab. XXXI [as *S. koningsbergeri*]; Bartram (1939) p. 185–186, pl. 14, fig. 231; Vitt et al. (1993) p. 19–23, figs. 8, 10; Eddy (1996) p. 88, fig. 389, p. 88–90, fig. 390 [as *S. koningsbergeri*].

Distribution: Endemic to Malesia. As. 4: Indonesia (Sulawesi, West Irian), Malaysia (Borneo), Papua New Guinea, Philippines (Luzon, Mindanao, Negros).

Habitat and ecology: The plant is either epiphytic, found growing on trunks and branches in montane forest, or epilithic, quite often found growing on rocks and boulders, in partially exposed or much open sites. In New Guinea, it occurs up to 3600 m (Vitt et al., 1993). Although this is the commonest *Schlotheimia* species in the region, with a wide elevation range from the lower montane to subalpine zones, it appears to be less common and is often collected from lower elevations than is *S. rubiginosa* on

Mount Kinabalu.

Notes:

1. This species is characterized by its robust size and oblong branch leaves that have abruptly narrowed to long-aristate apices (with excurrent costa). This species has branch leaves that tightly curl around branches, imparting a rope-like general appearance, a character shared with a few other Malaysian Orthotrichaceae (*Groutiella tomentosa*, both varieties of *Macromitrium blumei* and *M. densum*). However, *Schlotheimia wallisii* is easily distinguished from these other taxa by the robust plants and leaves, prorate basal laminal cells, and unique sporophytic structures that characterize the genus.

2. Superficially *S. wallisii* appears like a smaller form of *S. rubiginosa*, which it resembles in many features; however, *S. wallisii* has long-excurrent costae on all branch leaves, whereas *S. rubiginosa* is similarly costate only on perichaetial leaves. Apparently smaller forms of this species have been collected from the Maliau Basin (*Lunggat & Tinggi 283*, KLU) in Borneo as well as New Guinea (*Streimann 20537*, NY).

3. Here, I follow Eddy (1996) in listing S. splendida as a synonymy. A lectotype needs to be chosen, from the syntype at the BM, to fix the identity of this name.

Specimens examined:

INDONESIA. Sulawesi: Latimojong Mts., Mt. Rantemario (Pokapindjang), Nanemori, 3150 m, 24.X.1969, *Eddy 5063* [*c.fr.*] (BM!). **MALAYSIA. Borneo (Sabah):** Maliau Basin, Eucalyptus Camp, trail 4, 23.VI.2006, *Lunggat & Tinggi 283* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, 9600 ft [=2926 m], II.1973, *Shea 3099* (SAN!); *ibidem*, 10200 ft [=3109 m], II.1973, *Shea 2720* (SAN!); Ranau, Kinabalu Park, Mt. Kinabalu, Maraiparai ridge, 5000 ft [=1524 m], 22.XI.1931, *Holttum 25175* (NY! SING!); Ranau, Kinabalu Park, Mt. Kinabalu, Timpohon Gate to Laban Rata, 2960 m, 9.V.2005, *Yong 6301*, [*c.fr.*] (KLU!); Ranau, Kinabalu Park, Mt. Tombuyukon, Musang Camp (km 10) to the summit, 1480 m, 14.VIII.2008, *Suleiman 3665*, [*c.fr.*] (BORH, KLU! SNP);

ibidem, 1500 m, 14.VIII.2008, *Suleiman 3672* (BORH, KLU! SNP); *ibidem*, 1520 m, 14.VIII.2008, *Suleiman 3675* (BORH, KLU! SNP); Tambunan, Crocker Range Park, Mount Alab, 1720 m, 9.IX.2008, *Suleiman & Masundang 3839* (BORH!); Tambunan, Crocker Range Park, Mount Alab Permanent Research Plot, 1770 m, 5.VII.2006, *Suleiman 1844* (BORH!). **PAPUA NEW GUINEA:** *s.loc*., *Giulianetti 1896* [*c.fr*.], *1897* [*c.fr*.] (BM!); *s.loc*., 1920, *Lam 1730 ex Hb. Dixon ex Fleisch*. [*c.fr*.] (original material of *S. lamii*: BM!); Hellwiggereberg, 2500–3000 m, *Römer 1266* [*c.fr*.] (isotype of *S. gigantea*: NY!). **Central:** Owen Stanley Range, *MacGregor 10* (isolectotype of *S. pilicalyx*: BM!); Mt. Albert Edward, 3680 m, V–VII.1933, *Brass 4474* [*c.fr*.] (NY!); Mt. Tafa, V–IX.1933, *Brass 4047a* [*c.fr*.] (NY!). **Eastern Highlands:** Bismark Ranges, Mt. Wilhelm, Bogonota Ridge just below outlet of Lake Aunde, 11300 ft [=3444 m], 29.VI.1968, *Weber 4795*, [*c.fr*.] (TNS!); Bismark Ranges, Mt. Wilhelm, Lake Aunde, 11700 ft., VI.1966, *Wade 8027* (COLO, NY!); Goroka, Gahavisuka Provincial Park, above Nagamiza village, 1900 m, 8.IV.1982, *Streimann 18233* (H, LAE, NICH, NY!); Mt. Wilhelm, 3650 m, 27.II.1965, *Eddy 2525* (BM!); Mt. Wilhelm, 4250 m, 2.III.1965, *Eddy 2642* [*c.fr*.] (BM!); Mt. Wilhelm, Guraguragukl valley, Lake Aunde, 3700 m, 25.VI.1965, *Balgooy 878A* [*c.fr*.] (NY!); Mt. Wilhelm, Lake Aunde, 3600 m, 26.IV.1965, *Balgooy 107* [*c.fr*.] (NY!); *ibidem*, 3700 m, 28.IV.1965, *Balgooy 127* [*c.fr*.] (NY!); *ibidem*, 3850 m, 14.VI.1965, *Balgooy 683A* [*c.fr*.] (NY!). **Madang:** Finisterre Range, Mt. Abilala (above Moro village), 2500 m, 13.XI.1964, *Eddy 1037* [*c.fr*.] (BM!); Finisterre Range, Lake Naho, 2750 m, 17.XI.1964, *Eddy 1364* [*c.fr*.] (BM!). **Morobe:** Aseki, Aiuwa-Bakia Track, 1500 m, 22.I.1981, *Streimann & Tamba 12254* (H, LAE, NICH, NY!); Aseki, Angabena Ridge, Aseki-Bulolo Road, 1750 m, 4.XII.1982, *Streimann 25908* (ALTA, H, NICH, NY!); Bulolo, Ekuti Divide, Bulolo-Aseki Road, 2260 m, 16.VI.1982, *Streimann 20181* (H, LAE, NICH, NY!); Bulolo, Mt. Amungwiwa, 2900 m, 1.IV.1984, *Bellamy 1551* [*c.fr*.] (ALTA, LAE, NICH, NY! TAL); Mt.

Sarawaket Southern Range, 4 km SE of Lake Gwam, headwaters of Busu River, 6.VII.1981, *Koponen 32015* (H, HSC, NY!); Rawlinson Range, 7000–12000 ft [=2134–3658 m], 18–20.V.1940, *Clemens 41377* [*c.fr*.] (NY!); Siwea, E part of Cromwell Mts., 2200–2300 m, 13.VI.1981, *Koponen 30512* (H, HSC, NY!), *30602* (TNS! H, HSC); Wau, Mt. Kaindi Repeater Station, 2230 m, 22.V.1982, *Streimann 19850* [*c.fr*.] (H, LAE, NICH, NY!). **Simbu:** Mt. Wilhelm, Kegsugl Forest, 7500 ft [=2286 m], 4.VIII.1994, *Tan 94-4120* (SING!); Mt Wilhelm, sentier entre Keglsugl et le lac Piunde, 2850 m, 6.IV.1987, *de Sloover 42.950* (NY!). **Southern Highlands:** Massif du mont Giluwe, entre Karil (15 km au nord-est de Mendi) et le sommet, 2700 m, 20.IV.1987, *de Sloover 43.165* (NY!); Mt. Giluwe, 5 km SSE of summit, 3450 m, 12.IX.1982, *Streimann & Garin 24097* [*c.fr*.] (H, LAE, NICH, NY!); Paunde Logging area, 15 km NNW of Ialibu, 2400 m, 14.XII.1982, *Streimann 32284* (H, LAE, NY!); track between Omin and Mt. Giluwe, 2400 m, 12.IX.1984, *Bellamy 1643*, *1645* (ALTA, LAE, NICH, NY!). **West Sepik:** Kubor Range, Mt. Kinkain, 3640 m, 15.VII.1963, *Vink 16087* (NY!); Kubor Range, Nona-Minj-Divide, 3250 m, 6.VII.1963, *Vink 16052* [*c.fr*.] (NY!); Nebilyer River, 28 km WNW of Mt. Hagen, 2760 m, 23.VI.1982, *Streimann 20537* (H, LAE, NICH, NY!); S slopes of Mt. Hagen, 2700 m, 19.VII.1957, *Robbins 491* [*c.fr*.] (EGR, H, KRAM, NY! TAL); Star Mts., Folongonam, 2250 m, 13.V.1975, *Touw 17936* [*c.fr*.] (NY!); Star Mts., Tel Basin, 3350 m, 7.IV.1975, *Touw 15851* [*c.fr*.] (NY!); Star Mts., Mt. Capella Base Camp, 3500 m, 17.IV.1975, *Touw 16337* [*c.fr*.] (NY!); Star Mts., Mt. Antares, west summit, 3400 m, 21.VII.1959, *van Zanten 664* [*c.fr*.] (NY!); Star Mts., Sililkatibin, NW of Mt. Auriga, 3550 m, 25.IV.1975, *Touw 16702* [*c.fr*.] (NY!); *ibidem*, 27.IV.1975, *Touw 16891* (NY!). **PHILIPPINES. Luzon:** Benguet, XII.1908, *Ramos 5868* [*c.fr*.] (NY!); Benguet, Mt. Pulog, I.1909, *Curran et. al 16397* [*c.fr*.], *16401* [*c.fr*.], *16415* [*c.fr*.] (NY!); *ibidem*, VII.1909, *McGregor 8907* [*c.fr*.] (NY!); Benguet, Mt. Pulog, Bokod, trail to summit from Babadak Lake, 2400 m, 13.V.1982, *Tan et al. 82-*

209 [*c.fr*.] (TNS!); Laguna, Mt. Banajao, I.1909, *Robinson 6600* [*c.fr*.] (NY!); *ibidem*, I.1913, *Ramos 19608* [*c.fr*.] (NY!); Mt. Tabayoc, 19.II.1968, Jacobs B602 (L, NY!); Mt. Tabayoc, Lake Ingcolos, 2420–2450 m, 15.II.1968, *Jacobs B367* [*c.fr*.] (TNS! L); Zambales, XI–XII.1907, *Curran & Merill 8191* [*c.fr*.] (NY!); *ibidem*, XII.1907, *Ramos 5141* [*c.fr*.] (NY!). **Mindanao:** Misamis Oriental, Mt. Lumot (Via Haruhay Trial), Barangay Lunutan, 25.VIII.1999, *Schumm & Schwarz 4823* (SING!).

5.3.5 *Ulota* D. Mohr ex Brid.

Muscol. Recent. Suppl. 4: 112 (1819 [1818]). TYPE: *U. crispa* (Hedw.) Brid.

Bryodixonia Sainsbury, Trans. & Proc. Roy. Soc. New Zealand 75: 177 (1945). TYPE: *B. perichaetialis* Sainsbury.

Weissia (Ehrh.) Lindb., Utkast: 39 (1878), *nom. illeg*., non *Weissia* Hedw. (1801). TYPE: *W. ulophylla* Ehrh.

Plants acrocarpous, medium to large, loose- to dense-tufted. Stem (primary axis) branched sympodially, orthotropic, erect or ascending, simple or sparingly branched, with 1–2 subsequent branches formed almost immediate or short distance beneath perichaetium or perigonium. Plant not tomentose, rhizoids abundant only at stem base. Stem and branch leaves not differentiated, leaves uniform in shape, ligulate-lanceolate with a concave and much wider base, leaf base not decurrent, and leaf lamina unistratose thick. Leaf cells parenchymatous, upper laminal cells short and papillose, basal laminal cells long and smooth; juxtacostal cells and basal marginal cells not differentiated. Plant autoicous, both perigonium and perichaetium located closely to each other; perigonial leaves much smaller than the perichaetial leaves; perichaetial leaves not sharply differentiated from vegetative leaves, inconspicous. Vaginula short, sparsely covered by long and rough paraphysis; paraphysis bi- to multiseriate, never branched. Seta short, extended. Capsule exerted, urn gradually narrowed to seta through a long neck; exothecial cells incrassate; stomata phaneroporous, many, commonly found near urn base; operculum rostrate with a long-, oblique beak. Peristome double. Teeth 16, fused into eight pairs, exostome alternate with endostome. Isospory. Calyptra mitrate, completely covering the urn, plicate, pilose, base deeply dissected into several lobes.

Notes:

1. A genus of about 35 species worldwide (Vitt, 1982a), mainly found in temperate regions, from low to high elevations and mostly epiphytic. For Malesia, five species were formerly reported (Iwatsuki, 1969; Vitt et al, 1993); however, *Ulota hattori* is here synonymized under *U. splendida*, extending the species range from New Guinea to Borneo. All four species in Malesia appear endemic and restricted above 3000 m (subalpine elfin forest to alpine grassland).

2. *Ulota* and *Zygodon* (see later) are the only representatives of Subfamily Orthotrichoideae (distinguished by an acrocarpic habit from other Orthotrichaceae) in Malaysia. The loosely erect or ascending (orthotropic), sparingly branched stems also give a character absent in any Macromitrioideae. In addition, they differ from most other cladocarpic Orthotrichaceae (i.e., Subfamily Macromitrioideae) by their tufted, often cushion-forming habit.

1. *Ulota splendida* E.B. Bartram (Figs. 5.60)

Lloydia 5: 269, fig. 27 (1942). TYPE: Indonesia, West Irian, Jayawijaya, Mt. Wilhelmina, abundant as an epiphyte in subalpine forest, 2 km E of Wilhemina-top, 3800 m, *Brass 10137* (holotype FH; isotype BM!).

U. hattorii Iwats., J. Hattori Bot. Lab. 32: 280, fig. 7 (1969), ***syn. nov***. TYPE: North Borneo, Mount Kinabalu, Sayat-Sayat, *Iwatsuki 949* (holotype NICH!).

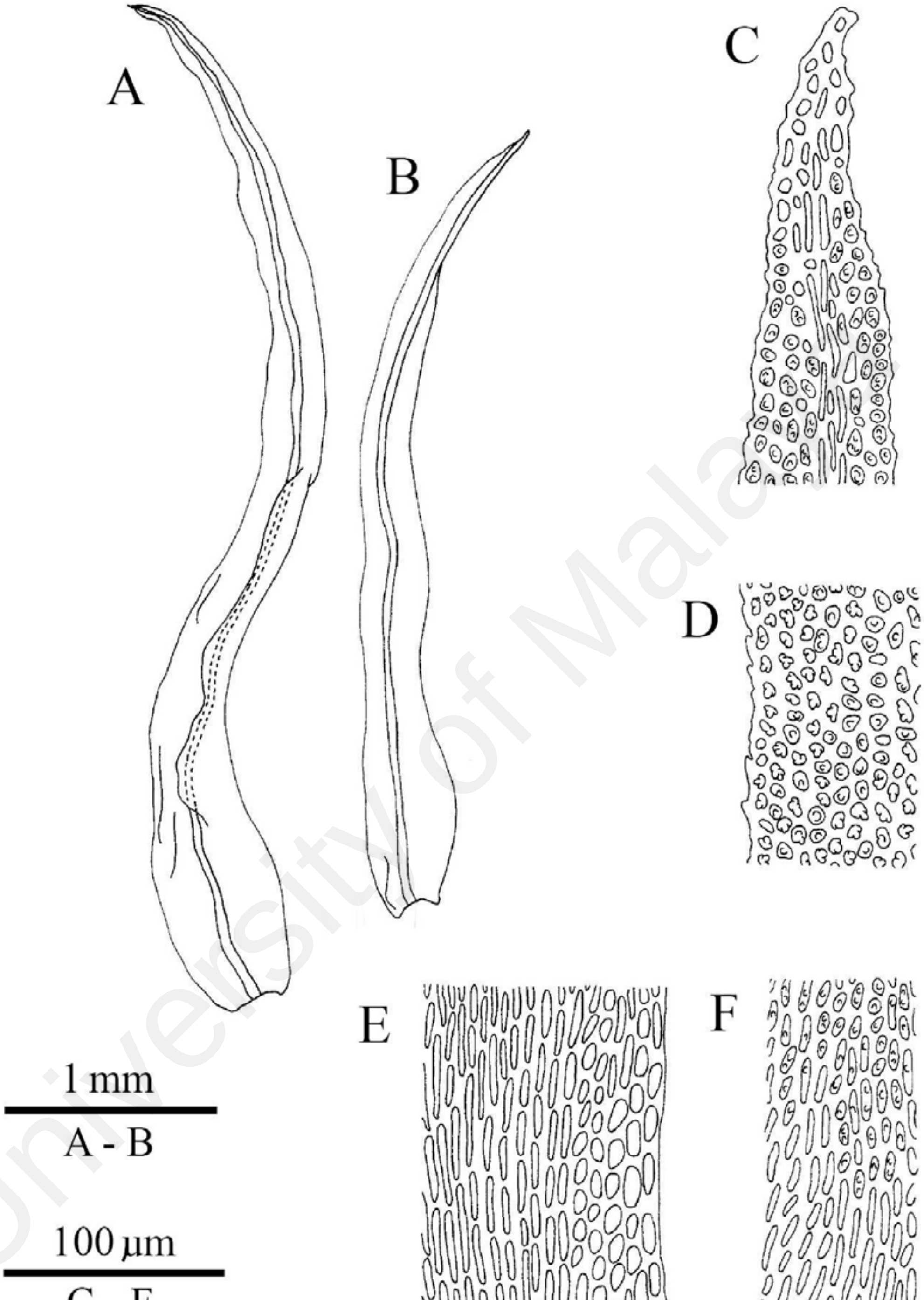

Figure 5.60. Illustrations of *Ulota splendida* E.B. Bartram — A-B, branch leaves; **C,** leaf apex; **D,** upper laminal cells; **E,** mid-leaf cells; **F,** basal laminal cells. [All from *Iwatsuki 949* (NICH)]

Plant medium-sized to fairly large, forming loose to dense, tall turf; young shoots yellowish-green, gradually turning to brownish at mature portions, brownish to darker below. Stems erect, up to 5 cm tall and 6–10 cm wide, not tomentose, sparsely branched.

Leaves spirally inserted on stem and branches, loosely arranged, leaves erect-twisted, flexuose-twisted to twisted-contorted, with most apices strongly involute-twisted (when dry), erect-spreading to recurved-spreading from a suberect leaf base (when moist); leaves (3.5–)3.8–5.0 × 0.4–0.5 mm, length-width ratio 8–10:1, long, slender-lanceolate to linear-lanceolate with a short and more or less sudden widened base, leaf base about 1/6 to 1/5 of leaf length, leaf lamina straight to flexuose, smooth or lightly undulate near leaf margin; apex firm, weakly incurved, slender, long-acuminate; margin irregular notched, denticulate to serrulate most of the part, but entire below, mostly plane, occasionally recurved only near leaf base; costa percurrent or filling the acumen. Upper and middle laminal cells irregular in length, 8–15 × 5–7 µm, length-width ratio 1:2, oblate, elliptic to short-rectangular, evenly incrassate, walls not pitted, cells flat, 1–2-papillate, papillae often tall, cells clear; cells grading from oblate or short-rectangular to gradually elongate very closed to the basal lamina; basal laminal cells 30–55 × 4–6 µm, length-width ratio 7–9:1, generally long-rectangular, with shorter cells, at time it can be quadrate to short-rectangular, found toward leaf margin and alar region, incrassate, walls either even or unevenly thickened, lumina 2–3 µm wide, linear to vermicular, pitted only near juxtacostal region and insertion, cells flat, smooth.

Autoicous, perigonium always located at short-distance beneath archegonium of the same branch. Perigonial leaves 1.1–1.2 mm × 0.4–0.5 mm, broadly ovate with acuminate apex, margin entire, costa percurrent or vanish short distant below leaf tip, upper lamina cell 6–8 µm × 4–10 µm, quadrate to rhomboid, moderately thick-walled, cell gradually elongate toward leaf base up to 40 µm long, thin-walled, smooth.

Perichaetial leaves inconspicuous, loosely erect to flexuose, loosely sheathing the seta, 3.5–5.0 × 0.4–0.5 mm, long, slender-lanceolate to linear-laceolate, upper lamina long and narrow, expanding gradually only at leaf base to form a short-ovate base, leaf base without plications; apex slender acuminate; margin notched, plane; costa percurrent; laminal cells character similar to its vegetative leaf, except elongated, smooth basal laminal cells occupied a larger region nearly up to mid-leaf, incrassate, lumen narrow to linear, pitted only at leaf base. Vaginula 0.9–1.0 mm long; paraphyses scarce, 1.8–2 mm long, long and coarse, made of 20–30 long-rectangular cells. Seta 7–8 mm long, smooth, dextrorse-twisted. Capsule urns 2.6–2.8 × 0.8–0.9 mm, broad-cylindric, deeply 8-plicate, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–4:1; stomata 10–16, phaneroporous; operculum rostrate, beak 0.8–1.1 mm. Exostome teeth eight, geminated but separated on top when old, strongly recurved to urn when dry, straight in wet conditions, teeth without distinct medial furrow and indistinctly articulated on dorsal face; dorsal side of teeth densely recticulate-papillose, papillae simple to compound; ventral side of teeth with tall horizontal ridges on top, irregular roughened below by low papillae, some part smooth; remnants of original cell-wall obscure on dorsal side, but marked by low and thin horizontal ridges on the ventral. Endostome segments eight, thin, filiformis, basal membrane absent, straight in both dry and wet conditions, segment keeled with a vertical divisural line on dorsal face; dorsal and ventral side of segment smooth or irregular roughened on the ventral; remnants of original cell-wall marked by low and thin horizontal ridges on both dorsal and ventral sides. Spores 26–36 µm in diameter. Calyptra mitrate, plicate, densely hairy, hairs erect and long, originated from ridges near calyptra base, calyptra base deeply clefted into 4–6 lobes.

Other descriptions and illustrations: Vitt et al. (1993) p. 12–13, figs. 4, 10; Eddy (1996) p. 25, fig. 342.

Distribution: Endemic to Malesia. As. 4: Malaysia (Borneo), Indonesia (Irian Jaya, Sulawesi), Papua New Guinea.

Habitat and ecology: Epiphytic on branches and twigs of trees and bushes, in elfin forest patches in the subalpine zone above 3250 m.

Notes:

1. *Ulota splendida* is the only species of its genus known for Malaysia, and has only been collected from higher elevation on Mount Kinabalu, Sabah. The plant is apparently rare there and has not been recollected in later surveys (Frahm et al., 1990; Akiyama et al., 2001; Higuchi et al., 2008). The species is very distinctive and easy to distinguish from other Orthotrichaceae by its a) robust structure, often more than 4 cm tall with several slender branches; b) long, slender lanceolate leaves with a suddenly widened leaf base 4–5 times shorter than the upper lamina; c) quadrate to short-rectangular cells in and near the leaf alar region, that are well differentiated from other long-rectangular basal lamina cells; d) multiseriate paraphyses longer than the vaginula when present; e) capsule connected to its seta by a long and narrow neck; f) double peristome, with strongly recurved exostome teeth in dry specimens and erect, filiform endostome segments.

2. In the original publication of *U. hattori*, Iwatsuki (1969) did not explain how it differed from other New Guinea congeners, but suggested it was related to the Pacific North American *U. obtusiuscula*; we have not verified this. However, a detailed comparison of type material showed that *U. hattori* was the same as *U. splendida*. Thus, *U. splendida* is the only one among four endemic Malesian *Ulota* spp. with a wide distribution.

3. *Orthotrichum brassii* appears to be very similar to *U. splendida*. Interestingly, both species were published by Bartram (1942) at the same time. In the original publication, Bartram (1942) noted that they were closely related and that *U. splendida* could be distinguished from *O. brassii* by a differentiated border at the leaf base, longer seta, a

distinctly sulcate capsule with stomata confined to the base of the urn, and the narrow and smooth cilia. However, a study of the type and other material of *O. brassii* and *U. splendida* for the present work showed that some of the leaf characteristics are variable and not distinctive. Old bigeminated teeth (teeth arranged as pairs) are often apically unjoined in *U. splendida*. In the revision of Asiatic *Orthotrichum* by Lewinsky (1992), there was no comparison of *O. brassii* with related taxa, but its exostome was said to have “8 pairs of bigeminated teeth that do not split”. However, the isotype of *O. brassii* (*Brass & Myer-Drees 10165*, BM) examined in the present study lacks sporophyte material, so we are as yet unable to confirm this apparent difference. More materials are needed to further understand the relationship of these taxa.

4. The paraphyses of *U. splendida* always exceed the vaginula and have 2–3 rows of cells (i.e., are never uniseriate like all other Orthotrichaceae). In addition, its paraphyses are always few and easily shed, so that Eddy (1996) has mistakenly described the species as having no paraphyses. The paraphyses, which can be observed using hand-lens, are distinct as a bunch of rough, erect, yellowish or golden hairs that form a good field character.

5. Vitt et al. (1993) was wrong in describing the calyptra of *U. splendida* as having smooth hairs. In fact, the calyptra hairs are roughened as in *O. brassii*, where each hair cell has a protruding distal end that contributes to a scabrous appearance under high magnification.

<u>Specimen examined</u>:

INDONESIA. **West Irian:** Jayawijaya, Mt. Wilhelmina, Wilhemina-top, 3800 m, *Brass 10137* (isotype of *U. splendida*: BM!). MALAYSIA. **Sabah:** Mt. Kinabalu, Sayat-Sayat, *Iwatsuki 949* [*c.fr.*] (holotype of *U. hattori*: NICH!). PAPUA NEW GUINEA. **Eastern Highlands:** Mt. Wilhelm, 4300 m, 2.III.1965, *Eddy 2650* (BM!). **Morobe:** Mt. Sarawaket, Lake Gwam, 8.VII.1981, *Koponen 32361* [*c.fr.*] (NY!); *ibidem*, 3400 m, 9.VII.1981, *Norris 63314* [*c.fr*.] (NY!). **Southern Highlands:** Lalibu, Mt. Gluwe, 12700 ft [=3871 m], 19.VII.1969, *Coode & Wardle 3727* (BM!).

5.3.6 *Zygodon* Hook. & Taylor

Muscol. Brit. 70 (1818). TYPE: *Z. conoideus* (Dicks.) Hook. & Taylor

Stenomitrium (Mitt.) Broth., Nat. Pflanzenfam.1(3): 464 (1902). TYPE: *S. pentastichum* (Mont.) Broth.

Leptodontiopsis Broth., Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot. 2: 146 (1910). TYPE: *L. fragilifolia* Broth.

Pleurozygodontopsis Dixon, Ann. Bryol. 12: 51 (1939). TYPE: *P. decurrens* Dixon.

Plants acrocarpous, small to fairly large, always form dense-tufted. Stem (primary axis) branched sympodially, orthotropic, erect or ascending, simple or sparingly branched, with 1–2 subsequent branches formed almost immediate or short distance beneath perichaetium or perigonium. Plant often tomentose, rhizoids abundant covering lower half or sometime extending to higher portion of stem and branches. Stem and branch leaves not differentiated, leaves uniform in shape, leaves in various sizes and shape varied from oblanceolate, oblong-lanceolate to narrow-lanceolate, leaf base more or less decurrent, and leaf lamina unistratose thick. Leaf cells parenchymatous, upper and basal laminal cells either not distinctly differentiated (in *Z. intermedius* and *Z. reinwardtii*), or clearly differentiated (in *Z. orientalis*), laminal cells short and pluripapillose throughout, except in latter case where basal laminal cells always long and smooth; juxtacostal cells and marginal cells at basal lamina not distinctly differentiated. Plant dioicous (in *Z. intermedius* and *Z. orientalis*) or autoicous (in *Z. reinwardtii*), if autoicous, both perigonium and perichaetium distantly located to each other with perichaetium always occupied a higher position then the perigonium; perigonial leaves about the size or smaller than the perichaetial leaves; perichaetial leaves inconspicous. Vaginula short, densely covered by short and filamentous paraphysis; paraphysis uniseriate, never branched. Seta short to long, extended. Capsule exerted, urn narrowed to seta short distance; exothecial cells incrassate; stomata phaneroporous, many, commonly found near urn base; operculum rostrate with a long-, oblique beak. Peristome single or double. Exostome absent or both exostome and endostome rudimentary, often giving a gymnostomous perspective. Isosporous. Calyptra cucullate, covering 1/3 of urn, smooth, naked, base entire.

Notes:

1. A cosmopolitan genus of about 52 species (Vitt, 1982a), with its centre of diversity (over 50% of the species) in the South American Andean region (Lewinsky 1990; Calabrese 2006). The species are widely distributed, from sea level to alpine elevations, mostly epiphytic but occasionally growing on rocks. However, all seven *Zygodon* species reported for Malesia (Eddy 1996) are either corticolous or occasionally epilithic and confined to higher-elevation forest in the upper montane and subalpine zones. Only three species are recorded for Malaysia, all collected from Mount Kinabalu, Sabah.

2. When sterile, many *Zygodon* species can resemble *Anoectangium* Schwägr. and *Leptodontium* (Müll. Hall.) Hampe *ex* Lindb. (Pottiaceae) (Zander & Vitt, 1979). In Malaysia, both *Anoectangium* and *Leptodontium* (both represented by single species) have only been reported from Mount Kinabalu at 2000 m and higher (Dixon, 1935; Akiyama et al., 2001). They overlap in distribution with the three Malaysia *Zygodon* species. In the absence of sporophytic structure, *Zygodon* is best separated from *Anoectangium* by the absence of a central strand in cross-sectional views of the stem, and lack of an adaxial stereid band that is found in the leaf costa of *Leptodontium*. In addition to this, the angular and weakly bulging upper lamina cells in *Anoectangium* and *Leptodontium*, combined with their often epilithic and terrestrial habit, are useful

for distinguishing them from *Zygodon* species, which have oval upper lamina cells and are usually epiphytic (Zander & Vitt, 1979).

3. Gradual evolutionary loss of peristome parts in a number of *Zygodon* species has been speculated by Calabrese (2006). Among Malaysian *Zygodon*, *Z. intermedius* is reported as having a double peristome with a exostome but rather well-developed endostome segments; whereas *Z. orientalis* and *Z. reinwardtii* have a single peristome with only endostome present (i.e., without exostome). However the peristome of these three species is usually rudimentary and often broken, giving the misimpression that the capsule is gymnostomous (Sainsbury, 1955; Lewinksy, 1990; Calabrese, 2006).

4. *Zygodon tetragonostomus* Braun *ex* B.S.G. (common in Sri Lanka and Southern India) is uncommon in Malesia, reported for Java at elevations above 2500 m (Fleischer, 1904). Eddy (1996) also recorded it for the Malay Peninsula without mentioning specimens. It is not likely that *Zygodon* is found in the Malay Peninsula as there, the mountains are generally lower than 2000 m, so the required conditions for *Zygodon* species are apparently absent.

1. *Zygodon intermedius* Bruch & Schimp. (Figs. 5.61 & 5.62)

Bryol. Europ. 3: 41 (Fasc. 4 Monogr. 9) (1838). LECTOTYPE (Lewinsky, 1990): New Zealand, Dusky Sound, *Menzies s.n*. (BM).

Z. affinis Dozy & Molk. *ex* Bosch. & Sande Lac., Bryol. Jav. 1: 107, tab. 85 (1859). LECTOTYPE (Touw, 2006): Java, e summo monte Pangerango, *Teysmann s.n.* ex *Hb. Dozy & Molk*. (L) — fide Fleischer (1904).

Z. pangerangensis M. Fleisch., Musci Buitenzorg 2: 395, fig. 74 (1904). LECTOTYPE (***hic designatus***): Am Pangerango auf morschem Holz abgestorbener Bäume, 2900 m, VII.1898, *Fleischer exsiccata no. 280* (NY!).

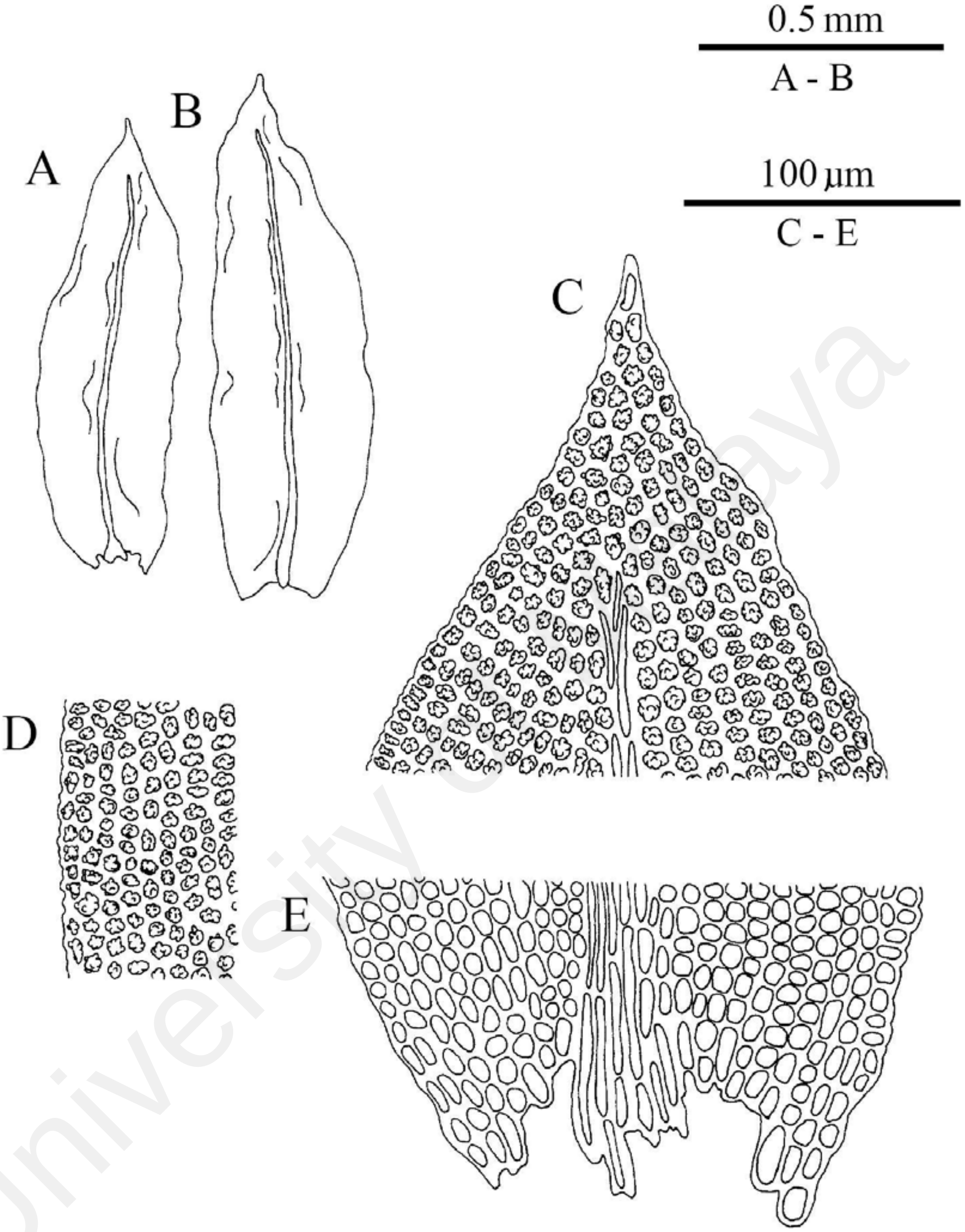

Figure 5.61. Illustrations of *Zygodon intermedius* Bruch & Schimp. — A-B, branch leaves; **C,** leaf apex; **D,** mid-leaf cells; **E,** basal laminal cells. [All from *Yong 6412* (KLU)]

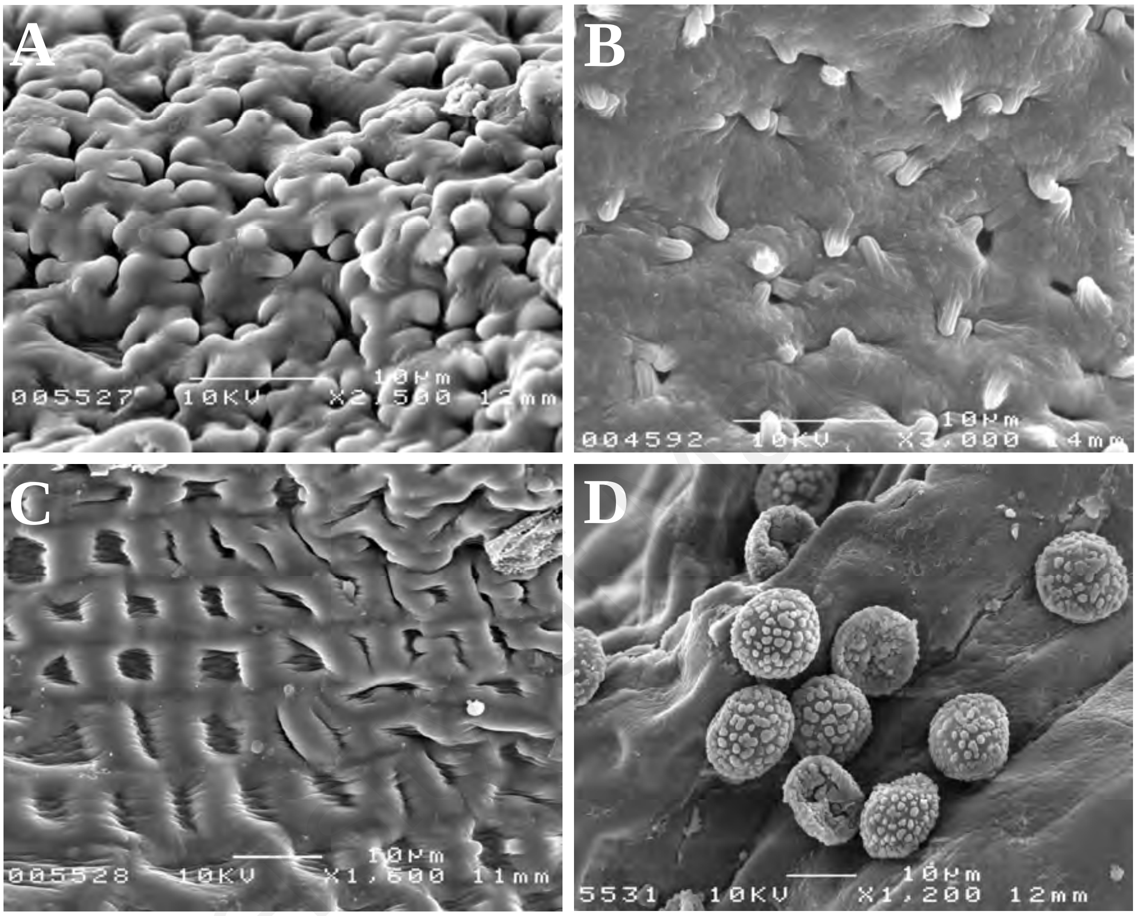

Figure 5.62. SEM images of *Zygodon intermedius* Bruch & Schimp. — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** spores. [All from *Eddy 5082* (BM)]

Z. stresemannii Herzog, Hedwigia 57: 233 (1916). TYPE: Mittel-Ceram, Epiphyt der Baumfarnregion am Gunung Pinaia, 2530–2750 m, *Stresemann 311 u. 328* (isotype JE) — fide Malta (1926).

Plant small, forming compact turf, short to tall; young shoots yellowish-green, gradually turning from light-green to yellowish-brown at mature portions, reddish below due to the dense tomentum. Stems erect, up to 0.5–3 cm tall and 0.5–1 mm wide, sparsely branched.

Leaves spirally inserted on stem and branches, loosely arranged, leaves erect-appressed, flexuose or loosely curled, with lightly incurved or straight apices (when dry), erecto-patent to erect-spreading (when moist); leaves 0.9–1.0 × 0.2–0.4 mm, length-width ratio 3–4:1, long, elliptic-lanceolate to lingulate, lamina straight, smooth or lightly undulate near leaf margin; apex firm, acute to acuminate; margin entire to crenulate, plane; costa failing, terminates at some distance below leaf tip. Upper and middle laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, oblate to short- or wide-rectangular, evenly incrassate, walls not pitted, cells flat, pluripapillose, papillae minute and many, 5–8 on each cell, cells clear; basal laminal cells not distinctly elongated except near extreme base, not pigmented, 8–20 × 8–12 µm, length-width ratio 1–2:1, quadrate, short- to long-rectangular, evenly incrassate, lumina not distinctly narrow, pitted only near leaf insertion, cells flat, smooth.

Dioicous. Perigonial leaves 1.1–1.2 mm × 0.4–0.5 mm, ovate-lanceolate with acuminate apex, margin entire, incurved, costa terminates short distance below leaf tip, upper lamina cells 6–8 µm × 4–10 µm, quadrate to rhomboid, moderately thick-walled, cells gradually elongate toward leaf base up to 20 µm long, thin-walled, smooth.

Perichaetial leaves and sporophytic structure not available among Malaysia’s collection, following description are based on materials from neighbouring regions.

Perichaetial leaves erect, loosely sheathing the seta, not differentiated from branch leaves, 1.0–1.2 × 0.4–0.5 mm, ovate-lanceolate to lanceolate, upper lamina broad, leaf base more or less concave and not plicate; apex acuminate; margin entire, plane; costa percurrent; laminal cells grading from long-elliptic and pluripapillose at upper lamina to long-rectangular and smooth at leaf base, incrassate, lumen narrow to linear, pitted only at extreme base. Vaginula 0.9–1.0 mm long; paraphyses many, 0.4–0.5 mm long, made of 7–9 short- or long-rectangular cells. Seta 5–7 mm long, smooth, dextrorse-twisted. Capsule urns 1.2–1.3 × 0.4–0.5 mm, narrow cylindric, distinctly 8-plicate, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–3:1; stomata 10–14, phaneroporous; operculum rostrate, beak 0.9–1.0 mm. Peristome double. Exostome rudimentary, usually absent. Endostome of 4–8 thin and short segments, 2–3 cells tall from a very low basal membrane, smooth, without medial divisural line; both dorsal and ventral face smooth or weakly ornamented by low and scattered papillae; remnants of original cell-wall marked by low and thin horizontal ridges on both dorsal and ventral side. Spores 22–26 µm in diameter. Calyptra cucullate, smooth, naked, base entire.

Other descriptions and illustrations: Müller (1849) p. 671–672; Fleischer (1904) p. 394–395; Malta (1926) p. 75–81, figs. 38–40; Sainsbury (1955) p. 202–204, fig. 2; Lewinsky (1990) p. 131–133, figs. 27–30, 131–155; Eddy (1996) p. 14–15, fig. 334; Calabrese (2006) p. 490–494, figs. 17, 18A–B.

Distribution: Widespread. Am. 2: Mexico; Am. 4: Bolivia; Am. 6: Argentina, Chile; Afr. 4: South Africa; As. 3: Sri Lanka, Thailand (Northern); As. 4: Indonesia (Bali, Flores, Java, Lombok, Seram, Sumatra), Malaysia (Borneo), Philippines (Mindanao); Austr. 1: Australia, Tasmania; Austr. 2: New Zealand.

Habitat and ecology: Mostly epiphytic on tree trunks and branches, often along the underside of leaning trunks and branches, as noted by Lewinsky (1990). Outside of

Malaysia, the species has been found over rotten trunks and rocks (*van Zanten & Brill 657*, NY) (Lewinsky, 1990). In Malaysia, the species is only known above 3000 m, in the upper montane and subalpine zones, although elsewhere it has been collected as low as 1000 m (Eddy 1996).

Notes:

1. *Zygodon intermedius* can be recognized by its a) delicate, tufted structure and cushion-forming habit; b) elliptic-lanceolate to lingulate leaves that are usually less than 1 mm long; c) costa that terminates some distance below the leaf tip; d) entire margin; e) oblate or oval laminal cells with distinctly thickened walls; f) upper laminal cells with abundant, minute papillae.

2. This species is related to *Z. gracillimus* Broth. *ex* M. Fleisch. (Java, New Zealand and Bolivia), *Z. novo-guinensis* E.B. Bartram (New Guinea) and *Z. hookeri* Hampe (Australasian region). Its pluripapillose laminal cells distinguish it from *Z. gracillimus* and *Z. novo-guinensis*, which have consistently smooth laminal cells. Its dioicous habit, small spores, and short seta and capsule distinguish it from *Z. hookeri*, which has a synoicous behaviour, larger spores, and longer seta and capsule (Lewinsky, 1990).

3. The original description and illustration of *Z. pangerangensis* (by Fleischer, 1904) refer to *Z. intermedius*, under which synonymy it has been placed (Malta, 1926; Eddy, 1996). However, the syntype material of *Zygodon pangerangensis* M. Fleisch. distributed by Fleischer (*Musci Frond. Archipelagi Indici, serie VI, no. 280*) to different herbaria is of different species. The set at NY is *Z. intermedius*, but that at BM is here identified as *Z. gracillimus*. As a result of this, lectotypification is required (here provided; see above).

Specimens examined:

AUSTRALIA. Tasmania: Guy Hawkes Rivulet, 3.IX.1892, *Weymouth 2931* [*c.fr.*] (BM!). **INDONESIA, Java**: Gedeh, Kandang Badak, 18.VII.1898, *Nyman 171* [*c.fr.*]

(NY!); Gedeh, Kandang Badak, 2400 m, 26.VI.1911, *Fleischer s.n.* [*c.fr.*] (NY!); Pangerango, *s.date*, *Wichura 2534* [*c.fr.*] (BM!); Mt. Pangerango, 2900 m, VII.1898, *Fleischer 280* (lectotype of *Z. pangeragensis*: NY!); *ibidem*, 3050 m, VII.1898, *Fleischer 279* [*c.fr.*] (NY!); Tjibodas, 1550 m, 29.IX.2001, *Tan s.n.* (KLU!). **Sulawesi**: Latimojong, Gg. Rantemario, Nanemori, 3150 m, 24.X.1969, *Eddy 5082 p.p.* [*c.fr.*] (BM!). **Sumatra:** Mt. Korinchi, 2700–2900 m, VII.1956, *Meijer 7885* (NY!); Mt. Merapi, 1600–1800 m, 31.VII.1894, *Schiffner 10697* [*c.fr.*] (NY!); Urwälder am Südosthang des Singalang, 25.VII.1894, *Schiffner 4100* [*c.fr.*] (NY 2 sheets! TNS!). **MALAYSIA. Borneo, Sabah**: Ranau, Kinabalu Park, Mt. Kinabalu, II.1973, *Shea 2819* (SAN!); Ranau, Kinabalu Park, Mt. Kinabalu, Laban Rata, 3010 m, 12.V.2005, *Yong 6412* (KLU!); 3000–3050 m, 30.VIII.1986, *Menzel et al. 4727* (KLU!). **NEW ZEALAND:** Great Barrier Island, *s.date*, *Kirk & Hellen 97* [*c.fr.*], *106e* [*c.fr.*] (NY!); Hawker Bay, Near Lake Waikariti, 8.I.1926, *Sainsbury 366* [*c.fr.*] (BM!); Wairarapa, Bank of Kopuasanga River, 22.IX.1924, *Gray 269* [*c.fr.*] (BM!). **PAPUA NEW GUINEA. Western Highland:** Mt. Wilhelmina, 3450 m, IX.1938, *Brass & Myer-Drees 9756* [*c.fr.*] (BM!). **West Sepik:** Star Mts., Mt. Antares above bivouac 42, 3400 m, 21.VII.1959, *vanZanten & Bril 657* [*c.fr.*] (NY! L). **PHILIPPINES, Mindanao:** Nord Cotabato, Mt. Apo, Lake Venado, 2210 m, 20.III.1999, *Schwarz 3782* (SING!). **SRI LANKA. Central Province**: Horton Plains, Nuwara Eliya, track to North Cove from Farr Inn, 7000 ft [=2134 m], 4.III.1973, *IPSE 73/1284* (SING!). **THAILAND. Northern Thailand:** Payap, Mt. Suthep, summit of Doi Pui, 1600–1650 m, 28.XI.1965, *Touw 8666* (NY! L).

2. ***Zygodon orientalis*** **(Dixon) Goffinet** (Figs. 5.63 & 5.64)

Monogr. Syst. Bot. Missouri Bot. Gard. 98: 287 (2004). *Leptodontiopsis orientalis* Dixon, J. Linn. Soc., Bot. 50: 91 (1935). TYPE: Borneo, Kinabalu, 11500 ft [=3505 m], 14.XI.1931, *Holttum 25668* (holotype BM! isotype SING!).

Plant medium to fairly large, forming compact turf, mostly tall; young shoots yellowish-green, gradually turning from light-green to yellowish-brown at mature portions, reddish below due to the dense tomentum. Stems erect, up to 3–6 cm tall and (3–)5–10 mm wide, sparsely branched.

Leaves spirally inserted on stem and branches, loosely arranged, leaves erect-flexuose, flexuose-twisted or loosely curled, with lightly incurved, deflexed or variously twisted apices (when dry), wide-spreading to recurved-spreading from suberect base (when moist); leaves variable in length, (2.2–)2.8–5.5(–5.9) × 0.4–0.6 mm, length-width ratio 5–10:1, long, lingulate-lanceolate, slender lanceolate to linear-lanceolate, lamina straight to recurved, often twisted, smooth or lightly undulate near leaf margin; apex firm, acuminate; margin irregular notched, crenulated to serrulate at upper lamina, entire below, plane; costa percurrent or filling the acumen. Upper and middle laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, oblate to short- or wide-rectangular, evenly incrassate, walls not pitted, cells flat, pluripapillose, papillae minute and many, 5–8 on each cell, cells clear; cells grading from short-rectangular to gradually elongate only near basal laminal, basal laminal cells often strongly pigmented especially toward leaf insertion, orange or reddish, 50–78(–86) × 10–14 µm, length-width ratio 5–7:1, long-rectangular, evenly incrassate, lumina not distinctly narrow, pitted only near leaf insertion, cells flat, smooth.

Dioicous, both male and female plants often occurred in same population. Perigonial leaves 1.1–1.2 mm × 0.4–0.5 mm, ovate to ovate-lanceolate with acuminate

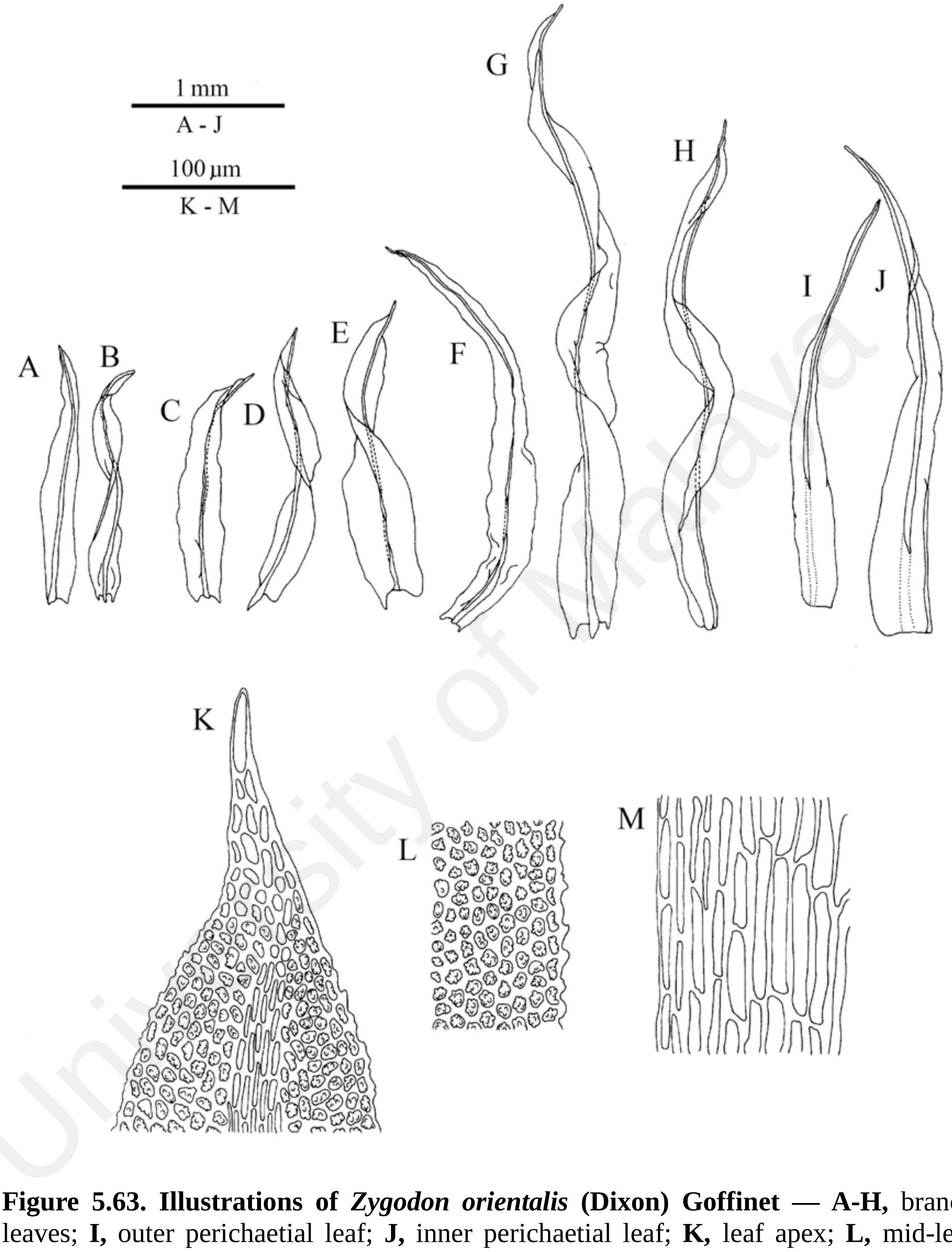

Figure 5.63. Illustrations of *Zygodon orientalis* (Dixon) Goffinet — A-H, branch leaves; **I,** outer perichaetial leaf; **J,** inner perichaetial leaf; **K,** leaf apex; **L,** mid-leaf cells; **M,** basal laminal cells. [**A-B** from *Holttum 25689* (SING, isotype); **C** from *Yong 6331* (KLU); **D, I-M** from *Yong 6368* (KLU); **E** from *Yong 6371* (KLU); **F** from *Holttum 25668* (SING, holotype); **G** from *Yong 6370* (KLU); **H** from *Yong 6374* (KLU)]

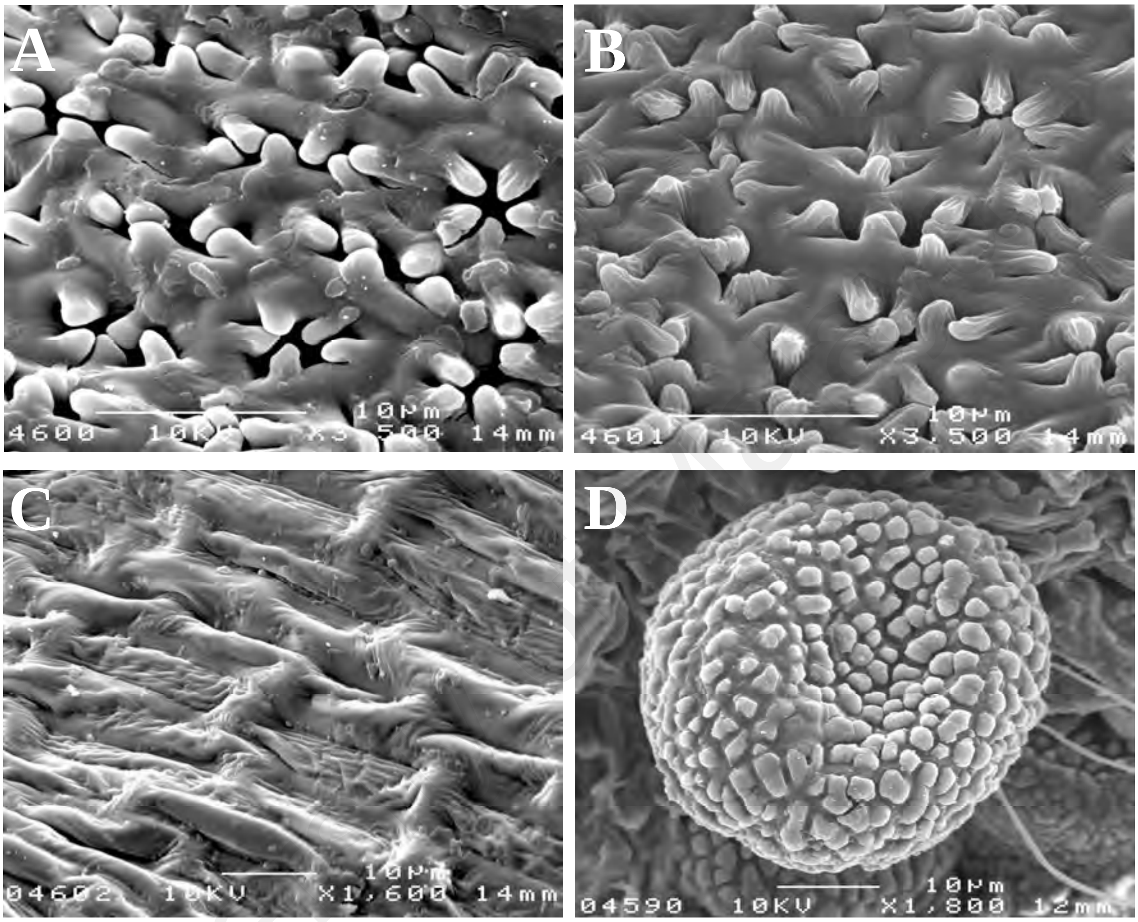

Figure 5.64. SEM images of *Zygodon orientalis* (Dixon) Goffinet — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** macrospore. [All from *Yong 6371* (KLU)]

apex, margin entire, incurved, costa vanish short distant below leaf tip, upper laminal cells 5–8 µm × 4–10 µm, quadrate to rhomboid, moderately thick-walled, cells gradually elongate toward leaf base up to 50 µm long, moderately thick-walled, smooth. Perichaetial leaves loosely erect to flexuose with recurved upper lamina, loosely sheathing the seta, often shorter than branch leaves, 1.1–1.8 × 0.5–0.7 mm, slender lanceolate to linear-lanceolate, upper lamina narrow, gradually expanded only near mid-leaf to form a long oblong base, leaf base more or less concave and not plicate; apex slender, long-acuminate; margin entire to subentire, plane; costa percurrent; laminal cells grading from long-elliptic and pluripapillose at upper lamina to long-rectangular and smooth at leaf base, incrassate, lumen narrow to linear, pitted only at extreme base. Vaginula 1.1–1.2 mm long; paraphyses abundant, 0.8–0.9 mm long, made of 9–11 short- or long-rectangular cells. Seta 16–22 mm long, smooth, dextrorse-twisted. Capsule urns 1.5–2.4 × 0.5–0.8 mm, narrow cylindric, distinctly 8-plicate, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–3:1; stomata 12–16, phaneroporous; operculum rostrate, beak 0.9–1.2 mm. Peristome single. Exostome absent. Endostome of 4–8 thin and short segments, 2–3 cells tall from a very low basal membrane, smooth, without medial divisural line; both dorsal and ventral faces smooth or weakly ornamented by low and scattered papillae; remnants of original cell-wall marked by low and thin horizontal ridges on both dorsal and ventral sides. Spores 38–42 µm in diameter. Calyptra cucullate, smooth, naked, base entire.

Other description and illustration: Eddy (1996) p. 22, fig. 341 as *Leptodontiopsis orientalis*.

Distribution: Endemic to Malesia, only known from a few high mountains in Malesian region. As. 4: Indonesia (Sulawesi), Malaysia (Sabah), Papua New Guinea.

Habitat and ecology: Mostly epiphytic on tree trunks and branches, rarely documented on granitic rock. The species has only been collected at 3000 m and above, in upper montane and subalpine vegetation.

Notes:

1. *Zygodon orientalis* can be recognized by its a) medium-sized to large plants in tufted habit; b) long and slender-lanceolate stem leaves; c) sharply acuminate leaf apex with percurrent costa; d) distinct upper and basal laminal cells (basal laminal cells often orange-reddish); e) long seta, 2 cm or longer.

2. This is the largest *Zygodon* species in Malesia, and easily distinguished from *Z. intermedius* and *Z. reinwardtii* by its percurrent costa and often strongly pigmented leaf base. However, the species can have variable plant and leaf sizes often found together.

3. The smaller forms of *Z. orientalis* might be confused with *Z. tetragonostomus*, a common species in Sri Lanka, India and Indochina (Eddy, 1996). However *Z. orientalis* is distinct from the latter by its strongly pigmented and distinctly elongated basal laminal cells, absent in the latter.

Specimens examined:

INDONESIA. Sulawesi: Latimojong Mts., Nanemori (above Rantelemo), 2950 m, 24.X.1969, *Eddy 5090 p.p*. [*c.fr*.] (BM!); Latimojong Mts., Nanemori (Gunung Rantemario, above Rantelemo), 3100 m, 24.X.1969, *Eddy 5047 p.p*. [*c.fr*.] (BM!). **MALAYSIA. Borneo, Sabah**: Ranau, Kinabalu Park, Mt. Kinabalu, 11500 ft [=3505 m], 14.XI.1931, *Holttum 25668* [*c.fr*.] (holotype of *Leptodontiopsis orientalis*: BM! isotype of *L. orientalis*: SING!), *25689* [*c.fr*.] (BM! SING!); Ranau, Kinabalu Park, Mt. Kinabalu, Gurulan spur, above Pinokok River, 12–13000 ft [=3658–3962 m], 16.XII.1933, *Clemens 51197* [*c.fr*.] (BM!); Ranau, Kinabalu Park, Mt. Kinabalu, Laban Rata, 7.VI.2000, *Jonima & Benedict 15387* (TNS!); Ranau, Kinabalu Park, Mt. Kinabalu, Paka Cave, 3130 m, 10.V.2005, *Yong 6331* (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, Sayat-Sayat Checkpoint, 3260 m, 11.V.2005, *Yong 6360* [*c.fr*.], *6361* [*c.fr*.], *6371* [*c.fr*.] (KLU!); *ibidem*, 3330 m, 11.V.2005, *Yong 6370* [*c.fr*.] (KLU!);

ibidem, 3335 m, 11.V.2005, *Yong 6359*, *6365* [*c.fr*.], *6366* [*c.fr*.], *6368* (KLU!); *ibidem*, 3345 m, 11.V.2005, *Yong 6364* [*c.fr*.], *6374* [*c.fr*.], *6375* [*c.fr*.] (KLU!).

3. *Zygodon reinwardtii* (Hornsch.) A. Braun (Figs. 5.65 & 5.66)

Bryol. Europ. 3: 41 (Fasc. 4 Monogr. 9) (1838). *Syrrhopodon reinwardtii* Hornsch., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14 (2): 700, tab. 39, fig. a. (1829). LECTOTYPE (***hic designatus***): Tab. 39, fig. a, in Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14(2): 700.

Z. cylindricarpus Müll. Hal., Bot. Zeitung (Berlin) 11: 59 (1853). TYPE: Nilghiri, *s. coll*. (B, destroyed) — fide Malta (1926).

Z. breviciliatus Thwaites & Mitt., J. Linn. Soc., Bot. 13: 304 (1873). TYPE: Ceylon, *Thwaites s.n*. (holotype NY) — fide Fleischer (1904).

Pleurozygodontopsis decurrens Dixon, Ann. Bryol. 12: 51 (1939). LECTOTYPE (Goffinet, 1998): Sumatra, Mt. Losir, Atjeh, Gajolanden, 2940 m, 5.II.1937, *van Steenis 10159* (BM!) — fide Eddy (1996).

Plant small to medium-sized, forming compact turf, mostly short; young shoots yellowish-green, gradually turning from light-green to yellowish-brown at mature portions, reddish below due to the dense tomentum. Stems erect, up to 2 cm tall and 2–3 mm wide, sparsely branched.

Leaves spirally inserted on stem and branches, loosely arranged, leaves erect-flexuose or loosely curled, with lightly incurved or deflexed apices (when dry), recurved-spreading to squarrose-spreading from suberect base (when moist); leaves variable in length, 1.6–2.3 × 0.5–0.7 mm, length-width ratio 3–4:1, elliptic-lanceolate to oblanceolate, lamina straight to recurved, smooth or lightly undulate near leaf margin; apex firm, acuminate; margin remotely dentate at apex, irregular crenulate or

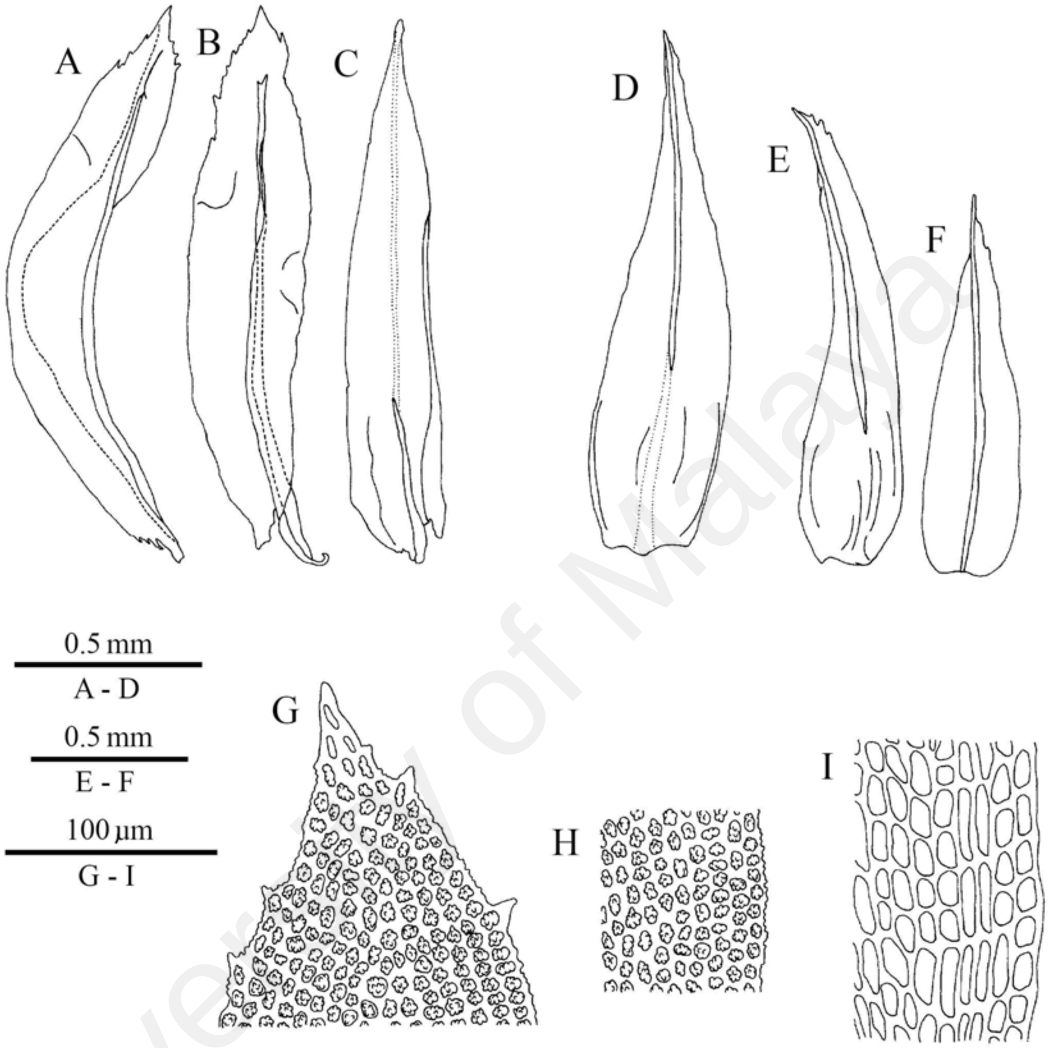

Figure 5.65. Illustrations of *Zygodon reinwardtii* (Hornsch.) A. Braun — A-B, branch leaves; **C-E,** outer perichaetial leaves; **F,** inner perichaetial leaf; **G,** leaf apex; **H,** mid-leaf cells; **I,** basal laminal cells. [**A-C, G-I** from *Damanhuri s.n.* (KLU); **D** from *Yong 6374* (KLU); **E-F** from *Yong 6331* (KLU)]

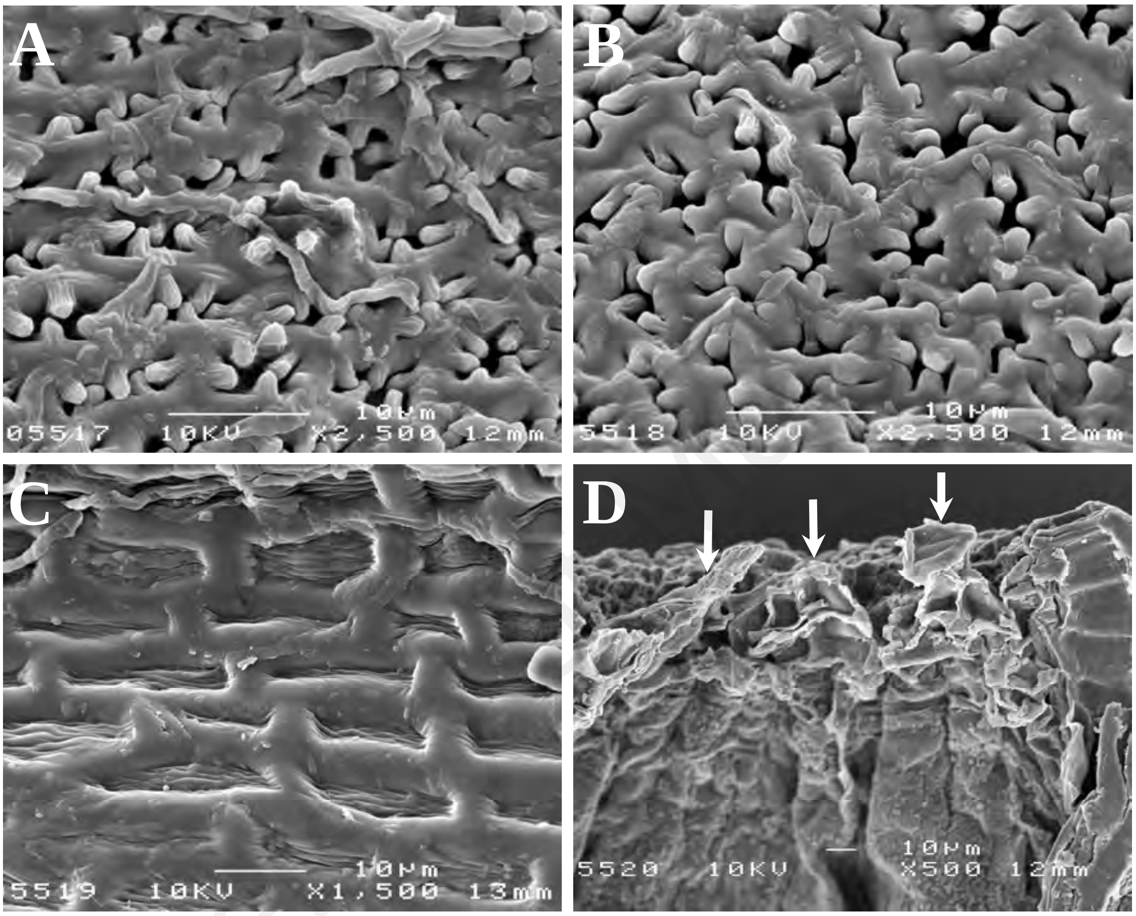

Figure 5.66. SEM images of *Zygodon reinwardtii* (Hornsch.) A. Braun — A, upper laminal cells; **B,** mid-leaf cells; **C,** basal laminal cells; **D,** inner view of urn, mouth part with vestigial peristome teeth (pointed with arrow). [All from *Yong 6330* (KLU)]

denticulate below, entire at leaf base, plane; costa failing, terminates at some distance below leaf tip. Upper and middle laminal cells 8–10 × 8–10 µm, length-width ratio 1:1, oblate, oval to short- or wide-rectangular, evenly incrassate, walls not pitted, cells flat, pluripapillose, papillae minute and many, 5–8 on each cell, cells clear; cells grading from short-rectangular to gradually elongate only near basal laminal, basal laminal cells not distinctly elongated except near extreme base, not pigmented, 12–22 × 8–12 µm, length-width ratio 1–2:1, quadrate, short- to long-rectangular, evenly incrassate, lumina not distinctly narrow, pitted only near leaf insertion, cells flat, pluripapillose, cells smooth only at extreme leaf base.

Autoicous or synoicous, perigonia normally located far below the perichaetia on a same branch. Perigonial leaves 1.0–1.2 mm × 0.3–0.4 mm, ovate to ovate-lanceolate with acuminate apex, margin entire, incurved, costa percurrent or terminates short distance below leaf tip, upper laminal cells 5–8 µm × 4–10 µm, quadrate to rhomboid, moderately thick-walled, cells gradually elongate toward leaf base up to 40 µm long, moderately thin-walled, smooth. Perichaetial leaves erect, loosely sheathing the seta, often smaller than branch leaves, 1.0–1.5 × 0.4–0.5 mm, typically lanceolate, leaf base more or less concave and not plicate; apex acuminate, apiculate; margin entire to subentire, plane; costa percurrent to short-excurrent with a few cells extending beyond leaf tip; laminal cells grading from long-elliptic and pluripapillose at upper lamina to long-rectangular and smooth at leaf base, incrassate, lumen narrow to linear, pitted only at extreme base. Vaginula 0.9–1.0 mm long; paraphyses many, 0.5–0.6 mm long, made of 7–9 short- or long-rectangular cells. Seta 10–12 mm long, smooth, dextrorse-twisted. Capsule urns 1.5–2.3 × 0.6–0.8 mm, narrow cylindric, distinctly 8-plicate, rim rounded when dry; exothecial cells irregularly rectangular to elliptic, generally long, length-width ratio 2–3:1; stomata 10–12, phaneroporous; operculum rostrate, beak 1.0–1.1 mm. Peristome single. Exostome absent. Endostome of 4–8 thin and short segments, 2–3 cells tall from a very low basal membrane, smooth, without medial divisural line; both dorsal and ventral face smooth or weakly ornamented by low and scattered papillae; remnants of original cell-wall marked by low and thin horizontal ridges on both dorsal and ventral side. Spores 20–24 µm in diameter. Calyptra cucullate, smooth, naked, base entire.

Other descriptions and illustrations: Müller (1849) p. 678; Dozy & Molk. (1861) p. 109–110, tab. 87; Fleischer (1904) p. 399–401; Malta (1926) p. 118–124, figs. 68–70; Eddy (1996) p. 16–17, fig. 335; Calabrese (2006) p. 497–501, figs. 2A, 3A, 20.

Distribution: Pantropic to almost cosmopolitan. Am. 1: Alaska; Am. 2: Costa Rica, Guatemala, Mexico; Am. 3: Cuba, Dominican Republic, Haiti; Am. 4: Bolivia, Colombia, Ecuador, Peru, Venezuela; Am. 5: Brazil; Am. 6: Argentina, Chile, Tierra del Fuego; Afr. 2: Democratic Republic of Congo; Afr. 3: Madagascar; As. 2: China; As. 3: India, Sri Lanka; As. 4: Indonesia (Java, Sumatra), Malaysia (Borneo), Papua New Guinea, Philippines (Luzon, Mindanao); OC.: Hawaii; Austr 2: New Zealand.

Habitat and ecology: Epiphytic on small branches and twigs of shrubs and trees, and sometimes on ferns; occasionally on soil and rocky sites with other mosses (Calabrese, 2006). The species is usually found above 2500 m in Malesia (Eddy 1996), but may occur at lower elevations in temperate regions (e.g., 457 m at Mount Cargill, *s.coll.*, NY).

Notes:

1. *Zygodon reinwardtii* is characterized by its a) elliptic-lanceolate to oblanceolate leaves; b) costa that terminates some distance below the leaf tip; c) dentate leaf margin; d) mostly pluripapillose laminal cells (smooth cells found only in a small region near to the leaf insertion). This combination of characters adequately distinguishes *Z. reinwardtii* from all other congeners in the Malesian region. The only species with some similarity is *Z. tetragonostomus* Braun *ex* B.S.G., which has a percurrent to short-

excurrent costa and entire leaf margin that clearly distinguishes it from *Z. reinwardtii*.

2. In *Z. reinwardtii*, seta length is variable and not correlated with plant size. Although plants collected from Malaysia have setae consistently shorter than 1.2 cm, those from neighbouring regions often have longer setae, e.g., *Van Steenis 10159*, *10161* from Sumatra (BM!); *Eddy 5065* from Sulawesi (BM!); *Fleischer 31* from Java (NY!). Although propagules are absent from all specimens examined in this study, the plant has been reported to possess fusiform to clavate-fusiform, hyaline or greenish-hyaline propagules (Calabrese, 2006).

3. Dale Vitt has placed a short note next to the specimen on the sheet "*N.H.M. London no.: BM00085458*" suggesting it as possible lectotype material if Hornschuch's herbarium no longer existed. However this specimen is not *Z. reinwardtii* and is here identified as *Z. tetragonotomus*, and so inappropriate for lectotypification. The *tabula* in the original publication clearly shows all the important features that characterize *Z. reinwardtii*. In the absence of the type specimen, this *tabula* counts as original material and is therefore appropriate as a lectotype.

<u>Specimens examined</u>:

INDONESIA. Java: *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe ex Dozy & Molk*. [*c.fr*.] (BM-N.H.M. no.: BM000858461!); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Hampe ex Lacoste* [*c.fr*.] (BM-N.H.M. no.: BM000858459!); *s.loc*., *s.date*, *s.coll*., *ex Hb*. *Hampe ex Nees* [*c.fr*.] (BM-N.H.M. no.: BM000858460!); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Jaeger* [*c.fr*.] (NY!); *s.loc*., *s.date*, *s.coll*. *ex Hb*. *Nees in Hook*. [*c.fr*.] (NY!); *s.loc*., *s.date*, *s.coll*., *H1229*, *ex Hb*. *Wilson ex Nees* [*c.fr*.] (BM-N.H.M. no.: BM000858454!), *H1229*, *ex Hb*. *Wilson ex Nees* [*c.fr*.] (BM!-N.H.M. no.: BM000858455!), *H1229*, *ex Hb*. *Wilson* [*c.fr*.] (BM!-N.H.M. no.: BM000858457!); Gipfel des Pangerango, 3000 m, 17.VII.1898, *Fleischer 31* [*c.fr*.] (NY 2 sheets!). **Sulawesi**: Latimojong, Mt. Rantemario, Nanemori, 3200 m, 24.X.1969, *Eddy 5065* [*c.fr*.] (BM!). **Sumatra**: Mt. Losir, Atjeh, Gajolanden, 2940 m, 5.II.1937, *van Steenis 10159 (Hb. Bogoriense 4044)* [*c.fr.*] (lectotype of *Pleurozygodontopsis decurrens*: BM!), *van Steenis 10161 (Hb. Bogoriense 4041)* [*c.fr.*] (syntype of *Pleurozygodontopsis decurrens*: BM!). **INDIA:** Peninsular India, *s.date, s.coll. 158(108) ex Hb. Wilson* (BM!), *s.coll. 133 &197(108) ex Hb. Wilson* [*c.fr.*] (BM!). **Madras State:** Madura District, Palni Hills, Kodaikanal and surrounding region, Shembaganur, *Foreau s.n.* (TNS!). **MALAYSIA. Borneo, Sabah:** Ranau, Kinabalu Park, Mt. Kinabalu, *s.date*, *Damanhuri s.n.* (UKMB!); Ranau, Kinabalu Park, Mt. Kinabalu, Paka Cave, 10000 ft [=3048 m], *s.date, Littke WL61* (UKMB!); *ibidem*, 3130 m, 10.V.2005, *Yong 6315* [*c.fr.*], *6330* [*c.fr.*], *Yong 6331* [*c.fr.*] (KLU!); Ranau, Kinabalu Park, Mt. Kinabalu, Laban Rata, 3185 m, 11.V.2005, *Yong 6367a* [*c.fr.*] (KLU!); *ibidem*, 3345 m, 11.V.2005, *Yong 6364*, *6374* [*c.fr.*] (KLU!). **NEW ZEALAND:** Mount Cargill, 1500 ft [=457 m], III.1888, *s.coll.* [*c.fr.*] (NY!). **PAPUA NEW GUINEA. Milne Bay:** Maneau Range, Mt. Dayman, 2230 m, V.1953, *Brass 22419* (TNS!). **Simbu:** Mt. Wilhelm, Kergsugl Forest, 7500 ft [=2286 m], 4.VIII.1994, *Tan 94-4460* [*c.fr.*], *Tan 94-4820A* [*c.fr.*] (SING!).

CHAPTER 6

MOLECULAR PHYLOGENETIC ANALYSES AND A CLADISTIC MORPHOLOGICAL STUDY

6.1 General introduction

Orthotrichales was raised from subordinal position (Orthotrichineae sensu Fleischer, 1920a) to ordinal position and separated from Order Isobryales by Dixon (1932a). Initially, Dixon (1932a) included members of three families under the Orthotrichales, i.e., Erpodiaceae, Ptychomitriaceae and Orthotrichaceae. He concluded that the members of that order are characterized by unique diplolepideous peristome teeth, with the outer teeth often united in eight pairs and shorter than the inner teeth. However, the order is not always an easily defined group, due to its highly polymorphic gametophytic characters, which include the presence of both acrocarpic and cladocarpic members. In spite of this, affinities between members that have well-developed peristome, with members with heavily reduced or rudimentary peristome or which lack peristome teeth (i.e., are gymnostomous) are always difficult to determine. Hence, the total number of families accepted for the Orthotrichales has fluctuated from time to time, from one to seven families (Dixon, 1932a; Reimers, 1954; Robinson, 1971; Walther, 1983; Vitt, 1984).

Recently, molecular information has been generated in larger datasets and also incorporated with morphological data to infer relationships within the Orthotrichales. Consequently, several families were removed from the Orthotrichales, for example, Erpodiaceae, Rhachitheciaceae and Wardiaceae (based on molecular inference: Goffinet et al., 1998; Hedderson et al., 1999), Microtheciellaceae (based on comparative morphology: Goffinet, 1998), and Hedwigiaceae (based on combined morphological and molecular analyses: De Luna, 1995; Goffinet et al., 1998; Cox & Hedderson, 1999). The Orthotrichales, as generally recognized today, is only represented by its type family, viz., Orthotrichaceae (Goffinet & Buck, 2004).

Vitt (1981, 1984) considered that peristomial architecture of the Orthotrichaceae is unique and distinct from the other diplolepideous mosses, which he recognized as an "orthotrichaceous peristome type". This type of peristome was thought to have evolved independently from an ancestral diplolepideous peristome, and not from the other two peristome types, i.e., the funariaceous and bryaceous types recognized for diplolepideous mosses (Vitt, 1984; Lewinsky, 1989). However, the above hypothesis is rejected by later phylogenetic studies inferences, where Orthotrichaceae often was placed in a position either nested in, or near the base of the Bryales clade (Cox & Hedderson, 1999; Cox et al., 2000; Newton et al., 2000; Goffinet et al., 2001). Thus, the Orthotrichales (or Orthotrichaceae) are generally accepted as a member of Subclass Bryidae, characterized by a diplolepideous alternate peristome (or "bryaceous peristome type") (Goffinet & Buck, 2004). Nevertheless, whether the peristomial architecture of Orthotrichaceae resembles an ancestral or derivative form of bryaceous peristome, the ordinal position of Orthotrichales within Subclass Bryidae, remains controversial (Goffinet et al., 1999). There is available molecular evidence based on single plastid markers, or parsimony analyses of combined markers of different genes, indicating a closer relationship of the Orthotrichales with the Splachnales (e.g., Cox et al., 2000; Newton et al., 2000; Tsubota et al., 2004), which is likely to have been an earlier evolved order in Subclass Bryidae that possesses opposite peristome (Goffinet et al., 2004). In contrast, there are other molecular findings, both using either mitochondrial information, or combined plastid/mitochondrial markers, that have demonstrated that the Orthorichales is, in fact, sister to the pleurocarpic mosses characterized by an alternate peristome with cilia, a derived form of the bryaceous peristome type (Beckert et al., 2001; Goffinet et al., 2001; Quandt et al., 2007; Stech & Frey, 2008). However, both alternatives have usually received poor statistical support**;** and good support has been obtained only with specific phylogenetic optimality criteria (Bell et al., 2007). Hence, much further work is still needed to determine the ordinal position of the Orthotrichales within Subclass Bryidae.

The presence of both acrocarpic and cladocarpic members in the Orthotrichaceae has long given the impression that the Orthotrichales (or Orthotrichaceae) represent the transition group between the typical acrocarpic and pleurocarpic mosses in evolution (Crum & Anderson, 1981; La Farge-England, 1996). On the other hand, the monophyly of Orthotrichaceae was questioned by Churchill and Linares (1995) and De Luna (1995). Using morphological data, the acrocarpous genera of Orthotrichaceae form a sister group to a larger clade composed of members of cladocarpous Orthotrichaceae, Hedwigiaceae, and the less related Leucodontineae and Hypnales (De Luna, 1995). This led to the suggestion by Churchill and Linares (1995) to segregate Orthotrichaceae into two separate families, each comprising only either acrocarpous or cladocarpous members.

However, the latest molecular findings have rejected the above hypothesis and supported a monophyletic origin for the Orthotrichaceae, with members of the Hedwigiaceae forming a sister group to these pleurocarpic mosses (Cox & Hedderson, 1999; Cox et al., 2000; Goffinet et al., 2001; Bell et al., 2007; Stech & Frey, 2008). Nevertheless, De Luna (1995) demonstrated that the Orthotrichaceae would be better subdivided into two distinct lineages (i.e., subfamilies Macromitrioideae and Orthotrichoideae), a position also supported by the most recent molecular findings

(Goffinet et al., 1998; Hu et al., 2008 and the present study). According to Goffinet and Vitt (1998), the ancestor of Orthotrichaceae is postulated to have 1) thick-walled and smooth laminal cells which are isodiametric on the upper lamina but differentiated into rectangular cells on the basal lamina, 2) terminal cauline perichaetia, 3) diplolepideous peristomes with an exostome of 16 free teeth and endostome of 16 segments alternate to the exostome teeth.

The speciose genera of the family, such as *Macromitrium*, *Orthotrichum, Ulota* and *Zygodon*, were suggested to be either paraphyletic or polyphyletic in origin (Goffinet et al., 1998). This is supported by later phylogenetic inferences made on the Subfamily Orthotrichoideae, where members of *Orthotrichum* and *Zygodon* are resolved in paraphyletic or polyphyletic grades (Goffinet et al., 2004).

Macromitrium, is by far the largest genus of Orthotrichaceae with 368 accepted specific names (Crosby et al., 1999), has not been thoroughly revised. The genus, as well as other Macromitrioideae members, is usually not represented in cladograms constructed for the Orthotrichaceae (Goffinet et al., 1998; Goffinet et al., 2004; Hu et al., 2008). In phylogenetic trees constructed using the rbcL region, Goffinet et al. (1998) have shown that members of Macromitrioideae, viz., *Cardotiella, Desmotheca, Groutiella, Macrocoma,* either positioned themselves as the sister taxa to, or nested together with, *Macromitrium* species in a clade. Except for the genus *Schlotheimia*, the only Macromitrioideae genus that consistently forms a well-supported clade that is sister to other Macromitrioideae genera in all analyses (Goffinet et al., 1998).

Due to the large number of species described and highly diversified plant characters, *Macromitrium* has been subdivided into various formal or informal infra-generic groups by many authors (e.g., Müller, 1845; Fleischer, 1904; Brotherus, 1925; Vitt, 1984; Allen, 2002). Müller (1845) was the first to recognize infra-generic categories in *Macromitrium*. Nevertheless, four out of his five infra-generic groups have later been raised to recognized genera (e.g., Brotherus, 1902-1910; Grout, 1944). Mitten (1869), based on the *Macromitrium* members that were known to him from continental America and Australasia, had divided the genus into four different sections, viz., *Goniostoma*, *Leiostoma*, *Macrocoma*, *Micromitrium*. His subdivision was based on the branching pattern, leaf orientation, and features of capsule mouth and calyptra. Likewise, some of the sections recognized by Mitten (1869) were later treated as genera, i.e., *Macrocoma* (from sect. *Macrocoma*) and *Groutiella* (from sect. *Micromitrium*).

In a global treatment of all moss species known at that time, Brotherus (1925) erected five subgenera to accommodate the many *Macromitrium* species recognized, among which subgenus *Macrocoma* was later elevated to a genus (Grout, 1944). Subgenus *Eumacromitrium*, the largest recognized in Brotherus' work, was further subdivided into three sections (Brotherus, 1925), including two of which (*Goniostoma* and *Leiostoma*) were proposed by Mitten (1869) and section *Teichodontium*, which was earlier considered by Herzog (1916) as a distinct subgenus of *Macromitrium*.

From a different perspective, Fleischer (1904) had categorized the many *Macromitrium* species of Java and adjacent islands into two subgenera, viz., Subgenus *Diplohymenium* and Subgenus *Haplodontiella* (=*Macromitrium s.str.*). Unlike earlier workers, Fleischer’s work (1904) had emphasized peristomial features in the infra- generic classification of *Macromitrium*. Under the subgenus *Diplohymenium*, Fleischer (1904) further segregated members into two sections (*Epilimitrium* and *Cometium*) and he recognized two subsections (viz., *Macro*- and *Micro-Cometium*) under section

Cometium. Section *Cometium* was first created by Mitten (1873) to accommodate small-sized *Macromitrium* taxa which often had forked branches and serially arranged leaves on branches (e.g., *M. orthostichum*).

Due to the general lack of sporophytic structures among collections, Grout (1944) subdivided the North American *Macromitrium* into three informal groups mainly using vegetative characters. Most subsequent workers also preferred such informal groupings to formal taxonomic subgroups. Vitt (1984) recognized three distinctive groups out of the ten *Macromitrium* species known in Mexico. Vitt and Ramsay (1985) subdivided the 32 *Macromitrium* species known for Australasia with many endemics, into seven informal groups based on a morphological cladistic analysis. However, the proposal of Vitt and Ramsay (1985) only partly corresponded to infra-generic classifications earlier proposed by Fleischer (1904) and Brotherus (1925).

Allen (2002) segregated 31 Central American *Macromitrium* taxa into seven informal groups. Likewise, the informal classification of Allen (2002) dealt only with *Macromitrium* taxa of limited neotropical distribution. The different criteria used by Allen (2002) meant that his subdivision did not correspond to any of the earlier published ones.

The objectives of this study were to use the *rps*4 gene and *trn*L-*trn*F interspacer region and morphological data to: 1) test the monophyly of *Macromitrium*; 2) assess the various infra-generic groupings in *Macromitrium* proposed by different authors; and 3) infer the phylogenetic relationships among *Macromitrium* and other Orthotrichaceae taxa treated in the present revision.

6.2 Results

6.2.1. Size of dataset

The complete matrix based on molecular information is composed of 56 taxa (including seven out-group taxa) and 113 sequences of two genes, of which 35 sequences are newly constructed (Table 6.1). Sequence information of the out-group taxa and most of the Orthotrichoideae representatives included in the analysis was downloaded from the DDBJ/EMBL/GenBank. The size and variation of the three data matrixes (*rps*4, *trn*L-*trn*F, *rps*4+*trn*L-*trn*F) analyzed are summarized in Table 6.2. Total taxa included in the individual and combined analyses of gene sequences vary from 50 to 56 taxa depending on the availability of the sequence information (Table 6.1). Sequence information for *rps*4 region is not available for *Macromitrium ochraceum*, while sequence information of *trn*L-*trn*F region is lacking for *Codonoblepharon menziesii*, *M. fuscescens, M. levatum, M. richardii*, *Schlotheimia rubiginosa*, and *Zygodon orientalis*. However, all listed taxa were included in the combined analysis of gene and morphological characters, even though only partial information was available for some taxa mentioned above.

The *rps*4 region has an invariant length of 547 base-pairs (bp) of nucleotides in all taxa included in the present analysis. Meanwhile, the *trn*L-*trn*F region consisted of 419 bp with a variable number of 241 to 289 bp of unaligned nucleotides across the taxa studied. The primer annealing sites were excluded from analysis, while the many gaps encountered in the alignment were treated with a simple indel coding method following Simmons & Ochoterena (2000). There are regions where nucleotides could not be properly arranged even by inducing new gaps. Such ambiguous regions were excluded from the analysis.

Table 6.1. List of the taxa represented in present analyses. Specimen voucher information (*Yong* numbers) is given for newly obtained sequences, while sequences downloaded from GenBank are indicated with their accession numbers. All the voucher materials are deposited with KLU.

		GenBank accession / Voucher No.	
	Taxa	***rps*4**	***trn*L-*trn*F**
	Family Orthotrichaceae		
	Subfamily Macromitrioideae		
1.	*Cardotiella quinquefaria* (Hornsch.) Vitt	AY618362	AY636032
2.	*Desmotheca apiculata* (Dozy & Molk.) Lindb.	*Yong 5766*	AY636028
3.	*Groutiella chimborazensis* (Spruce ex Mitt.) Florsch.	AY618380	AY636033
4.	*G. tomentosa* (Hornsch.) Wijk & Margad.	Peninsular Malaysia (A):	
		Yong 6124	*Yong 6124*
		Borneo (B):	
		Yong 6224	*Yong 6224*
5.	*Leiomitrium plicatum* (P. Beauv.) Mitt.	AY618359	AY636029
6.	*Macrocoma tenuis* (Hook. & Grev.) Vitt	AY618361	AY606030
7.	*Macromitrium angustifolium* Dozy & Molk	Lower elevation (A):	
		Yong 6215	*Yong 6215*
		Higher elevation (B):	
		Yong 6409	*Yong 6409*
8.	*M. blumei* Nees ex Schwägr. var. *blumei*	*Yong 6122*	*Yong 6122*
9.	*M. blumei* var. *zollingeri* (Mitt. ex Bosch & Sande Lac.) S.L. Guo, B.C. Tan & Virtanen	*Yong 6201*	*Yong 6201*
10.	*M. cuspidatum* Hampe	*Yong 6117*	*Yong 6117*
11.	*M. fuscescens* Schwägr.	*Yong 5762*	—
12.	*M. incurvifolium* (Hook. & Grev.) Schwägr.	AF226754	AF231162
13.	*M. levatum* Mitt.	AF023813	—
14.	*M. longicaule* Müll. Hal.	Peninsular Malaysia (A):	
		Yong 6127	*Yong 6127*
		Borneo (B):	
		Yong 6210	*Yong 6210*
15.	*M. orthostichum* Nees ex Schwägr.	Peninsular Malaysia (A):	
		Yong 6116	*Yong 6116*
		Borneo (B):	
		Yong 6211	*Yong 6211*
16.	*M. ochraceoides* Dixon	*Yong 6329*	*Yong 6329*
17.	*M. ochraceum* (Dozy & Molk.) Müll. Hal.	—	*Yong 6123*
18.	*M. richardii* Schwägr.	AF306975	—
19.	*M. salakanum* Müll. Hal.	*Yong 6125*	*Yong 6125*
20.	*Matteria gracillima* (Besch.) Goffinet	AY618360	AY636031
21.	*Schlotheimia rubiginosa* C.H. Wright	*Yong 6333*	—
22.	*S. torquata* (Sw. ex Hedw.) Brid.	AY618378	AY636027
23.	*S. wallisii* Müll. Hal.	*Yong 6301*	*Yong 6301*

Table 6.1, continued.

		GenBank accession / Voucher No.	
	Taxa	***rps*4**	***trn*L-*trn*F**
	Subfamily Orthotrichoideae		
24.	*Codonoblepharon forsteri* (Dicks. ex With.) Goffinet [syn. *Zygodon forsteri* (Dicks. ex With.) Mitt.]	AY618376	AY636006
25.	*C. menziesii* Schwägr.	AY908175	—
26.	*C. pungens* (Müll. Hal.) A. Jaeger	AY618383	AY636005
27.	*Nyholmiella obtusifolia* (Brid.) Holmen & Warncke [syn. *Orthotrichum obtusifolium* Brid.]	AF306969	AY636014
28.	*Orthotrichum anomalum* Hedw.	AF306970	AY636019
29.	*O. affine* Schrad. ex Brid.	AY618365	AY636021
30.	*O. alpestre* Hornsch. ex B.S.C.	AF306971	AY636017
31.	*O. crassifolium* Hook. f. & Wilson [syn. *Muelleriella crassifolia* (Hook. f. & Wilson) Dusén]	AY618377	AY636018
32.	*O. jetteae* B.H. Allen [syn. *Orthomitrium tuberculatum* Lewinsky-Haapasaari & Crosby]	AY618368	AY636016
33.	*O. lyellii* Hook. & Taylor	AY618367	AY636023
34.	*O. laevigatum* J.E. Zetterst.	AY618366	AY636022
35.	*Pleurorthotrichum chilense* Broth.	AY618375	AY636011
36.	*Sehnemobryum paraguense* (Besch.) Lewinsky-Haapasaari & Hedenas	AY618382	AY636013
37.	*Stoneobryum mirum* (Lewinsky) D.H. Norris & H. Rob.	AY618381	AY636012
38.	*Ulota crispa* (Hedw.) Brid.	AF306972	AY636026
39.	*U. hutchinsiae* (Sm.) Hammar	AY618370	AY636025
40.	*U. phyllantha* Brid.	AY618369	AY636024
41.	*Zygodon bartramioides* Malta	AY618371	AY636007
42.	*Z. fragilifolius* Broth. ex Malta [syn. *Leptodontiopsis fragilifolia* Broth.]	AY618374	AY636010
43.	*Z. inermis* Malta	AF618372	AY636008
44.	*Z. intermedius* Bruch & Schimp.	AF223061	AF229918
45.	*Z. pentastichus* (Mont.) Müll. Hal. [syn. *Pentastichella pentasticha* (Mont.) Müll. Hal. ex Thér.]	AY618373	AY636009
46.	*Z. orientalis* (Dixon) Goffinet	*Yong 6365*	—
47.	*Z. reinwardtii* (Hornsch.) A. Braun	*Yong 6331*	*Yong 6331*
	Taxa of uncertain position		
48.	*Leratia exigua* (Sull.) Goffinet [syn. *Orthotrichum exiguum* Sull.]	AY626223	AY636034
49.	*L. obtusifolia* (Hook.) Goffinet [syn. *Bryomaltaea obtusifolia* (Hook.) Goffinet]	AY618358	AY636004

Table 6.1, continued.

Taxa		**GenBank accession / Voucher No.**	
		***rps*4**	***trn*L-*trn*F**
Out-groups:			
	Family Bartramiaceae		
50.	*Bartramia halleriana* Hedw.	EF107539	EF107539
	Family Calymperaceae		
51.	*Mitthyridium undulatum* (Dozy & Molk.) H. Rob.	AF226775	AF231188
	Family Dicranaceae		
52.	*Dicranoloma blumii* (Nees) Paris	AF435281	AF435318
	Family Hedwigiaceae		
53.	*Hedwigia ciliate* (Hedw.) P. Beauv.	AF306997	AF233587
	Family Meesiaceae		
54.	*Leptobryum wilsonii* (Mitt.) Broth.	AF306992	AY501424
	Family Pottiaceae		
55.	*Hyophila involuta* (Hook.) A. Jaeger	AY950357	AY950403
	Family Rhizogoniaceae		
56.	*Pyrrhobryum spiniforme* (Hedw.) Mitt.	AF023832	AF023751

Table. 6.2. Summary of sequence length and characters for regions used in phylogenetic analyses of Orthotrichaceae, and principal indicators obtained.

Regions	***No. taxa***	***Tree length***	***Variable characters***	***Parsimony informative characterss***	***GC content (%)***	***Transition / transversion ratio (ti/tv)***	***Best trees***	***Consistency Index (CI)***	***Retention Index (RI)***	***Homoplasy Index (HI)***
*rps*4	55	547	226	121	26.009	1.976	11	0.617	0.792	0.383
*trn*L-*trn*F	50	496	232	141	25.512	2.093	8	0.650	0.812	0.350
Combined	56	1043	458	262	25.861	1.955	5	0.624	0.794	0.376
Morphology	33	43	43	39	–	–	22	0.442	0.723	0.558

A preliminary run showed that ambiguous regions where many gaps are present, included or not, did not alter the resulting topologies. However, the simple indel coding approach resulted in better supported trees (Simmons & Ochoterena, 2000). The total length of the *trn*L-*trn*F region included in the analysis is 496 bp, where 77 additional positions are of binary data (indel information). In conclusion, the total length of combined data used in analyses is actually made of 1043 bp, viz., 547 bp from the *rps*4 region and 496 bp from the *trn*L-*trn*F region, after considering the indel information.

Results from separate and combined analyses of *rps*4 and *trn*L-*trn*F are given in Table 6.2. The tree topologies obtained under different datasets are largely congruent and are found to have no significant conflicts. However, the analyses of separate datasets produced branches resolving with relatively low support value, under both maximum parsimony (MP) and Bayesian reconstructions. Hence, results from analyses of the combined *rps*4 and *trn*L-*trn*F regions are preferred and discussed here. The results from separate datasets are discussed only when necessary and the trees are not shown. Phylogenetic trees reconstructed based on the combined region, under the MP and MrBayes approaches, are presented in Figs. 6.1 and 6.2.

In another cladistic analysis based on morphological data, a total 43 characters in 33 taxa were considered (Tables 6.3 and 6.4). Morphological characters were sampled from all 30 Orthotrichaceae taxa revised in the present work, with additional information obtained from *Orthotrichum anomalum*, the type species of *Orthotrichum*. The two out-group taxa chosen for this analysis were *Hyophila involuta* (Pottiaceae) and *Mitthyridium undulatum* (Calymperaceae).

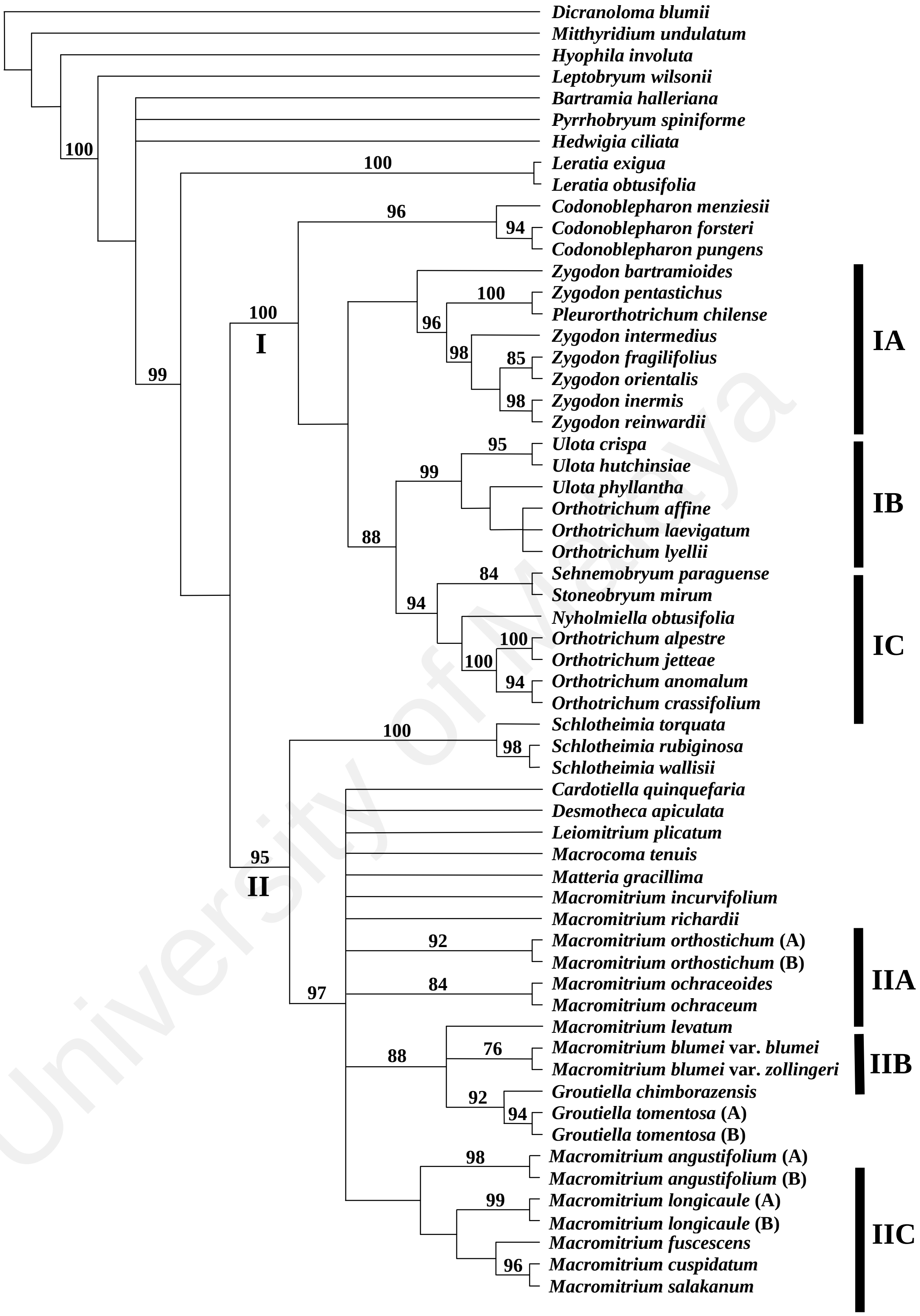

Figure 6.1. Majority rule consensus tree of five equally most parsimonious trees (MPTs) retained by the parsimony ratchet analysis performed based on the combined *rps*4 and *trn*L-*trn*F regions. Bootstrap support values (>70%) of 1000 replications are indicated above branches. Labels I–II denote clades, while IA-IC and IIA-IIC denote groups discussed in the text.

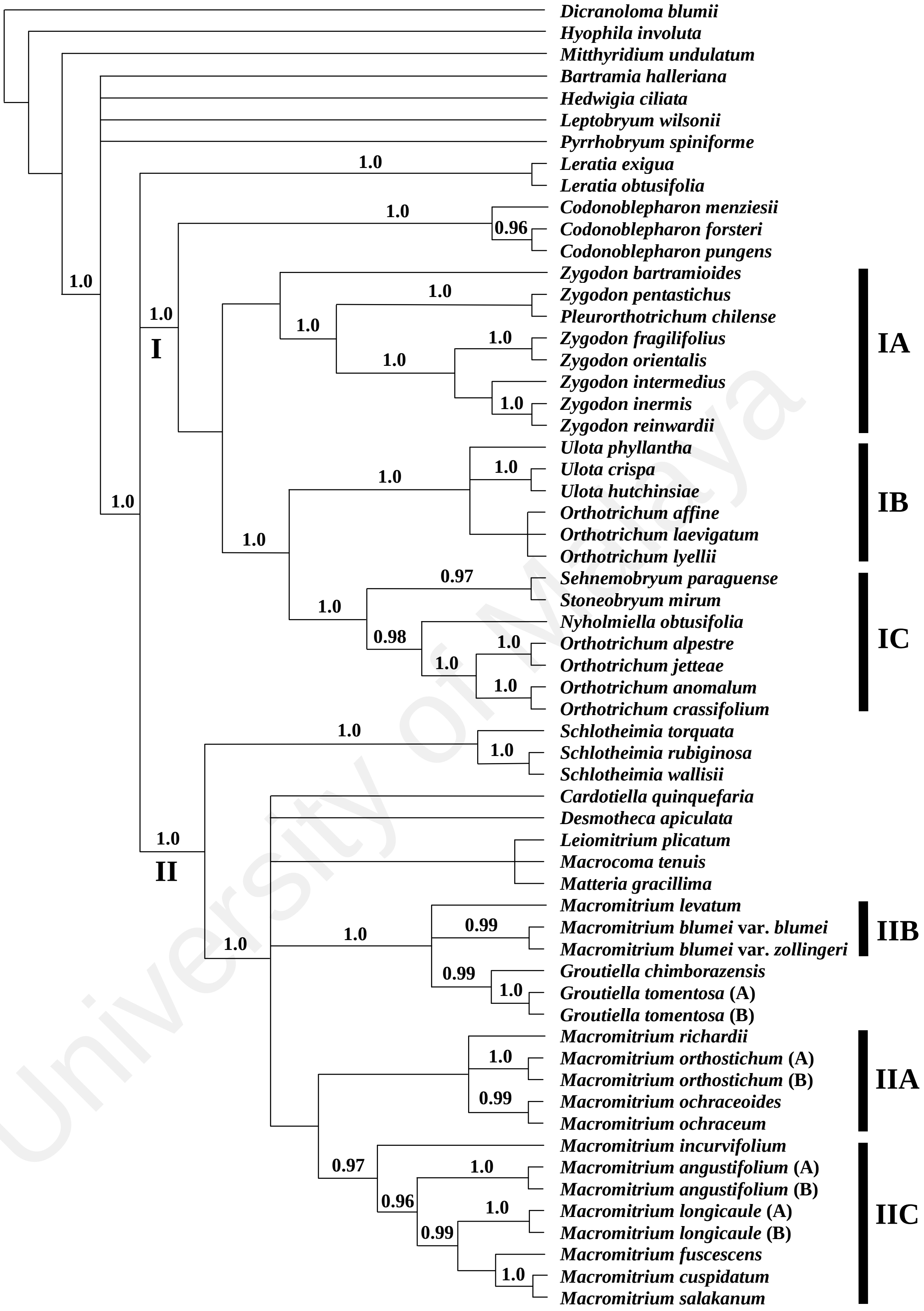

Figure 6.2. Phylogenetic tree obtained by Bayesian inference on the combined *rps*4 and *trn*L-*trn*F regions. Posterior probability values (>0.95) are depicted above the branches. Labels I–II denote clades, while IA-IC and IIA-IIC denote groups discussed in the text.

Table 6.3. Characters and character states used in a cladistic analysis of Malaysian Orthotrichaceae.

Character code	Character and states (the latter numbered in parentheses)
1.	Stem orientation: orthotropic (1); plagiotropic (2).
2.	Central strand: present (1); absent (2).
3.	Branching of the secondary axis: sympodial (1); monopodial (2).
4.	Leaf dimorphism: stem and branch leaves identical (1); stem and branch leaves dimorphic (2).
5.	Terminal branch leaf differentiation: much shorter than those found at the lower portion of branches (1); not differentiated from those found at the lower portion of branches (2).
6.	Leaf base morphology: leaf base decurrent (1); leaf base not decurrent (2).
7.	Branch leaf arrangement when dry: tightly coiled on branches (1); imbricate or loosely-erect (2), variously curved, or flexuose, or twisted-contorted (3).
8.	Branch leaf arrangement when moist: inserted in five distinctive ranks (1); spirally inserted on branch (2).
9.	Thickness of leaf lamina: bistratose, at least at upper lamina (1); unistratose throughout (2).
10.	Leaf apex: broad, blunt, obtuse to round-pointed (1); slender, acute to acuminate (2).
11.	Costa: terminating below leaf apex (1); consistently percurrent (2); occasionally excurrent to long-excurrent (3).
12.	Chlorophyllous epidermal cells of costa: present (1); absent (2).
13.	Upper laminal margin: entire to crenulated (1); regularly serrulate to serrate (2); strongly and irregularly toothed (3).
14.	Limbidium at upper laminal margin: present (1); absent (2).
15.	Basal laminal margin: plane (1); weakly recurved or incurved (2).
16.	Overall leaf morphology: basal part much wider than upper lamina and sharply contracted into the narrower upper lamina (1); basal part more or less as wide as upper lamina (2).
17.	Overall laminal cell size: short throughout (1); long throughout (2); basal laminal cells long and upper laminal cells short (3).

Table 6.3, continued.

Character code	Character and states (the latter numbered in parentheses)
18.	Ornamentation of upper laminal cells: flat or smooth (1); bulging or mammillose (2); unipapillose (3); pluripapillose (4).
19.	Size and shape of upper laminal cells: short, round, polygonal (1); elongate or long (2); irregular in size and shape (3). [Only those plants with upper laminal cells of different size and shape on the same leaf were coded as 3.]
20.	Basal laminal cells: equally thick-walled (1); unevenly thick-walled (2); thin-walled (3).
21.	Basal laminal cells lumen: wider than cell wall (1); narrower than cell wall (2).
22.	Shape of basal laminal cells: cells rounded, oblate or oval (1); long-rectangular (2).
23.	Ornamentation of basal laminal cells: smooth (1); unipapillose or tuberculate (2); prorate (3).
24.	Morphology of basal marginal cells: cells differentiated, usually long-slender and having thinner cell wall (1); cells not differentiated from inner laminal cells (2).
25.	Position of perichaetia: acrocarpy, terminal on main axis (1); cladocarpy, terminal on lateral branches (2).
26.	Relative length of perichaetial to vegetative leaves: shorter than vegetative leaf (1); as long as or longer than vegetative leaf (2).
27.	Sexual condition: autoicous (1); dioicous (2); phyllodioicous (3).
28.	Calyptra shape: cucullate (1); mitrate (2).
29.	Calyptra size: covering only the operculum or half of the urn (1); completely covering the urn (2).
30.	Calyptra surface ornamentation: smooth (1); plicate (2).
31.	Calyptra surface appendages: naked (1); few hairs (2); many hairs (3).
32.	Outline of calyptra base: entire or slightly dissected (1); fringed or lacerated (2); deeply lobed (3); shallowly lobed (4).
33.	Capsule position: immersed (1); short-exerted, $\leq$ 0.8 mm long (2); long-exerted, $\geq$ 1.2 mm long (3).
34.	Opercular rostrum length: short, $\leq$ 0.5 mm (1); long, > 0.6 mm (2).

Table 6.3, continued.

Character code	Character and states (the latter numbered in parentheses)
35.	Opercular rostrum orientation: oblique or curved (1); perpendicular to operculum base (2).
36.	Number of stomata on capsule: many, ≥ 10 stomata (1); few, ≤ 6 stomata (2).
37.	Stomatal exposure: phaneropore (1); cryptopore (2).
38.	Twisting of the distal portion of the seta: dextrorse (1); sinistrorse (2); both directions (3).
39.	Seta surface ornamentation: papillose (1); smooth (2).
40.	Exostome: lack of peristome (1); reduced (2); fully developed (3).
41.	Fusion of exostome teeth: with 16 free teeth (1); fused into 8 free pairs (2); fused into a peristomial lamella (3).
42.	Endostome: present (1); absent (2).
43.	Spore size: isosporous (1); anisosporous (2).

Table 6.4. The data matrix for morphological character states used in a cladistic analysis of Malaysian Orthotrichaceae. Character states are coded with (1), (2), (3) and (4). (?) denotes unknown information and (–) denotes inapplicable characters.

Taxa	Characters																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Hyophila involuta	1	1	1	1	2	2	3	2	2	1/2	2	1	2	2	1	2	1	2	1	1	1	1/2
Mitthyridium undulatum	2	2	1	1	2	2	3	2	2	1/2	1	1	2	1	1	1	3	4	1	3	1	2
Zygodon intermedius	1	2	1	1	2	1	2	2	2	1/2	1	2	1	2	1	2	1	4	1	1	1	1
Z. orientalis	1	2	1	1	2	1	3	2	2	2	2	2	1/2	2	1	2	3	4	1	1	1	2
Z. reinwardtii	1	2	1	1	2	1	3	2	2	1/2	1	2	3	2	1	2	3	4	1	1	1	1
Ulota splendid	1	2	1	1	2	2	3	2	2	2	2	2	1/2	2	1	1	3	1/3/4	3	1	2	2
Orthotrichum anomalum	1	2	1	1	2	2	2	2	2	1/2	1	2	1	2	2	2	3	4	1	1	1	2
Macromitrium angustifolium	2	2	2	2	2	2	3	2	2	2	2/3	2	1	2	2	2	3	4	1	1/2	2	2
M. salakanum	2	2	2	2	2	2	3	2	2	2	3	2	1	2	2	2	3	4	1	2	2	2
M. fuscescens	2	2	2	2	2	2	3	2	2	1/2	3	2	1	2	2	2	3	4	1	2	2	2
M. cuspidatum	2	2	2	2	2	2	3	2	2	2	3	2	1	2	2	2	2/3	1/4	1/2	2	2	2
M. incurvifolium	2	2	2	2	2	2	3	2	2	2	2/3	2	1	2	2	2	3	4	1	1/2	2	2
M. longicaule	2	2	2	2	2	2	3	2	2	2	1/2	2	1/2	2	2	2	3	4	1	2	2	2
M. falcatulum	2	2	2	2	2	2	3	2	2	1/2	3	2	1	2	2	2	1	2/4	1	1	1	1
M. nepalense	2	2	2	2	2	2	3	2	2	1/2	3	2	1	2	2	2	3	2/4	1	1	2	2
M. ochraceoides	2	2	2	2	2	2	3	2	2	2	3	2	2	2	2	2	3	1/4	1	1	2	2
M. ochraceum	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	3	1/4	1	1	2	2
M. papillisetum	2	2	2	2	2	2	3	2	2	1	3	2	1	2	2	2	1	2/4	1	1	2	2
M. orthostichum	2	2	2	2	2	2	2	1	2	1/2	3	2	2	2	2	2	1	2/4	1	1	1	1/2
Desmotheca apiculata	2	2	2	2	1	2	2	1	2	2	3	2	1	2	2	2	3	2/4	1	1	1	1/2
D. mohamedii	2	2	2	2	1	2	2	1	2	2	3	2	1	2	2	2	3	2/4	1	1	1	2

Table 6.4, continued.

	Characters																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Macromitrium densum	2	2	2	2	2	2	1	2	2	1	3	2	1	2	2	2	1	2	1	1	2	1/2
M. longipilum var. *ligulatum*	2	2	2	2	2	2	3	2	2	2	3	2	1	2	2	2	2/3	1	1/2	1	2	2
M. longipilum var. *longipilum*	2	2	2	2	2	2	3	2	2	2	3	2	1	2	2	2	2/3	1/3/4	1/2	1/2	2	2
M. longipilum var. *rugosum*	2	2	2	2	2	2	3	2	2	1/2	3	2	1	2	2	2	2/3	1	1/2	1	2	2
M. macrosporum	2	2	2	2	2	2	3	2	2	2	2	2	1	2	2	2	3	2/3	1	1	2	2
M. parvifolium	2	2	2	2	2	2	3	2	2	1/2	2	2	1	2	2	2	3	1/2	1	1	2	2
M. blumei var. *blumei*	2	2	2	2	2	2	1	2	2	1	3	2	1	2	2	2	3	1/2	1	1	2	2
M. blumei var. *zollingeri*	2	2	2	2	2	2	1	2	2	1	3	2	1	2	2	2	3	1/2	1	1	2	2
Groutiella kelantanense	2	2	2	2	2	2	1	2	2	2	1	2	1	2	2	2	1/3	1/2	1	1	2	1/2
G. tomentosa	2	2	2	2	2	2	1	2	1	2	1	2	1	2	2	2	1/3	1/2	1	1	2	1/2
Schlotheimia rubiginosa	2	2	2	2	2	2	1	2	2	1	3	2	1	2	2	2	3	1	1/2	1	2	2
S. wallisii	2	2	2	2	2	2	1	2	2	1	3	2	1	2	2	2	3	1	1/2	1	2	2

Table 6.4, continued.

	Characters																				
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Hyophila involuta	1	2	1	1	2	1	2	1	1	1	3	2	1	2	1	3	2	1	-	2	1
Mitthyridium undulatum	1	1	1	2	2	1	2	1	1	2	2	2	1	2	2	3	2	2	1	2	1
Zygodon intermedius	1	2	1	2	2	1	1	1	1	1	2	2	1	1	1	1	2	2	?	1	1
Z. orientalis	1	2	1	1	2	1	1	1	1	1	3	2	1	1	1	1	2	2	?	1	1
Z. reinwardtii	1	2	1	1	1	1	1	1	1	1	3	2	1	1	1	1	2	2	?	1	1
Ulota splendid	1	2	1	2	1	2	2	2	3	3	2	2	1	1	1	1	2	3	2	1	1
Orthotrichum anomalum	1	2	1	2	2	2	2	2	3	2	2	1	2	1	2	2	2	3	1	?	1
Macromitrium angustifolium	1	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2
M. salakanum	1	2	2	2	3	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	2
M. fuscescens	1	2	2	1/2	3	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	2
M. cuspidatum	1	2	2	1	3	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2
M. incurvifolium	1	2	2	1	3	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2
M. longicaule	2	2	2	1	3	2	2	2	2	2	2	2	2	2	2	2	2	3	1	2	2
M. falcatulum	2	2	2	1	3	2	2	2	3	2	2	2	2	2	2	3	2	2	1	2	2
M. nepalense	2	2	2	2	3	2	2	2	3	2	2	2	2	2	1	3	2	2	1	2	2
M. ochraceoides	1	2	2	2	3	2	2	2	3	2	3	2	2	2	2	2	1	2	3	2	2
M. ochraceum	2	2	2	2	3	2	2	2	3	2	2	2	2	2	2	2	1	2	3	2	2
M. papillisetum	2	2	2	2	3	2	2	2	3	2	2	1	2	2	2	2	1	1	-	2	2
M. orthostichum	2	2	2	1	3	2	1	2	3	3	2	1	2	2	1	2	1	2	3	2	2
Desmotheca apiculata	2	2	2	2	3	2	1	2	3	4	1	1	2	2	1	-	-	1	-	2	2
D. mohamedii	2	2	2	1	3	2	1	2	3	4	1	1	2	2	1	-	-	1	-	2	2

Table 6.4, continued.

	Characters																				
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Macromitrium densum	2	2	2	2	3	2	2	2	1	2	2	2	2	2	2	2	2	2	3	2	2
M. longipilum var. *ligulatum*	2	2	2	2	3	2	2	2	1	2	3	2	2	2	1	3	2	2	3	2	2
M. longipilum var. *longipilum*	2	2	2	2	3	2	2	2	1	2	3	2	2	2	1	3	2	2	3	2	2
M. longipilum var. *rugosum*	2	2	2	2	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. macrosporum	2	2	2	1	3	2	2	2	1	2	3	2	2	2	2	2	2	2	3	2	2
M. parvifolium	2	2	2	1	3	2	2	2	1	3	3	2	2	2	2	3	2	2	3	2	2
M. blumei var. *blumei*	2	2	2	2	1/3	2	2	2	1	2	3	2	2	2	2	2	2	2	3	1	2
M. blumei var. *zollingeri*	2	2	2	2	3	2	2	2	1	2	3	2	2	2	2	2	2	2	3	1	2
Groutiella kelantanense	2	1	2	1	2	2	1	2	1	4	2	2	2	2	2	1	2	2	3	1	1/2
G. tomentosa	2	1	2	1	2	2	1	2	1	4	3	2	2	2	2	1	2	2	3	1	1
Schlotheimia rubiginosa	3	2	2	2	3	2	2	1	1	4	3	2	2	1	1	1	2	3	1	1	2
S. wallisii	3	2	2	2	3	2	2	1	1	4	3	2	2	1	1	1	2	3	1	1	2

The level of variation of the data matrix based on morphological character is summarized in Table 6.2, while the strict consensus tree is shown in Fig. 6.3.

6.2.2. Phylogenetic inferences using molecular information

In general, topologies retrieved from different methods of analyzing the combined dataset are highly similar, except for some minor details. The Orthotrichaceae consistently formed a well-supported monophyletic assemblage (BS 99, PP 1). Meanwhile, the two subfamilies of Orthotrichaceae, viz., Macromitrioideae and Orthotrichoideae, resolved as well-supported clades (BS 100, PP 1 for Clade I, Orthotrichoideae; BS 95, PP 1 for Clade II, Macromitrioideae). The only Orthotrichaceae genus with an ambiguous position is *Leratia*, which in the present analyses is basal to the clade containing both subfamilies (in the MP analysis), or resolved in a trichotomy together with the two subfamilies (in the Bayesian analysis) (Figs. 6.1 and 6.2).

Within the Orthotrichoideae (Clade I in Figs. 6.1 and 6.2), *Codonoblepharon* forms a well-supported clade in both analyses (BS 96, PP 1). On the other hand, currently recognized species of *Zygodon* (group IA in Fig. 6.1 and 6.2) do not form a well-supported clade. In the *Zygodon* group, *Z. bartramioides* is resolved basally to a well-supported clade that comprises the other species of *Zygodon* together with *Pleurorthotrichum chilense* (i.e., unless the latter is transferred to *Zygodon*, the main part of *Zygodon* would be paraphyletic).

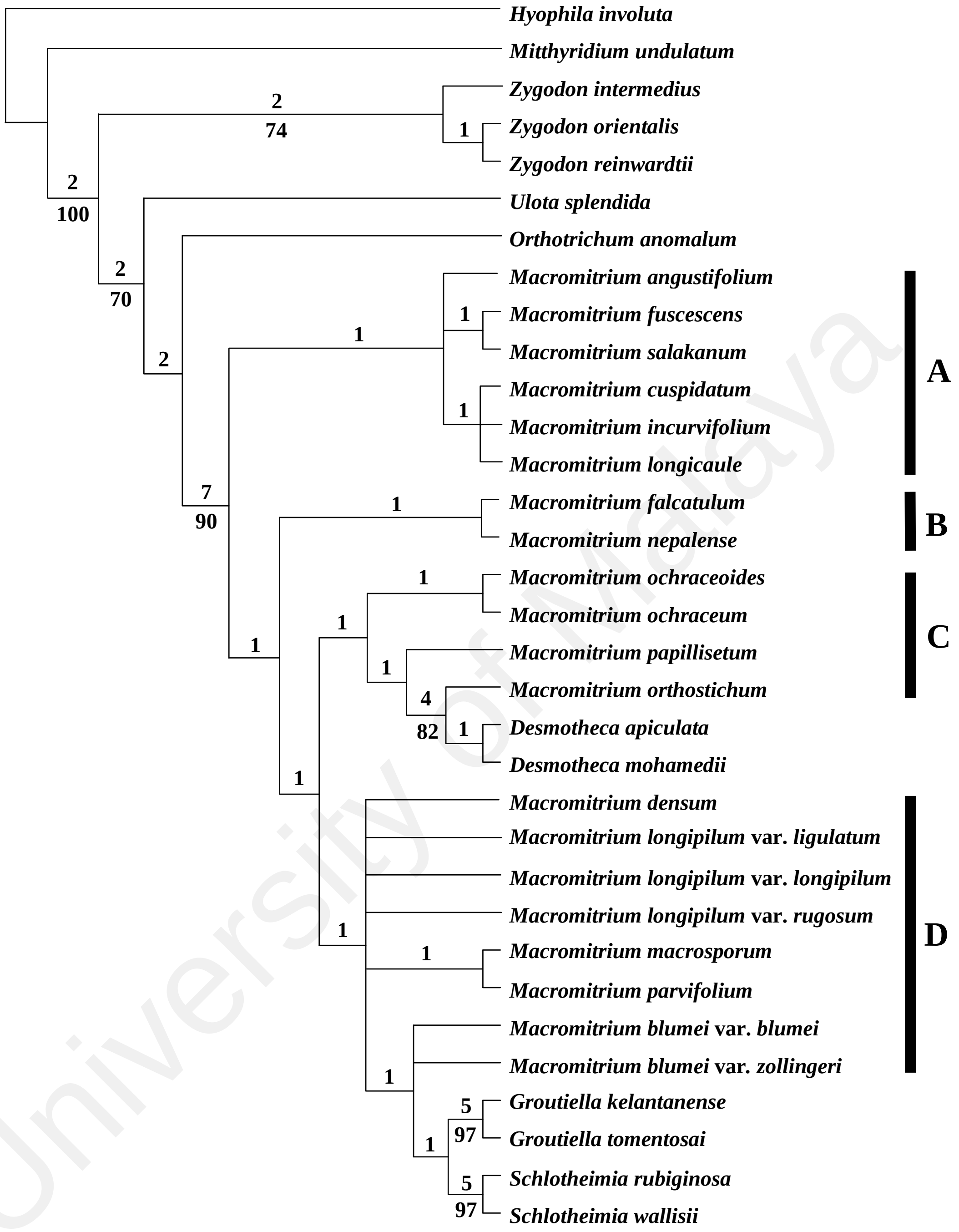

Figure 6.3. Strict consensus tree of 22 equally most parsimonious trees (MPTs) retained by the parsimony ratchet analysis based on morphological information (43 characters in 33 OTUs). Numbers above branches are estimated values of the decay index (>1) while those below branches are bootstrap support values (>70%). Labels A–D denote groups discussed in the text.

The other Orthotrichoideae members, viz., *Ulota*, *Sehnemobryum*, *Stoneobryum* and *Orthotrichum*, form the next larger clade in the subfamily (BS 88, PP 1). Within this assemblage, *Orthotrichum* is paraphyletic, its species split into groups IB (BS 99, PP 1) and IC (BS 94, PP 1) (Figs. 6.1 and 6.2). In group IB, *Ulota* also appears to be paraphyletic as one of its species (Fig. 6.1) clusters with *O. affine*, *O. lyelii* and *O. laevigatum*. In group IC, *Nyholmiella obtusifolia* and all the remaining *Orthotrichum* members form a monophyletic group with equivocal statistical support (PP 0.98, but poor BS value of 65). Meanwhile, *Sehnemobryum* and *Stoneobryum* form a well-supported terminal clade (BS 84, PP 0.97), sister to the *Nyholmiella*-*Orthotrichum* clade (group IC in Figs. 6.1 and 6.2).

Within the Subfamily Macromitrioideae (Clade II in Figs. 6.1 and 6.2), *Schlotheimia* is consistently resolved at the most basal position, as a well-supported monophyletic clade (BS 100, PP 1) that is sister to all other Macromitrioideae genera. These other Macromitrioideae, viz., *Cardotiella, Desmotheca, Leiomitrium, Macrocoma, Matteria, Macromitrium* and *Groutiella*, were resolved as a polytomy (Figs. 6.1 and 6.2). It is clear that *Macromitrium* as it is known is not monophyletic. The genera *Cardotiella*, *Desmotheca, Leiomitrium, Macrocoma*, and *Matteria* were not resolved (Fig. 6.1 and 6.2). In this assemblage, a clade (group IIB in Figs. 6.1 and 6.2) consisting of two *Macromitrium* branches (*M. levatum* and *M. blumei*) in a polytomy with *Groutiella* was resolved. Overall, in this subfamilial assemblage (Clade II in Figs. 6.1 and 6.2), the primary resolutions are not clear, so it is not possible to conclude on generic circumscriptions, including of *Groutiella* and *Macromitrium*. Only better resolution in further analyses that utilize more informative gene regions and involve a larger taxon set may be able to help resolve these relationships.

6.2.3. Cladistic analysis using morphological characters

The strict consensus tree from the maximum parsimony analysis of 43 morphological characters (Figure 6.3) has generally poor resolution. The nodes have poor bootstrap support, with most clades having a decay index of 2 or lower. However, both the outgroup taxa, viz., *Hyophila involuta* and *Mitthyridium undulatum*, resolved at the most basal position of the cladogram, with high support value (BS 100), so that it is clear the Orthotrichaceae are a monophyletic group. *Zygodon* (*Z. intermedius*, *Z. orientalis* and *Z. reinwardtii* in a well-supported clade), *Ulota* (*U. splendida*) and *Orthotrichum* (*O. anomalum*), are members of Subfamily Orthotrichoideae and were resolved basal to the Macromitrioideae members, so that all Macromitrioideae taxa form a monophyletic group.

In the present study, the monophyletic group representing Subfamily Macromitrioideae (BS 90, DC 7) is mostly represented by species placed in *Macromitrium*; whereas the other small genera, i.e., *Desmotheca*, *Groutiella* and *Schlotheimia*, are each only represented by two taxa. *Macromitrium* is clearly paraphyletic. It is not possible to make definitive conclusions regarding the circumscription of these smaller genera, which are embedded within the various clusters of so-called *Macromitrium* species, within a poorly resolved topology. A larger taxon sampling and additional morphological characters in future analyses may produce better resolution. The morphological analyses mainly support the overall monophyly of the Orthotrichaceae and the monophyly of the Subfamily Macromitrioideae.

Within this poorly resolved topology, it is not possible to be certain if characters that appear to divide *Macromitrium* into major groups are phylogenetically meaningful. For example, *Macromitrium* species treated in the present study can be generally separated into two apparently distinctive groups by their peristomial structure. The first group is made of *Macromitrium* species that have single peristome with teeth divided into 16 separate units and only connected at its basal portion, forming a low basal membrane. The second group is represented by *Macromitrium* species that are either gymnostomous or have single or double peristome with all their teeth fused into a low peristomial membrane. Very often, *Macromitrium* species with divided peristome teeth have branch leaves with pluripapillate upper laminal cells, whereas those *Macromitrium* species with fused peristome teeth are usually characterized by branch leaves with smooth, bulging to unipapillate upper laminal cells. Such characters, therefore, have to be viewed as possibly homoplasious (repeatedly present in different lineages and not unique to, and universally present in, a particular lineage only) or only taxonomically useful at the finer level.

6.3 Discussion

6.3.1. Subfamilial classification

The phylogenetic analyses based on both molecular and morphological datasets support the monophyly of the Orthotrichaceae (Figs. 6.1, 6.2, 6.3). The highly supported monophyletic clade representing this family is clearly distinguished from the outgroup including representatives from two sister-orders of the Orthotrichales (*Leptobyum wilsonii*, Splachnales, and *Hedwigia ciliata*, Hedwigiales). The present results are congruent with Goffinet et al.'s (1998 & 2004) findings that Orthotrichaceae is a well-defined family. Consequently, there is little support for the contention of Churchill & Linares (1995) and De Luna (1995) that the Orthotrichaceae have a polyphyletic origin.

The monophyly of the two groups recognized as subfamilies Orthotrichoideae and Macromitrioideae are also well-supported in all analyses. The two subfamilies can be easily distinguished by several morphological characters (the potential morphological synapomorphies). The Macromitrioideae clade is characterized by: plagiotropic stems, monopodial branches, differentiated stem and branch leaves, and cladocarpic perichaetia. Synapomorphies for the Orthotrichoideae clade include: orthotropic stems, sympodial branches, uniform stem and branch leaves, and acrocarpic perichaetia.

The doubtful position of *Leratia* has been addressed by Goffinet et al. (2004), who noted that both molecular and morphological studies (Crum, 1987) suggest a transitional position for the genus between the two major subfamilies in Orthotrichaceae. However, whether the genus should be accorded subfamilial position would depend on further critical examination of the phylogeny of Orthotrichaceae, with increased taxon sampling and the use of more informative gene regions.

6.3.2. The monophyly of genera in Orthotrichoideae

Codonoblepharon Schwägr. was established based on the old *Zygodon* section *Bryoides* Malta (see Müller, 1849; Brotherus, 1925; Malta, 1926) by Goffinet and Vitt (1998). There is considerable support for this change, as in the present analyses *Codonoblepharum* was consistently resolved as a well-supported monophyletic clade (BS 96, PP 1); that is sister to all other Orthotrichoideae genera (Figs. 6.1, 6.2). This corroborates the results of Goffinet et al. (2004), even though Allen (2002) and Calabrese (2006) have questioned the legitimacy of segregating *Codonoblepharum* from *Zygodon* based on a single morphological character, viz., the consistently smooth laminal cells in *Codonoblepharum* (pluripapillate in *Zygodon*).

On the other hand, Goffinet et al. (2004) also anticipated a wider generic concept for *Zygodon* by subsuming two genera (*Pentastichella* and *Pleurorthotrichum*) with cladocarpic habit, atypical for Orthotrichoideae, into that subfamily. This is supported by all phylogenetic analyses performed so far (Goffinet et al., 2004; present study), in which both *Pentastichella* (*P. pentasticha* sensu Goffinet et al., treated here as *Zygodon pentastichus*) and *Pleurorthotrichum* (represented by *P. chilense*) consistently form a monophyletic lineage with other *Zygodon* species.

Orthotrichum was clearly paraphyletic in the present study, with presently named species distributed into separate clades (Groups IB and IC in Figs. 6.1 and 6.2). This result agrees with the earlier cladistic phylogenetic conclusions of Goffinet et al. (1998, 2004). As currently understood, *Orthotrichum* is a highly speciose genus with many infra-generic groupings based on either single or a combination of character-states of the following: immersed or superficial stomata, exserted or immersed capsules, and various peristome structures (see Lindberg, 1879; Delogne, 1885; Venturi, 1887; Hagen, 1908; Brotherus, 1925). Vitt (1973) presented the first classification of the genus based on phylogenetic data and later revised by Lewinsky (1977, 1993). More recently, as many as eight informal groups were recognized by Lewinsky-Haapasaari & Hedenäs (1998) based on cytological information and cladistic analyses using morphological data.

As in Goffinet et al. (1998; 2004), the present study has affirmed that *Ulota*, characterized by superficial (phaneroporic) stomata, is nested within a clade (Group IB in Figs. 6.1 and 6.2) together with several phaneroporic *Orthotrichum* taxa (*Orthotrichum* subgenus *Phaneroporum*, represented by *O. laevigatum*; and subgenus *Gymnoporous*, represented by *O. affine* and *O. lyellii*). Since the first establishment of *Ulota* by Mohr (1806), its status had been contentious (Lindberg, 1879; Delogne, 1885; Venturi, 1887; Malta, 1927), and it has also been subsumed under *Orthotrichum* (Hooker & Greville, 1824; Schimper, 1848; Müller, 1849; Kindberg, 1897). Lewinsky

(1977) also pointed out that the strongly contorted leaf habit and plicate calyptra with deep-incised bases that were used to distinguish *Ulota* from *Orthotrichum* were in fact highly variable among the species and of little taxonomical utility.

In spite of this, *Ulota* and *Orthotrichum* are more consistently differentiated by cytological characteristics. The chromosome number for *Ulota* species is typically n=10 or more (Fritsch, 1991), except *U. japonica*, which has n = 8–10 (Yano, 1951, 1957). On the other hand, phaneroporic *Orthotrichum* spp. appear to consistently have n=6 (Lewinksy, 1993). A shared ancestry for *Orthotrichum* and *Ulota* has been suggested by Goffinet et al. (1998 & 2004) and the present study follows Goffinet et al. (2004) in preferring to maintain a distinct *Ulota* based on cytological differences from *Orthotrichum*. More representatives of both phaneroporic *Orthotrichum* and *Ulota* will need to be included in future phylogenetic analyses, and further informative gene regions explored, to clarify these taxonomic relationships.

Meanwhile, several cryptoporic *Orthotrichum* species. (i.e., with immersed stomata) were resolved in a monophyletic terminal clade together with three other genera, viz., *Nyholmiella*, *Sehnemobryum* and *Stoneobryum* (Group IC in Fig. 6.1 and 6.2). The cryptoporic *Orthotrichum* spp. included subgenus *Pulchella* (represented by *O. alpestre*) and subgenus *Orthotrichum* (represented by *O. anomalum, O. crassifolium* that was once treated under *Muelleriella*, and *O. jetteae*). *Nyholmiella* and *Sehnemobryum* have superficial stomata, whereas *Stoneobryum* has immersed stomata, but all were recently segregated from *Orthotrichum*. Not only are these genera morphologically related to *Orthotrichum* (Group IC in Fig. 6.3), their phylogenetic relatedness to *Orthotrichum* (Group IC in Figs. 6.1 and 6.2) also demonstrates that the subgeneric delimitations in use for *Orthotrichum* as well as characters for delimiting genera and groups, are questionable.

In conclusion, *Orthotrichum* is accepted here as a polyphyletic entity, while the status of *Nyholmiella, Sehnemobryum, Stoneobryum* and *Ulota* as distinct genera cannot be fully ascertained until further phylogenetic evidence is possible with a larger taxonomic sampling and the use of more informative gene regions.

6.3.3. Generic circumscription within Macromitrioideae

The strongly supported monophyly and basal position of *Schlotheimia* among Macromitrioideae (Clade II in Figs. 6.1 & 6.2) has also been noted by Goffinet et al. (1998; 2004). Goffinet & Vitt (1998) proposed a tribal position for it, viz., Schlotheimieae Goffinet. *Schlotheimia* is a considerably large genus in the Orthotrichaceae, with its highest diversity in the South America and Madagascar (Vitt, 1989). The genus is distinct due to the following characters: a) large, smooth, mitrate-campanulate calyptra with broadly lobed base; b) well-developed double peristome of 16 exostome teeth and 16 endostome segments either opposite or alternate to each other; c) generally smooth laminal cells (prorulose cells restricted to basal lamina in Malesian species). Smooth calyptra, well-developed double peristome teeth, and smooth laminal cells are the plesiomorphic (ancestral) characters recognized for Orthotrichaceae by Goffinet & Vitt (1998), so this basal position of *Schlotheimia* in the Macromitrioideae may well reflect this. In addition, there is a higher average difference in nucleotide bases (based on the rbcL region) between *Schlotheimia* and other Macromitrioideae genera (Goffinet et al., 1998), which suggests a longer evolutionary divergence of the genus from the main lineage.

Cardotiella has naked calyptra with broadly lobed base and well-developed double peristome teeth, and was thought to be evolutionarily closer to *Schlotheimia* (Vitt, 1981b; Allen, 2002). It is a small genus (7 species) in the tropical America, South Africa, Madagascar and the Mascarene Islands (Vitt, 1981b). However, the genus *Cardotiella* appears to be closer to *Macromitrum,* within the same robustly supported clade, either in a nested position (Goffinet et al., 1998) or unresolved (present study: Figs. 6.1 and 6.2). Morphologically, the genus is unique among Macromitrioideae and readily recognized by the combination of *Macromitrium*-like plant habit, decurrent leaf base and the *Schlotheimia*-like sporophyte. Thus, *Cardotiella* is treated here as a genus distinct from *Macromitrium* and related genera.

Another genus that appears unresolved among *Macromitrium* and its relatives is *Desmotheca* (Clade II, Figs. 6.1 and 6.2). *Desmotheca* is a small genus restricted to South East Asia (Vitt, 1990), distinguished by the following characters: dimorphic sterile and fertile branches, sessile and gymnostomous capsule, and mitrate and hairy calyptra that only covers the operculum. The genus has been removed to section *Cryptocarpon* of *Macromitrium* by Müller (1845) but is more commonly recognized as a good genus and placed in its own subfamily, Pseudo-Macromitrioideae Broth. (Fleischer, 1904; Brotherus, 1925; Walther, 1983) or Desmothecoideae Crum (Crum 1987). Vitt (1990) has argued that Macromitrioideae would become paraphyletic by the exclusion of genus *Desmotheca*. His argument was supported by later molecular phylogenetic studies, in which *Desmotheca* consistently was clustered with other Macromitrioideae (except *Schlotheimia*) (Goffinet et al. 1998, 2004; Hu et al., 2008; present study).

The two *Desmotheca* species were resolved in a terminal clade nested among *Macromitrium* in the present cladistic analysis using morphological characters (Fig. 6.3). *Desmotheca* appears to be most closely related to *M. orthostichum*, and share such character-states as pentastichous leaves (found on fertile branches for *Desmotheca* species), generally short laminal cells at leaf base, and short calyptra and phaneroporic stomata. However, such a close association is rejected by the molecular analyses, especially with Bayesian inference, which show *Desmotheca* and *M. orthostichum* as unresolved independent entities (Fig. 6.1) or the latter clustering with other *Macromitrium* taxa. The phylogenetic analysis used for the morphological dataset merely had a cladistic function (indicating relatedness by shared similarities) as evolutionary directions (ancestral vs. advanced states) and character weights were not indicated. *Desmotheca* is clearly distinguished from *M. orthostichum* and relatives by its dimorphic sterile and fertile branches and the immersed capsule that has its seta reduced into a junction between capsule and foot. In contrast, the branches are uniform and the capsule always exerted by adistinctly formed seta in *M. orthostichum* and relatives.

Leiomitrium, *Macrocoma* and *Matteria* are morphologically related genera. *Matteria* was previously *Macrocoma* subgenus *Trachyphyllum* (Broth.) Vitt (Goffinet and Vitt (1998). *Leiomitrium* is monotypic and resembles *Macrocoma* in many ways, including having imbricate leaves on branches, uniformly rounded and strongly unipapillate leaf cells, long ocrea, mitrate, plicate and hairy calyptrae (Vitt, 1981). Unlike *Macrocoma* and *Matteria*, laminal cells in *Leiomitrium* are not always unipapillate, but with a tendency to have 2–3 papillae developed on the laminal cells (Vitt, 1981). *Leiomitrium* is also recognized by its unique peristome structure, more similar to *Ulota* (Orthotrichoideae) than any Macromitrioideae, with exosotome teeth fused into 8 pairs and 16 free endostome segments (Vitt, 1980). *Leiomitrium* has been described as having a "*Ulota*-like capsule and peristome, but *Macromitrium*-like branching" by Vitt (1981) and is retained here as a distinct genus among the Macromitrioideae.

Macrocoma, was formerly included under *Macromitrium,* either as section (Müller, 1845) or subgenus (Brotherus, 1925) until 1944, when Grout made it a genus. It is morphologically related to *Macromitrium* but is distinguished by its widely spaced branches covered by imbricate leaves and the uniformly rounded to elliptic leaves cells that are either smooth, bulging or unipapillate (Grout, 1944; Vitt, 1980). Phylogenetically, the genus appears unresolved with *Macromitrium* and other *Macromitrium* related genera in both present and earlier studies (Goffinet et al., 1998).

Groutiella is a segregate of *Macromitrium* (Hornschuch, 1840) but is also considered as *Macromitrium* section *Micromitrium* by Mitten (1869). It was raised to the genus *Micromitrium* Schimp. ex Besch. (1872) and later transferred to *Craspedophyllum* Grout (1946), and finally was named *Groutiella* Crum & Steere (1950). The genus is most diverse in the neotropics, where 12 out of the known 14 species are found. *Groutiella* is distinguished from *Macromitrium* mainly by the bordered leaf base, and the short, naked calyptra that ends in several broad and rounded lobes. In molecular phylogenetic studies, *Groutiella* has always been resolved as nested among *Macromitrium* taxa (Goffinet et al., 1998; Hu et al., 2008). In the present study, *Groutiella* was part of a clade that included *M. levatum* and two varieties of *M. blumei* (Group IIB in Figs. 6.1 and 6.2).

Groutiella is related to some *Macromitrium* species by its peristome teeth structure, but it appears to also have unique character-states, such as a limbidium at leaf base and the short calyptrae that only covers the operculum and which ends in several broad and rounded lobes, features that are never present in *Macromitrium* generally. As *Macromitrium* is presently polyphyletic in its circumscription, and little resolution was obtained for clarifying the positions of several related genera including *Groutiella*, no firm taxonomic conclusions may be drawn prior to more critical studies as pointed out in previous sections.

6.3.4. The genus **Macromitrium**

Goffinet et al. (1998) has already suggested that *Macromitrium* is paraphyletic or polyphyletic, although they used very few *Macromitrium* taxa in their analysis with the *rbc*L (chloroplast) region. The present phylogenetic analyses included more species which were expected to reveal infra-generic relationships among *Macromitrium* spp. in Malaysia. The genus is not monophyletic and some grouping of species is apparent.

Within such a scenario, it is necessary to identify what may be the typical *Macromitrium* group. Although the type of the genus *Macromitrium*, *M. aciculare* Brid., is not included in the present study, all its key morphological features are found in members of Group A in Fig. 6.3 (analysis of morphological characters), which largely corresponds to Group IIC in Figs. 6.1 and 6.2 (molecular phylogenetic analyses). This group of taxa may therefore be considered the type alliance. Nomenclaturally, it is necessary to note that this group (*Macromitrium s.str.*) also corresponds well with the *Macromitrium* subgenus *Haplodontiella* of Fleischer (1904), who created this for taxa with single and divided peristome teeth. [This implies, too, that if subgenera are possible to recognize, then the type-including subgenus should be better named subgenus *Macromitrium*.] However, the composition of this putative typical group is by no means unequivocal. *Macromitrium incurvifolium* was resolved outside of Group IIC in the Maximum parsimony analysis (Fig. 6.1) but clustered with other members of this group in the Bayesian Inference analysis (Fig. 6.2). Morphologically, however, *M. incurvifolium* is well justified to be a member of this cluster, Group IIC (Fig. 6.2).

Fleischer (1904) created *Macromitrium* subgenus *Diplohymenium* for taxa with double peristome and teeth fused into a peristomial membrane. In the present molecular phylogenetic analyses, members of this subgenus were resolved in Figs. 6.1 and 6.2 as Group IIA (*M. orthostichum*, *M. ochraceoides*, *M. ochraceum*) and Group IIB (*M. levatum*, *M. blumei*), As such, the subgenus circumscription is, again, polyphyletic. Morphological circumscriptions may also remain difficult, as this subgenus was resolved in different clades in Fig. 6.3 (the morphological analysis) as Group C (corresponding to section *Cometium* Mitt. as accepted by Fleischer, 1904) and Group D (which corresponds to the section *Epilimitrium* erected by Fleischer in the same publication).

The phylogenetic relationship of the members in Group B, viz. *M. falcatulum* and *M. nepalense*, with other *Macromitrium* species is not clear at the moment. Both species are not represented in the molecular phylogenetic analyses and morphologically they resemble members of Group A, by having divided peristome; and members of Group C by having tuberculate basal laminal cells and densely hairy calyptra.

Sectional circumscriptions may be further considered. Mitten (1869) proposed *Macromitrium* section *Leiostoma* to include species with smooth theca and small to large rounded mouth. At the same time he erected section *Goniostoma* for species with intensely coloured theca and puckered capsule mouth. Mitten's sectional concepts were slightly modified by Brotherus (1925), who considered section *Leiostoma* to have double peristome teeth often fused into a peristomial layer, and section *Goniostoma* to have single peristome teeth where only an exostome is present. Most *Macromitrium* species treated in the present study were placed under section *Leiostoma* in Brotherus (1925), except *M. macrosporum* and *M. parvifolium* (treated under section *Goniostoma*) and *M. orthostichum* (section *Cometium*, a smaller section erected by Mitten, 1873).

The present cladistic analysis based on morphological characters appears to suggest that *Macromitrium* taxa in Malaysia segregate into several distinctive groups based on peristomial structure. On this basis, section *Leiostoma* appears to be paraphyletic and is represented by different lineages with divided peristome teeth (Groups A and B in Fig. 6.3) or fused peristome teeth (parts of Groups C and D in Fig. 6.3). Section *Goniostoma* does not appear to represent a natural group because its members (viz., *M. macrosporum* and *M. parvifolium*) cluster with other *Macromitrium* spp. that have fused peristome teeth (Groups C and D in Fig. 6.3). The original character-states used to define section *Goniostoma* (capsules with dark colour and puckered mouth) vary across different populations of a particular species, as revealed in the present study. A study of Australasian *Macromitrium* by Ramsay & Vitt (1986) also regarded puckered capsule mouth as a homoplasious character present in unrelated *Macromitrium* species, although prevalent in a specific group.

Macromitrium section *Cometium* was first created by Mitten (1873) to accommodate *M. orthostichum* and related taxa. Fleischer (1904) expanded Mitten’s sectional concept by dividing it into subsections *Micro-Cometium* and *Macro-Cometium*. Subsection *Macro-Cometium* was created for taxa that are large with branch leaves that are not five-ranked inserted on branches, although both subsections are characterized by papillose seta and densely hairy calyptra with toothed hairs. Present finding agrees with Fleischer (1904)’s suggestion that *M. ochraceum* and *M. ochraceoides* (the larger members of subsection

Macro-Cometium) were resolved sister to *M. orthostichum* (which represents the smaller species of subsection *Micro-Cometium*) (Figs. 6.2 & 6.3). Morphologically, *Macromitrium papillisetum,* a Bornean endemic species known only from its type, is positioned in between members of subsections *Macro-Cometium* and *Micro-Cometium* (Fig. 6.3). Like *M. orthostichum, M. papillisetum* has small plant size and oblong branch leaves. Nevertheless, its spirally inserted branch leaves and distinctly incrassate basal laminal cells with lumen narrower than its cell walls, do not support its placement within subsection *Micro-Cometium*. As such, it is also very difficult to have much confidence in the way finer-level grouping (such as subsections within sections) has been circumscribed.

The usefulness of taxonomic characters can be difficult to determine. Both molecular (Figs. 6.1, 6.2) and morphological analyses (Fig. 6.3) merely demonstrate the rare Malaysian endemic *M. ochraceum* and the widespread Malesian *M. ochraceoides* as a closely related pair of taxa. Their relationship could perhaps be further indicated by morphological character-states. Vitt (1984) and Vitt & Ramsay (1985) have recognized aristate leaf apex and long-excurrent costa as apomorphic (derived) characters for Australasian *Macromitrium*. This may support the suggestion that *M. ochraceoides* (restricted to Mount Trus Madi, Mount Kinabalu and Mount Tambuyokon in Sabah, north Borneo), which has an aristate leaf apex with long-excurrent costa, is derived from *M. ochraceum*, which has an acuminate apex with percurrent costa. In spite of this tenable suggestion, aristate leaf apices may have evolved in parallel among different *Macromitrium* groups. In the present study, this character is represented in almost every major clade of the morphological tree in Fig. 6.3: *M. cuspidatum* of Group A (representing subgenus *Haplodontiella*); *M. ochraceoides* of Group C (representing subgenus *Diplohymenium* section *Cometium*); and *M. longipilum* and its variety in

Group D (representing subgenus *Diplohymenium* section *Epilimitrium*). Piliferous leaf apices are also present in the two *Schlotheimia* species included in the present analysis, as well as in the other subfamily, Orthotrichoideae (e.g., *Orthotrichum armatum* Lewinsky & Van Rooy; Lewinsky, 1993). Thus, it would be appropriate to consider aristate or piliferous leaf apices as a homoplasious character (present in multiple lineages and not unique to a particular clade).

In fact, Vitt (1982) has considered parallel evolution as a significant factor in the evolution of the Orthotrichaceae. Another peculiar example is the fragile leaf tips that characterize *Groutiella tomentosa* and *Macromitrium angustifolium*. This is also present in *Macrocoma lycopodioides* (Schwägr.) Vitt, *Macromitrium fragilicuspis* Müll. Hal. and *Schlotheimia angustata* Mitt., and is believed to be an apomorphic character that has arisen separately in different Macromitrioideae genera, possibly due to selection toward xerophytism (Vitt, 1982).

Among Group D taxa (Fig. 6.3), *M. blumei* and *M. longipilum* are treated as members of *Macromitrium* section *Epilimitrium* by Fleischer (1904). The remaining ones, viz., *M. densum, M. macrosporum* and *M. parvifolium,* were not classified by Fleischer (1904) and they (as well as *M. longipilum*) have not been represented in molecular phylogenetic analyses. However, their position within Group D (Fig. 6.3) may seem to be supported by shared morphological character-states shared among taxa in the clade (see 6.2.3). For example, *M. blumei*, *M. densum* and *M. parvifolium* have branch leaves that are tightly whorled on branches and which appear rope-like. This character, however, may be homoplasious and could have evolved independently among different *Macromitrium* taxa, as well as other Malesian Macromitrioideae such as *Groutiella* and *Schlotheimia*.

The sectional concepts proposed by Mitten (1869) and later accepted by Brotherus (1925) are generally too broad and fail to reflect many of the evolutionary traits among the *Macromitrium* taxa that are treated in the present study. In fact, the four *Macromitrium* groups identified in the present study (Fig. 6.3) better correspond to Fleischer (1904)’s infrageneric classification. However, for a genus with pantropical distribution, a much complete picture of the phylogeny will only be obtained when taxonomic sampling adequately covers the morphological variation and geographical distribution, and informative gene regions are employed.

CHAPTER 7

GENERAL CONCLUSIONS

Overall, a total of 30 taxa in six genera of the Orthotrichaceae were investigated in the present study. Among these, two species, viz., *Desmotheca mohamedii* and *Groutiella kelantanense*, and two varieties, viz., *Macromitrium longipilum* var. *ligulatum* and *M. longipilum* var. *rugosum*, are proposed as new to science. Two new country records are reported: *M. densum* from Peninsular Malaysia and *M. parvifolium* from Borneo. Despite many synonymies that have been previously recorded and newly listed in the present study, 22 out of the 36 names that have been reported for Peninsular Malaysia and Borneo (Mohamed & Tan, 1988; Damanhuri, 2000; Suleiman et al., 2006) are maintained. In addition, three Orthotrichaceae taxa are synonymised under two species that were formerly not known to Malaysia, viz., *M. aspericuspis* and *M. kinabaluense* are reduced to the synonym of *M. macrosporum*, and *Ulota hattorii* is considered a synonym of *U. splendida*.

7.1 Systematic position and delimitation of Malaysian Orthotrichaceae genera

Among the six Orthotrichaceae genera reported for Malaysia, *Ulota* and *Zygodon* are members of Orthotrichoideae, while *Desmotheca*, *Groutiella*, *Macromitrium* and *Schlotheimia* belong to the Macromitrioideae. Their position within subfamilies and the monophyly of the Orthotrichaceae are very well supported in the present phylogenetic analyses using both molecular and morphological characters; this was also the case previously (Goffinet et al., 1998, 2004; Hu et al., 2008). *Zygodon* is well distinguished from *Ulota* by the pluripapillate upper laminal cells, smooth calyptra, reduced double peristome which often appears gymnostomous, and separate (not fused) exostome teeth (if these are present). *Ulota* is characterized by having uni- to bipapillate upper laminal cells, hairy calyptra, a well-developed double peristome where the exostome is always fused in pairs, forming 8 pairs of geminate teeth. Phylogenetically, members of *Zygodon* are resolved as a monophyletic group separated from other Orthotrichoideae genera. *Ulota* is phylogenetically closely related to phaneroporic species of *Orthotrichum* and these two groups consistently form a clade in all analyses (Goffinet et al., 2004; present study).

Among the Malaysian Macromitrioideae, *Schlotheimia* is very well-defined with all its members consistently forming a well-supported monophyletic group that is sister to all other Macromitrioideae genera (Goffinet et al., 1998, 2004; present study). Morphologically, the genus is easily distinguished from other Macromitrioideae genera by having large, smooth, mitrate-campanulate calyptra with a broadly lobed base, well-developed double peristome teeth with 16 exostome teeth and 16 endostome segments that are either opposite or alternate to each other. On the other hand, the phylogenetic relationships among *Desmotheca*, *Groutiella* and *Macromitrium*, as well as other *Macromitrium* related genera, remain unclear, as there was generally poor resolution in the phylogenetic study using molecular information. Morphologically, *Desmotheca* is unique in the Orthotrichaceae by its dimorphic sterile and fertile branches. Apart from this, the genus is also readily distinguished from *Macromitrium* and related genera by a combination of the following characters: sessile gymnostomous capsule, and mitrate hairy calyptra that only covers the operculum. *Groutiella* resembles *Macromitrium* in most of its morphological features, and can only be distinguished from the latter by the presence of a bordered leaf base, and the short, naked calyptra that ends in several broad, rounded lobes.

Macromitrium, the largest genus of the family, is not monophyletic according to present phylogenetic results using both molecular and morphological characters. In general, *Macromitrium* species can be segregated into four distinctive groups based on morphological characters. *Macromitrium* members are first separated into two major groups by the difference in their peristomial structure, viz., divided peristome teeth that only fuse at its base, and fused peristome teeth that developed into a peristomial membrane. Very often, those *Macromitrium* species with divided peristome are usually associated with pluripapillate upper laminal cells, whereas those species with their peristome fused into a peristomial membrane are often characterized by smooth, bulging to unipapillate upper laminal cells.

Those with divided peristome teeth are further segregated into two groups. The first group is associated with the type of *Macromitrium* and has been recognized as *Macromitrium* subgenus *Haplodontiella* (or *Macromitrium s. str.*) by Fleischer (1904). This group is characterized by having pluripapillate upper laminal cells that are, however, smooth at the basal lamina (except *M. longicaule*, which is tuberculate at the basal lamina), and sparsely hairy calyptra. The second group has pluripapillate upper laminal cells that are tuberculate at the basal lamina, and strongly pilose calyptra. In fact, this second group resembles a transition form between *Macromitrium* subgenus *Haplodontiella* and *Macromitrium* section *Cometium* sensu Fleischer (1904), which is further mentioned below.

Likewise, *Macromitrium* species that have teeth fused into a peristomial membrane, or *Macromitrium* subgenus *Diplohymenium* as recognized by Fleischer (1904), can be further separated into two smaller groups. The first group has smooth, unipapillate and occasionally pluripapillate upperlaminal cells, but consistently have unipapillate to tuberculate basal lamina cells, densely pilose calyptra, and generally short but papillose seta; Fleischer (1904) referred this group to section *Cometium*. The second group corresponds to Fleischer (1904)'s section *Epilimitrium*, which largely includes members with smooth upper laminal cells and unipapillate to tuberculate basal laminal cells, naked calyptra, and generally long and smooth seta.

Current phylogenetic findings largely agree with the infrageneric groupings that were proposed by Fleischer (1904), but reject those of Mitten (1869) and Brotherus (1925). However, the above-mentioned subgroups are generally Asiatic in distribution and largely overlap in their geographical range. Thus, at the moment, it is impossible to reconcile their apparent phylogenetic and morphological distinctions with biogeography. In fact, present study only provides a regional perspective of the phylogeny of this speciose pantropical genus. A more complete picture of the phylogeny of *Macromitrium* would only be obtained with a more complete sampling of representatives of the various morphological variations, as well as the use of more informative gene regions.

7.2 Biogeographical and conservation considerations

In general, most Orthotrichaceae treated in the present study are mainly confined to the tropics, with rare extensions to the subtropics or even temperate regions. *Macromitrium angustifolium* which is distributed in Malesia, Pacific Islands and South China is also known as far north as Honshu, Japan (Noguchi, 1967) and *M. orthostichum* that has been reported from North Island in New Zealand (as *M. wellingtonianum*; Vitt, 1983). Three of the 30 Orthotrichaceae taxa treated here are pantropical in distribution, viz., *Groutiella tomentosa*, *Zygodon intermedius* and *Z. reinwardtii*. *Macromitrium orthostichum* has a very wide paleotropical distribution from tropical Africa

(Wilbraham, 2007) eastwards to the Pacific Islands. Apart from these, the remaining Orthotrichaceae taxa are mainly Asiatic in distribution.

Several Orthotrichaceae species are widely distributed in tropical Asia, from India in the west, eastward to the Pacific Islands, and even to tropical Australia; these include *M. fuscescens, M. incurvifolium* and *M. nepalense*. In fact, *M. nepalense* is more commonly found in the Indian subcontinent and Indochinese region, but only sporadically reported for the Malesian islands (Gangulee, 1976; Eddy, 1996). Slightly narrower in distribution are *Desmotheca apiculata, M. cuspidatum, M. falcatulum, M. macrosporum, M. salakanum*, which range from Indochina, Malesia to the Pacific Islands. *Macromitrium densum* is the only species that is restricted to continental Asia and does not extend to insular South East Asia. The species is common in Indochina and has been reported for Nepal (Gangulee, 1976), but its southern-most extension appears to be the northern states of Peninsular Malaysia. On the other hand, *M. blumei* (including var. *zollingeri*) is widespread and common in insular South East Asia but has its western-most limit in Flores, just across the Wallace's Line.

Nearly half of the Orthotrichaceae treated in the present study are restricted to Malesia. Among these, *M. longicaule, M. ochraceum* and *Schlotheimia wallisi* are rather widespread and common, whereas *M. longipilum* var. *longipilum, M. parvifolium, Ulota splendida*, and *Z. orientalis* are only known from some localities in the region. Seven taxa are endemic to Malaysia, among them, *D. mohamedii, M. longipilum* var. *ligulatum, M. longipilum* var. *rugosum* are found in both Peninsular Malaysia and Borneo island. Three species are endemic to Borneo, viz., *M. ochraceoides, M. papillisetum, Schlotheimia rubiginosa*, and there is also a species, *G. kelantanense*, endemic to Peninsular Malaysia.

In Malaysia, Orthotrichaceae are more commonly found in the highlands, both within the montane forest or in relatively open sites where surrounding humidity is still high. However, a small number, viz., *Desmotheca apiculata, D. mohamedii, Groutiella kelantanense*, *M. densum, M. falcatulum*, *M. incurvifolium* and *M. papillisetum,* are confined to lower elevations, usually in lowland forest. On the other hand, there are also species that are known to occupy a wide range of elevation, for instance, *G. tomentosa* and *M. fuscescens* have been frequently collected from both lowlands and mountains.

Those species that are confined to lowland habitats and which have narrow distributional ranges are more vulnerable to human disturbance and habitat clearance. Among them, *G. kelantanense*, a proposed new species only known from the Gua Musang area, Kelantan, Peninsular Malaysia, is believed to be associated with limestone formations and would be very much threatened by the increasing destruction of limestone mountains by quarrying activities. On the other hand, *M. papillisetum*, an endemic Bornean species only known from its type specimen, may already be extinct in the wild. Its type locality, Bettotan, Sandakan, was heavily logged in the 1920s, and the species has never been recollected again. Likewise, highland species are threatened by extensive land conversion for agricultural purposes or even recreational purposes. For instance, *M. longipilum* var. *longipilum* that was once common near the summit area of Mount Ulu Kali, Selangor (judging from the extensive collections prior to 1987), has not been collected again even with frequent searches made during the present study. The species may have become extinct in the summit area due to extensive site alteration associated with development of a casino-hotel complex and telecommunications facilities over the past twenty years, which has cleared much natural vegetation around the summit.

7.3 Some suggestions for future work

The circumscription of a number of Macromitrioideae genera, excluding *Schlotheimia*, is still poorly defined at the moment. Hence, exploration of other gene regions, including both coding and non-coding regions of the plastid, mitochondrial and nuclear genomes, that may be more informative, should be useful. Likewise, this should also better illuminate the phylogenetic relationships among species in *Macromitrium*, the largest genus in the Orthotrichaceae. In fact, the analyses carried out presently only involve a limited sampling of the taxa. Hence, increased taxon sampling, particularly from a wider geographical context, should benefit further phylogenetic studies required for a better systematic understanding of the large genus *Macromitrium*.

Although there are scattered taxonomic revisions based on morphology of this large and very variable genus from Australasia, the Neotropics, East Asia and Malesia, the African and west Asian *Macromitrium* taxa are still very poorly understood. Hence, there is also a need for more revisionary work to be carried out (especially in the western part of the paleotropics) before all information could be incorporated towards an overall understanding of the genus, especially of morphological variation within the genus. Studies of ontogenetic characters, for instance, those associated with the development of peristome teeth, pilose calyptra and laminal cell papillae, may provide useful information for a natural classification of *Macromitrium*.

REFERENCES

Akiyama, H., Yamaguchi, T. & Suleiman, M. (2001). The bryophyte flora of Kinabalu National Park (Sabah, Malaysia), based on the collections by Japan-Malaysia collaborative expeditions in 1997. *Nature & Human Activities* 6: 83-99.

Allen, B. (2002). *Moss flora of Central America. Part 2. Encalyptaceae-Orthotrichaceae*. Monogr. Syst. Bot. Missouri Bot. Gard. Vol. 90. 699 p.

Anderson, L.E. (1980). Cytology and reproductive biology of mosses. In: Taylor, R.J. & Leviton, A.E. (eds.), *The Mosses of North America.* AAS Pacific Division, San Francisco. Pp. 37-76.

Anderson, L.E. & Crum, H. (1958). Cytotaxonomic studies on mosses of the Canadian Rocky Mountains. *Bull. Natl. Mus. Canada* 160: 1-89.

Arnott, G.A.W. (1825). Disposition Méthodique des Espèces de Mousses. *Mém. Soc. Hist. Nat. Paris.* 2: 1-410.

Bartram, E.B. (1936). Bornean mosses, principally from Mount Kinabalu. *Philipp. J. Sci.* 61: 235-250.

Bartram, E.B. (1939). Mosses of the Philippines. *Philipp. J. Sci.* 68: 1-437.

Bartram, E.B. (1942). Third Archbold Expedition mosses from the Snow Mountains, Netherlands New Guinea. *Lloydia* 5: 245-292.

Beckert, S., Muhle, D., Pruchner, D. & Knoop, V. (2001). The mitochondrial *nad2* gene as a novel marker locus for phylogenetic analysis of early land plants: A comparative analysis in mosses. *Mol. Phylogenet. Evol.* 18: 117-126.

Bell, N.E., Quandt, D., O'Brien, T.J. & Newton, A.E. (2007). Taxonomy and phylogeny in the earliest diverging pleurocarps: square holes and bifurcating pegs. *Bryologist* 110: 533-560.

Bescherelle, É. (1872). Prodromus bryologiae Mexicanae ou énumération des mousses de Mexique. *Mém. Soc. Sci. Nat. Cherbourg.* 16: 144-256.

Borsch, T., Hilu, K.W., Quandt, D., Wilde, V., Neinhuis, C. & Barthlott, W. (2003). Non-coding plastid *trn*T-*trn*F sequences reveal a well resolved phylogeny of basal angiosperms. *J. Evol. Biol.* 16: 558-576.

Bridel, S.E. (1819). Methodus Nova Muscorum ad Naturae Normam Melius Instituta et Muscologiae Recentiorum Accommodata. *Muscologiae Recentiorum Supplementum Pars IV seu Mantissa Generum Specierumque Muscorum Frondosorum Univers*. Gotha. 221 p.

Brotherus, V.F. (1909). Musci. In: Engler, A. & K. Prantl (eds.), *Die natürlichen Pflanzenfamilien*. Teil I, Abt. 3. W. Engelmann, Leipzig. Pp. 265-1246.

Brotherus, V.F. (1912). Musci—Beiträge der Flora und Pflanzengeographie von Borneo. III. *Bot. Jahrb.* 49: 349-352.

Brotherus, V.F. (1925). Musci. In: Engler, A. & K. Prantl (eds.), *Die natürlichen Pflanzenfamilien*. Band 11. W. Engelmann, Leipzig. Pp. 1-542.

Brotherus, V.F. (1928). Musci—Beiträge zur Kenntnis der Flora Von Borneo. *Mitteil. Inst. Allg. Bot., Hamburg* 7: 115-140.

Brummit, R.K. & Powell, C.E. (eds.) (1992). *Authors of Plant Names*. Royal Botanic Gardens, Kew. 732 p.

Buck, W.R., Goffinet, B. & Shaw, A.J. (2000). Testing morphological concepts of orders of pleurocarpous mosses (Bryophyta) using phylogenetic reconstructions based on *trnL-trnF* and *rps4* sequences. *Mol. Phylogenet. Evol.* 16: 180-198.

Calabrese, G.M. (2006). A taxonomic revision of *Zygodon* (Orthotrichaceae) in southern South America. *Bryologist* 109(4): 453-509.

Cardot, J. (1897). Contribution a la Flore Bryologique de Java Mousses Recoltees par M.J. Massart. *Ann. Jard. Bot. Buitenzorg Suppl.* 1: 1-31.

Churchill, S.P. & Linares, E.L. (1995). Prodromus Bryologiae Novo-Granatensis. Introduccion a la Flora de Musgos de Colombia. Parte II. *Bibliotheca "Jose Jeronimo Triana"* 12: 455-924.

Clarke, G.C.S. (1979). Spore morphology and bryophyte systematics. In: Clarke, G.C.S. & Duckett, J.G. (eds.), *Bryophyte Systematics*. The Systematics Association Special Vol. 14. Pp. 231-250.

Cox, C.J. & Hedderson, T.A.J. (1999). Phylogenetic relationships among the ciliate arthrodontous mosses: evidence from chloroplast and nuclear DNA sequences. *Pl. Syst. Evol.* 215: 119-139.

Cox, C.J. & Hedderson, T.A.J. (2003). Phylogenetic relationships within the moss family Bryaceae based on chloroplast DNA evidence. *J. Bryol.* 25: 31-40.

Cox, C.J., Goffinet, B., Newton, A.E., Shaw, A.J. & Hedderson, T.A.J. (2000). Phylogenetic relationships among the diplolepideous-alternate mosses (Bryidae) inferred from nuclear and chloroplast DNA sequences. *Bryologist* 103: 224-241.

Crosby, M.R., Magill, R.E., Allen, B. & He, S. (1999). *A Checklist of the Mosses*. Missouri Botanical Garden, St. Louis. 306 p.

Crum, H. (1972). A taxonomic account of the Erpodiaceae. *Nova Hedwigia* 23: 201-224.

Crum, H. (1987). *Leratia* and its place in the Orthotrichaceae, subfamily Macromitrioideae. *Mem. New York Bot. Gard.* 45: 602-606.

Crum, H. & Anderson, L.E. (1981). *Mosses of Eastern North America*. Vol. 1. Columbia University Press, New York. 663 p.

Crum, H.A. & Steere, W.C. (1950). Additions to the moss flora of Panama. *Bryologist* 53: 139-152.

Damanhuri, A. (2000). Mosses of Belum Forest Reserve, Perak, Peninsular Malaysia. *Malay. Nat. J.* 54(3): 211-221.

Damanhuri, A. & Maideen, H. (2001). Mosses of Perlis State Park at Wang Kelian, Perlis, Peninsular Malaysia. In: Faridah-Hanum, I., Osman, K. & Latiff, A. (eds.), *Biodiversity and management of Perlis State Park—physical, biological and social environments of Wang Mu*. Perlis Forestry Department, Kangar. Pp. 239-249.

De Luna, E. (1995). The circumscription and phylogenetic relationships of the Hedwigiaceae (Musci). *Syst. Bot.* 20(3): 347-373.

Delogne, C.-H. (1885). Flore Cryptogamique de Belgique (suite). Tribue 11. Grimmiaceae. *Ann. Soc. Belge Microscop.* 9: 7-220.

Dening, K. (1935). Untersuchungen über sexuellen Dimorphismus der Gametophyten bei heterothallischen, Laubmosen. *Flora, Jena* 30: 57-86.

Dixon, H.N. (1916). On a collection of Bornean mosses made by the Rev. C.H. Binstead. *J. Linn. Soc., Bot.* 43: 291-323.

Dixon, H.N. (1924). New species of mosses from the Malay Peninsula. *Bull. Torrey Bot. Club* 51: 225-259.

Dixon, H.N. (1926). A list of the mosses of the Malay Peninsula. *Gard. Bull. Straits Settlem.* 4: 1-46.

Dixon, H.N. (1932a). Classification of mosses. In: Verdoorn, F. (ed.), *Manual of Bryology*. Martinus Nijhoff, Hague. Pp. 397-412.

Dixon, H.N. (1932b). On the moss flora of Siam. *J. Siam Soc., Nat. Hist. Suppl.* 9(1): 1-51.

Dixon, H.N. (1935). A contribution to the moss flora of Borneo. *J. Linn. Soc., Bot.* 50: 57-140.

Doyle, J.F. & Doyle, J.L. (1990). Isolation of plant DNA from fresh tissue. *Focus* 12(1): 13-15.

Dozy, F. & Molkenboer, J.H. (1844). Muscorum Frondosorum Novae Species ex Archipelago Indico et Japonia. *Ann. Sc. Nat. Bot.*, Ser. 3, 2: 299-320.

Dozy, F. & Molkenboer, J. H. (1861). *Bryologia Javanica seu descriptio muscorum frondosorum Archipelagici Indici iconibus illustrata*. Vol. 1. A.W. Sythoff, Leiden. 161 p.

Duckett, J.G., Schmid, A.M. & Ligrone, R. (1998). Protonemal morphogenesis. In: Bates, J.W., Ashton, N.W. & Duckett, J.G. (eds.), *Bryology for the Twenty-first Century*. Maney Publishing, London. Pp. 223-246.

Eddy, A. (1996). *A handbook of Malesian mosses.* Vol. 3. HMSO, London. 277 p.

Edward, S.R. (1979). Taxonomic implications of cell patterns in Haplolepideous moss peristomes. In: Clarke, G.C.S. & Duckett, J.G. (eds.), *Bryophtye Systematics*. The Systematics Association Special Vol. 14. Pp. 317-346.

Ernst-Schwarzenbach, M. (1936). Zur heterosporie in der Laubmoos gattung *Macromitrium*. *Verh. Schweiz. Naturf. Ges.* 117: 310-311.

Ernst-Schwarzenbach, M. (1939). Zur kenntnis der sexuellen dimorphismus der Laubmoss. *Arch. Julius Klaus-Stift. VererbForsch.* 14: 362-474.

Ernst-Schwarzenbach, M. (1943). The sexual dimorphism of the tropical mosses of the genus *Macromitrium*. *Farlowia* 1: 195-198.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783-791.

Felsenstein, J. (1991). *PHYLIP (Phylogeny Inference Package).* Version 3.4. Program distributed by the author. University of Washington, Washington.

Fleischer, M. (1900). *Musci Archipelagi Indici*, exsiccata series III: no. 101-150. Batavia.

Fleischer, M. (1904). *Die Musci der Flora von Buitenzorg*. Vol. 2. Leiden: E.J. Brill. Pp. 381-643.

Fleischer, M. (1914). Laubmoose. In: Resultats de I'Expedition scientifique neerlandaise à la Nouvelle-Guinee. *Nova Guinea* 12: 109-128.

Fleischer, M. (1920a). Natürliches system der Laubmoose. *Hedwigia* 61: 390-400.

Fleischer, M. (1920b). Über die entwicklung der zwergmännchen aus sexuell differenzierten sporen bei den Laubmoosen. *Ber. dt. bot. Ges.* 38: 84-92.

Frahm, J.-P., Frey, W., Kurschner, W.H. & Menzel, M. (1990). *Mosses and liverworts of Mount Kinabalu*. Sabah Parks Publication no. 12. Sabah Parks Trustees, Kota Kinabalu. 91 p.

Fritsch, R. (1991). Index to bryophyte chromosome counts. *Bryophyt. Biblioth.* 40: 1-352.

Fröhlich, J. (1962). Musci novi Malesiani collecti a Dre Guil. Meijer. *Rev. Bryol. Lichenol.* 31: 91-94.

Gangulee, H.C. (1976). *Mosses of eastern India and adjacent regions*. Vol. 5. Calcutta. Pp. 1135-1462.

Goffinet, B. (1997a). *Circumscription and Phylogenetic Trends in the Orthotrichales (Bryopsida).* Ph.D. dissertation, unpublished, University of Alberta, Canada.

Goffinet, B. (1997b). The Rhachitheciaceae: Revised circumscription and ordinal affinities. *Bryologist* 100: 425-439.

Goffinet, B. (1998). A reconsideration of the affinities of *Kleioweisiopsis*, *Pleurozygodontopsis*, *Trigonodictyon* and the Microtheciellaceae (Bryopsida, Orthotrichales). *J. Bryol.* 20: 69-82.

Goffinet, B. & Buck, W.R. (2004). Systematics of the Bryophyta (mosses): from molecules to a revised classification. In: Goffinet, B., Hollowell, V.C. & Magill, R.E. (eds.), *Molecular Systematics of Bryophytes*. Monogr. Syst. Bot. Missouri Bot. Gard. Vol. 98. Pp. 205-239.

Goffinet, B. & Shannon, R.K. (2002). On the occurrence of an extensive but deciduous prostome in *Orthotrichum obtusifolium*. *Bryologist* 105(3): 349-352.

Goffinet, B. & Vitt, D.H. (1998). Revised generic classification of the Orthotrichaceae based on a molecular phylogeny and comparative morphology. In: Bates, J.W., Ashton, N.W. & Duckett, J.G. (eds.), *Bryology for the Twenty-first Century*. Maney Publishing, London. Pp. 143-159.

Goffinet, B., Bayer, R.J. & Vitt, D.H. (1998). Circumscription and phylogeny of the Orthotrichales (Bryopsida) inferred from rbcL sequence analyses. *Amer. J. Bot.* 85(9): 1324-1337.

Goffinet, B., Cox, C.J., Shaw, A.J. & Hedderson, T.A.J. (2001). The Bryophyta (mosses): systematic and evolutionary inferences from an *rps*4 gene (cpDNA) phylogeny. *Ann. Bot.* 87: 191-208.

Goffinet, B., Shaw, A.J., Anderson, L.E. & Mishler, B.D. (1999). Peristome development in mosses in relation to systematics and evolution. V. Diplolepideae: Orthotrichaceae. *Bryologist* 102(4): 581-594.

Goffinet, B., Shaw, A.J., Cox, C.J., Wickett, N.J. & Boles, S.B. (2004). Phylogenetic inferences in the Orthotrichoideae (Orthotrichaceae, Bryophyta) based on variation in four loci from all genomes. In: Goffinet, B., Hollowell, V.C. & Magill, R.E. (eds.), *Molecular Systematics of Bryophytes*. Monogr. Syst. Bot. Missouri Bot. Gard. Vol. 98. Pp. 270-289.

Goode, J.A., Stead, A.D. & Duckett, J.G. (1993). Studies of protonemal morphogenesis in mosses II. *Orthotrichum obtusifolium* Brid. *J. Bryol.* 17(3): 409-419.

Grout, A.J. (1903). *Orthotrichum*. *Bryologist* 6(1): 4-13.

Grout, A.J. (1908). Some relations between the habitats of mosses and their structure. *Bryologist* 6: 97-100.

Grout, A.J. (1944). Preliminary synopsis North American *Macromitriae*. *Bryologist* 47: 1-22.

Grout, A.J. (1946). Orthotrichaceae. *North American Flora*. Vol. 15A. New York Botanical Garden, Bronx. Pp. 1-62.

Guo, S.L., Enroth, J. & Koponen, T. (2007). Bryophyte flora of Hunan Province, China 11: Orthotrichaceae (Musci). *Ann. Bot. Fennici* 44: 1-34.

Guo, S.L., Enroth, J. & Virtanen, V. (2004). Bryophyte flora of Hunan Province, China 9: *Ulota gymnostoma sp. nov.* (Orthotrichaceae, Musci). *Ann. Bot. Fennici* 41: 459-463.

Guo, S.L., Tan, B.C. & Virtanen, V. (2006). Taxonomic and morphometric comments on *Macromitrium blumei*, *M. zollingeri* and *M. annamense* (Orthotrichaceae, Bryophyta). *Nova Hedwigia* 82: 467-482.

Guo, S.L., Cao, T., Tan, B.C. & Song, G.-Y. (2007). Taxonomic notes Asian species of Orthotrichaceae (Bryopsida): *Macromitrium* with gymnostomous capsules. *Gard. Bull. Singapore* 58(2): 155-178.

Hagen, I. (1908). Forarbejder til en norsk Iovmosflora. I. Orthotrichaceae. *Kongel. Norske Vidensk. Selsk. Skr. (Trondheim)* 13: 1-100.

Hall, T.A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids. Symp.* 41: 95-98.

Hedderson, T.A.J., Cox, C.J. & Gibbings, J.G. (1999). Phylogenetic relationships of the Wardiaceae (Musci): evidence from 18s rRNA and *rps*4 gene sequences. *Bryologist* 102(1): 26-31.

Hedwig, J. (1790). *Descriptio et Adumbratio Microscopico-Analytica Muscorum Frondosorum*. Vol. 2. Leipzig. 112 p.

Hedwig, J. (1801). *Species Muscorum Frondosorum descriptae et tabulis aeneis LXXVII coloratis illustratiae. (Opus posthumum editum a F. Schwaegrichen).* Lipsiae. 352 p.

Herzog, T. (1916). Die Bryophyten meiner zweiten Reise durch Bolivia. *Biblioth. Bot.* 87: 1-347.

Higuchi, M., Arikawa, T. & Suleiman, M. (2008). Mosses of Mt. Kinabalu, Borneo, Malaysia. *Mem. Natl. Mus. Nat. Sci., Tokyo* 45: 93-104.

Hirohama, T. & Iwatsuki, Z. (1980). Surface ornamentation of rhizoids of the species of Bartramiaceae (Musci). *J. Hattori Bot. Lab.* 48: 259-275.

Holder, M. & Lewis, P.O. (2003). Phylogeny estimation: traditional and Bayesian approaches. *Nature Review* 4: 275-284.

Holmgren, P.K. & Holmgren, N.H. (1998) [continuously updated]. *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden’s Virtual Herbarium. http://sweetgum.nybg.org/ih/

Holttum, R.E. (1927). A list of mosses collected in the Botanic Gardens, Singapore. *Gard. Bull. Straits Settlem.* 4: 88-91.

Hooker, W.J. & Greville, R.K. (1824). Sketch of the characters of the species of mosses, belonging to the genera *Orthotrichum* (including *Schlotheimia*, *Micromitrion* [sic] and *Ulota*), *Glyphomitrion*, and *Zygodon*. *Edinburgh J.Sci.* 1: 110-113.

Hornschuch, C.F. (1840). Musci. In: Martius, C.F.P. (ed.), *Flora Brasiliensis*. Vol. I(2). R. Oldenbourg, Leipzig. Pp. 1-105.

Hu, T.Y., Gou, S.L. & Shi, X.L. (2008). Phylogenetic analysis of Orthotrichaceae on generus level based on three gene sequences including chloroplast *rbcL*. *J. East China Normal Univ. (Nat. Sci.)* 1: 129-138.

Huelsenbeck, J.P., Larget, B., Miller, R.E. & Ronquist, F. (2002). Potential applications and pitfalls of Bayesian inference of phylogeny. *Syst. Biol.* 51: 673-688.

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & Bollback, J.P. (2001). Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294: 2310-2314.

Inoue, S. (1979). A preliminary report on moss chromosome numbers. *Misc. Bryol. Lichenol.* 8(6): 109-113.

Iwatsuki, Z. (1959). A revision of the Japanese species of the genus *Ulota*. *J. Hattori Bot. Lab.* 21: 138-156.

Iwatsuki, Z. (1969). Bryological miscellanies XIX-XX. XIX. Some interesting mosses from North Borneo. *J. Hattori Bot. Lab.* 32: 269-287.

Kindberg, N.C. (1897). *European and North American Bryineae—Acrocarpous*. Linköpings Lithografiska, Linköping. Pp. 153-410.

Kurma, S.S. & Verma, S.K. (1983). Cytological observations on some West Himalayan mosses VII. *J. Bryol.* 12: 487-490.

La Farge-England, C. (1996). Growth form, branching pattern, and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. *Bryologist* 99(2): 170-186.

Lara, F., Mazimpaca, V. & Garilleti, R. (1999). *Orthotrichum acuminatum* H. Philib. new to the Canary Islands. *J. Bryol.* 21: 75.

Lewinsky, J. (1976). On the systematic position of *Amphidium* Schimp. *Lindbergia* 3: 227-231.

Lewinsky, J. (1977). The genus *Orthotrichum*, morphological studies and evolutionary remarks. *J. Hattori Bot. Lab.* 43: 31-61.

Lewinsky, J. (1984). The genus *Orthotrichum* Hedw. (Musci) in Australasia. A taxonomic revision. *J. Hattori Bot. Lab.* 56: 369-460.

Lewinsky, J. (1989). Does the Orthotrichaceous type of peristome exist? A study of peristome evolution in the genus *Orthotrichum* Hedw. with a possible derivation of the haplolepideous peristome. *J. Hattori Bot. Lab.* 67: 335-363.

Lewinsky, J. (1990). *Zygodon* Hook. & Tayl. in Australasia: a taxonomic revision including SEM-studies of peristomes. *Lindbergia* 15: 109-139.

Lewinsky, J. (1992). The genus *Orthotrichum* Hedw. (Orthotrichaceae, Musci) in Southeast Asia. A taxonomic revision. *J. Hattori Bot. Lab.* 72: 1-88.

Lewinsky, J. (1993). A synopsis of the genus *Orthotrichum* Hedw. (Musci, Orthotrichaceae). *Bryobrothera* 2: 1-59.

Lewinsky-Haapasaari, J. (1994). The genus *Pleurorthotrichum* Broth. *Lindbergia* 19: 11-24.

Lewinsky-Haapasaari, J. & Crosby, M.R. (1996). *Orthomitrium tuberculatum* (Orthotrichaceae), a new genus and species from Guizhou, China. *Novon* 6: 1-5.

Lewinsky-Haapasaari, J. & Hedenäs, L. (1998). A cladistic analysis of the moss genus *Orthotrichum*. *Bryologist* 101(4): 519-555.

Lindberg, S.O. (1879). *Musci Scandinavici in Systemate Novo Naturali Dispositi*. Uppsala. 50 p.

Malcom, B. & Malcom, N. (2007). Mosses and Other Bryophytes—An Illustrated Glossary. 2nd Edition. Micro-Optics Press, Nelson. 336 p.

Malta, V.N. (1926). Die gattung *Zygodon* Hook. *et* Tayl.—eine monographische studie. *Latv. Univ. Bot. Dārza Darbi* 1: 1-184.

Malta, V.N. (1927). Die *Ulota*—Arten Süd-Amerikas. *Acta Horti. Bot. Univ. Latviensis* 2: 165-208.

Maniselvan, P. & Kumar, S.S. (1999). Cytological observation on some South Indian species of *Macromitrium* Brid. *Cryptog. Bryol.* 20(3): 185-187.

Manuel, M.G. (1981). A generic moss flora of Peninsular Malaysia and Singapore. *Fed. Mus. J.* 26(2): 1-163.

Mitten, W. (1859). Musci India Orientalis: an enumeration of the mosses of the East Indies. *J. Proc. Linn. Soc., Bot.* 1: 1-171.

Mitten, W. (1869). Musci Austro-americani. *J. Linn. Soc. Bot.* 12: 1-659.

Mitten, W. (1873). New species of Musci collected in Ceylon by Dr. Thwaites. *J. Linn. Soc. Bot.* 13: 293-326.

Mitten, W. (1879). Musci. An account of the petrological, botanical and zoological collections made in Kerguelen's Land and Rodriguez during the transit of Venus expeditions carried out by order of her Majesty's government in the years 1874-1875. *Philos. Trans.* 168: 388-396.

Mogensen, G.S. (1981). The biological significance of morphological characters in bryophytes: the spore. *Bryologist* 84(2): 187-207.

Mohamed, H. (1987). The limestone moss flora of Malaya. *Symp. Biol. Hung.* 35: 649-663.

Mohamed, H. & Tan, B.C. (1988). A checklist of mosses of Peninsular Malaya and Singapore. *Bryologist* 91(1): 24-44.

Mohamed, H. & Yong K.T. (2007). The moss flora of the southwestern Endau-Rompin National Park, Johor, Malaysia. In: Mohamed, H. & Zakaria-Ismail, M. (eds.), *The forests and biodiversity of Selai, Endau-Rompin*. Johor Bahru: Perbadanan Taman Negara Johor. Pp. 75-89.

Mohamed, H., Tan, B.C., Yong K.T. & Geri, C. (2004). Mosses. In: Yong H.S., Ng, F.S.P. (eds.), *Sarawak Bau Limestone Biodiversity*. Sarawak Mus. J. Vol. 59. Pp. 179-186.

Mohamed, H., Yong K.T. & Bakar, B. (2003). Mosses of Gunung Serapi, Sarawak. *Trop. Bryol.* 24: 139-145.

Mohr., D.M.H. (1806). XXXI. Observation on *Orthotrichum* and *Neckera*, together with some other genera of mosses. *Ann. Bot.* 2: 532-547.

Möller, H. (1919). Beiträge zur mossflora Javas, Straits Settlements und Birmas. *Hedwigia* 60: 313-330.

Müller, C. (1845). Synopsis macromitriorum hactenus cognitorum. *Bot. Zeit. (Berlin)* 3: 521-526, 539-545.

Müller, C. (1849). *Synopsis Muscorum frondosorum omnium hucusque cognitorum*. I. Alb. Foerstner, Berlin. 812 p.

Müller, K. (2004). PRAP—calculation of Bremer support for large data sets. *Mol. Phylogenet. Evol.* 31: 780-782.

Müller, K.F. (2005). SeqState—primer design and sequence statistics for phylogenetic DNA data sets. *Applied Bioinformatics* 4: 65-69.

Nadot, S., Bajon, R. & Lejeune, B. (1994). The chloroplast gene *rps*4 as a tool for the study of Poaceae phylogeny. *Pl. Syst. Evol.* 191: 27-38.

Newton, A.E., Cox, C.J., Duckett, J.G., Wheeler, J.A., Goffinet, B., Hedderson, T.A.J. & Mishler, B.D. (2000). Evolution of the major moss lineages: phylogenetic analyses based on multiple gene sequences and morphology. *Bryologist* 103: 87-211.

Nishida, Y. (1978). Studies on the sporeling types in mosses. *J. Hattori Bot. Lab.* 44: 371-454.

Nixon, K.C. (1999). The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistic* 15: 407-414.

Noguchi, A. (1967). Musci Japonici. VII. The genus *Macromitrium*. *J. Hattori Bot. Lab.* 30: 205-230.

Noguchi, A. (1968). Musci Japonici. VIII. The genus *Orthotrichum*. *J. Hattori Bot. Lab.* 31: 113-129.

Noguchi, A. (1972). Mosses of Thailand. *Lindbergia* 1: 169-183.

Noguchi, A. (1973). Mosses of Malaya collected by Dr. Hiroshi Inoue. *Bull. Natl. Sci. Mus., Tokyo* 16: 293-304.

Norris, D.H. & Robinson, H. (1981). *Stoneobryum*, a new genus of Orthotrichaceae from South Africa and southern Queensland. *Bryologist* 84: 95-99.

Nylander, J.A.A. (2004). *MrModeltest*. Version 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Paton, J.A. (1957). The occurrence, structure and functions of the stomata in British bryophytes. Part I. occurrence and structure. *Trans. Brit. Bryol. Soc.* 3: 228-242.

Philibert, H. (1884). Etudes sur le péristome. *Rev. Bryol.* 11: 81-87.

Philibert, H. (1888). Etudes sur le péristome. *Rev. Bryol.* 15: 6-93.

Posada, D. & Buckley, T.R. (2004). Model selection and model averaging in phylogenetics: advantages of Akaike Information Criterion and Bayesian Approaches over Likelihood Ration Tests. *Syst. Biol.* 53(5): 793-808.

Proctor, M.C.F. (1981). Physiological ecology of bryophytes. In: Schultze-Motel, W. (ed.) *Advances in bryology*. Vol. I. J. Cramer, Vaduz. Pp. 79-166.

Quandt, D. & Stech, M. (2005). Molecular evolution and secondary structure of the chloroplast *trn*L intron in bryophytes. *Mol. Phylogenet. Evol.* 36: 429-443.

Quandt, D., Bell, N.E. & Stech, M. (2007). Unravelling the knot: the Pulchrinodaceae *fam. nov.* (Bryales). *Nova Hedwigia Beiheft* 131: 21-39.

Ramsay, H.P. (1966). Sex chromosomes in *Macromitrium*. *Bryologist* 69(3): 293-311.

Ramsay, H.P. (1979). Anisospory and sexual dimorphism in the Musci. In: Clarke, G.C.S. & Duckett, J.G. (eds.), *Bryophyte Systematics*. Systematic Association Special Vol. 14. Pp. 281-316.

Ramsay, H.P. (1993). Chromosome studies on some Australasian Orthotrichaceae II. *Ulota* and *Zygodon* with additional studies on *Orthotrichum*, *Schlotheimia* and *Macromitrium*. *J. Hattori Bot. Lab.* 74: 183-192.

Ramsay, H.P. & Vitt, D.H. (1984). Distribution, cytology and sexuality of *Macromitrium* in the Pacific. *J. Hattori Bot. Lab.* 55: 13-33.

Ramsay, H.P. & Vitt, D.H. (1986). The *Macromitrium* complex in Australasia (Orthotrichaceae-Bryopsida). Part III. Cytotaxonomy. *J. Hattori Bot. Lab.* 61: 1-43.

Ramsay, H.P., Streimann, H. & Vitt, D.H. (1995). Cytological studies on mosses from Papua New Guinea 1: Introduction and the family Orthotrichaceae. *Trop. Bryol.* 11: 151-160.

Reese, W.D. (1997). Identity and lectotypification of *Orthotrichum undulatum* (Orthotrichaceae, Musci). *Taxon* 46: 249-252.

Reimers, H. (1954). Bryophyta. In: Melchior, H. & Wedermann, E. (eds.), *A. Engler's Syllabus der Pflanzenfamilien.* 12th edition. Gebrürder Bornträgger, Berlin. Pp. 218-268.

Robinson, H. (1971). A revised classification for the orders and families of mosses. *Phytologia* 21: 289-293.

Ronquist, F. & Huelsenbeck, J.P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572-1574.

Rodriguez, F., Oliver, J.L., Marin, A. & Menida, J.R. (1990). The general stochastic model of nucleotide substitution. *J. Theor. Biol.* 142: 485-501.

Rooy, J. & Wyk, A. E. (1992). A conspectus of the subfamily Macromitrioideae (Bryopsida: Orthotrichaceae) in Southern Africa. *Bryologist* 95(2): 205-215.

Sainsbury, G.O.K. (1955). A handbook of the New Zealand mosses. *Bull. Roy. Soc. New Zealand* 5: 1-490.

Sayre, G. (1977). Authors of names of bryophytes and the present location of their herbaria. *Bryologist* 80: 502-521.

Schimper, W.P. (1848). Recherches Anatomiques et Morphologies sur les Mousses. Strassbourg.

Shaw, J. (1986). Peristome structure in the Orthotrichaceae. *J. Hattori Bot. Lab.* 60: 119-136.

Shaw, J. & Rohrer, J.R. (1984). Endostomial architecture in diplolepideous mosses. *J. Hattori Bot. Lab.* 57: 41-61.

Simmons, M.P. & Ochoterena, H. (2000). Gaps as characters in sequence-based phylogenetic analyses. *Syst. Biol.* 49(2): 369-381.

Stafleu, F.A. & Cowan, R.S. (1976). *Taxonomic Literature*. Vol. 1: A–G. 2nd Edition. Bohn, Scheltema & Holkema, Utrecht. 1136 p.

Stafleu, F.A. & Cowan, R.S. (1979). *Taxonomic Literature*. Vol. 2: H–Le. 2nd Edition. Bohn, Scheltema & Holkema, Utrecht. 991 p.

Stafleu, F.A. & Cowan, R.S. (1981). *Taxonomic Literature*. Vol. 3: Lh–O. 2nd Edition. Bohn, Scheltema & Holkema, Utrecht. 980 p.

Stafleu, F.A. & Cowan, R.S. (1983). *Taxonomic Literature*. Vol. 4: P-SAK. 2nd Edition. Bohn, Scheltema & Holkema, Utrecht. 1214 p.

Stafleu, F.A. & Cowan, R.S. (1985). *Taxonomic Literature*. Vol. 5: Sal–Ste. 2nd Edition. Bohn, Scheltema & Holkema, Utrecht. 1066 p.

Stafleu, F.A. & Cowan, R.S. (1986). *Taxonomic Literature*. Vol. 6: Sti–Vuy. 2nd Edition. Bohn, Scheltema & Holkema, Utrecht. 1136 p.

Stafleu, F.A. & Cowan, R.S. (1988). *Taxonomic Literature*. Vol. 7: W–Z. 2nd Edition. Bohn, Scheltema & Holkema, Utrecht. 1136 p.

Stapf, O. (1894). On the flora of Mount Kinabalu, in North Borneo. *Trans. Linn. Soc. London, Bot.* 4(2): 69-261.

Staples, G.W., Imada, C.T., Hoe, W.J. & Smith, C.W. (2004). A revised checklist of Hawaiian mosses. *Trop. Bryol.* 25: 35-69.

Stech, M. (1999). A molecular systematic contribution to the position of *Amphidium* Schimp. (Rhabdoweisiaceae, Bryopsida). *Nova Hedwigia* 68 (3-4): 291-300.

Stech, M. & Frey, W. (2008). A morpho-molecular classification of the mosses (Bryophyta). *Nova Hedwigia* 86(1-2): 1-21.

Steenis, C.G.G.J. (1950). The delimination of Malaysia and its main plant geographical divisions. *Fl. Males.*, Ser. I, Vol. I: LXX-LXXV.

Suleiman, M., Akiyama, H. & Tan, B.C. (2006). A revised catalogue of mosses reported from Borneo. *J. Hattori Bot. Lab.* 99: 107-183.

Swofford, D.L. (2002). *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.

Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991). Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Mol. Biol.* 17: 1105-1109.

Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007). MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. *MBE* 24(8): 1596-1599.

Tan, B.C. (2005). New species records of Sri Lankan mosses. *Raff. Bull. Zool. Suppl.* 12: 5-8.

Taylor, E.C. (1962). The Philibert peristome articles. An abridged translation. *Bryologist* 65(3): 175-212.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997). The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucl. Acids Res.* 24: 4876-4882.

Tixier, P. (1971). A contribution to the bryological knowledge of Fraser's Hill station (Malaysia). *Gard. Bull. Singapore* 25: 335-353.

Tixier, P. (1980). Contribution to the bryological knowledge of Malaysia III. Cameron Highlands, mosses and epiphyllous liverworts. *Nova Hedwigia* 32: 377-392.

Touw, A. (1978). The mosses reported from Borneo. *J. Hattori Bot. Lab.* 44: 147-176.

Touw, A. (1992). A survey of the mosses of the Lesser Sunda Islands (Nusa Tenggara), Indonesia. *J. Hattori Bot. Lab.* 71: 289-366.

Touw, A. (2007). Original specimens kept in the Nationaal Herbarium Nederland (Universiteit Leiden Branch) of Asian and South American moss taxa published by F. Dozy, J.H. Molkenboer, R.B. van den Bosch and C.M. van der Sande Lacoste. *NHN-Electronic Publication* 1: 1-104.

Tsubota, H., Deluna, E., González, D., Ignatov, M.S. & Deguchi, H. (2004). Molecular phylogenetic and ordinal relationships based on analyses of a large-scale data set of 600 *rbcL* sequences of mosses. *Hikobia* 14: 149-170.

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

Tsubota, H., Nakao, N., Yamaguchi, T., Seki, T. & Deguchi, H. (2000). Preliminary phylogenetic relationships of the genus *Brotherella* and its allied genera (Hypnales, Musci) based on chloroplast *rbcL* sequence data. *J. Hattori Bot. Lab.* 87: 79-99.

Une, K. (1985a). Geographical distribution of male and female plants in species of *Macromitrium* Brid. (Musci: Orthotrichaceae) in Japan. *J. Hattori Bot. Lab.* 59: 515-521.

Une, K. (1985b). Sexual dimorphism in the Japanese species of *Macromitrium* Brid. (Musci: Orthotrichaceae). *J. Hattori Bot. Lab.* 59: 487-513.

Venturi, G. (1887). Orthotrichum. In: Husnot, T. (ed.), *Muscologia Gallica.* Vol. 1. Paris. Pp. 154-196.

Vitt, D.H. (1968). Sex determination in mosses. *The Michigan Botanist* 7: 195-203.

Vitt, D.H. (1972). A monograph of the genus *Drummondia*. *Canad. J. Bot.* 50: 1191-1208.

Vitt, D.H. (1973). A revision of the genus *Orthotrichum* in North America, North of Mexico. *Bryophyt. Biblioth.* 1: 1-208.

Vitt, D.H. (1976). A monograph of the genus *Muelleriella* Dusén. *J. Hattori Bot. Lab.* 40: 91-113.

Vitt, D.H. (1980). The genus *Macrocoma* I. Typification of names and taxonomy of the species. *Bryologist* 83(4): 405-436.

Vitt, D.H. (1981a). Adaptive modes of the moss sporophyte. *Bryologist* 84(2): 166-186.

Vitt, D.H. (1981b). The genera *Leiomitrium* and *Cardotiella* gen. nova (Orthotrichaceae). *J. Hattori Bot. Lab.* 49: 92-113.

Vitt, D.H. (1982a). The genera of Orthotrichaceae. *Beih. Nova Hedwigia* 71: 261-269.

Vitt, D.H. (1982b). On Neotropical Orthotrichaceae. *Beih. Nova Hedwigia* 71: 531-535.

Vitt, D.H. (1983). The New Zealand species of the pantropical genus *Macromitrium* (Orthotrichaceae: Musci): Taxonomy, phylogeny and phytogeography. *J. Hattori Bot. Lab.* 54: 1-94.

Vitt. D.H. (1984). Classification of the Bryopsida. In: Schuster, R.M. (ed.), *New Manual of Bryology*. Vol 2. Hattori Botanical Laboratory, Nichinan. Pp. 696-759.

Vitt, D.H. (1989). The genus *Schlotheimia* (Orthotrichaceae: Bryopsida) in Australia and New Zealand. *Bryologist* 92: 282-298.

Vitt, D.H. (1990). *Desmotheca* (Orthotrichaceae): Gondwanan fragmentation and the origin of a Southeast Asian genus. *Trop. Bryol.* 3: 79-88.

Vitt, D.H. (1993). Orthotrichaceae. In: Sharp, A.J., Crum H.A., Eckel, P.M. (eds.), *The moss flora of Mexico*. New York Botanical Garden, New York. Pp. 590-657.

Vitt, D.H. & Crum, H. (1970). *Groutiella tomentosa* new to the United States. *Bryologist* 73: 145-149.

Vitt, D.H. & Ramsay, H.P. (1985). The *Macromitrium* complex in Australasia (Orthotrichaceae, Bryopsida). Part I. Taxonomy and phylogenetic relationships. *J. Hattori Bot. Lab.* 59: 325-451.

Vitt, D.H., Koponen, T. & Norris, D.H. (1993). Bryophyte flora of the Huon Peninsula, Papua New Guinea. LIII. *Ulota* and *Schlotheimia* (Orthotrichaceae, Musci). *Acta Bot. Fennica* 148: 5-25.

Vitt, D.H., Koponen, T. & Norris, D.H. (1995). Bryophyte flora of the Huon Peninsula, Papua New Guinea. LV. *Desmotheca*, *Groutiella*, *Macrocoma* and *Macromitrium* (Orthotrichaceae, Musci). *Acta Bot. Fennica* 154: 1-94.

Walther, K. (1983). Bryophytina. Laubmoose. In: Gerloff, J. & Poelt, J. (eds.), *A. Engler's Syllabus der Pflanzenfamilien.* Aufl. 13, Vol. 2. Gebrüder Bornträger, Berlin. Pp. 1-108.

Werner, O., Ros, R.M., Cano, M.J. & Guerra, J. (2004). Molecular phylogeny of Pottiaceae (Musci) based on chloroplast *rps*4 sequence data. *Plant. Syst. Evol.* 243: 147-164.

Wijk, R., Margadant, W.D. & Florschütz, P.A. (1962). *Index Muscorum 2 (D–Hypnum)*. *Regnum Veg.* Vol. 26. 535 p.

Wijk, R., Margadant, W.D. & Florschütz, P.A. (1964). *Index Muscorum 3 (Hypnum–O)*. Regnum Veg. Vol. 33. 529 p.

Wilbraham, J. (2007). Taxonomic notes on the pantropical genera *Macromitrium* and *Macrocoma* (Bryopsida: Orthotrichaceae). *J. Bryol.* 29: 54-59.

Yano, K. (1951). On the chromosomes in some mosses I. *Bot. Mag. (Tokyo)* 64: 234-237.

Yano, K. (1957). Cytological studies on Japanese mosses III. Isobryales, Polytrichinales. *Me. Takada Branch, Niigata Univ.* 1: 129-159.

Yong, K.T., Damanhuri, A., Mohamed, H., Sadiah, H. & Idris, N. (2006). Towards a comprehensive moss flora of Gunung Jerai. In: Ismail, S.M., Ahmad, W.Y.W., Som, J.M., Muda, Y. & Latiff, A. (eds.), *Hutan Simpan Gunung Jerai, Kedah: Pengurusan, Persekitaran Fizikal dan Kepelbagaian Biologi*. Forestry Department of Peninsular Malaysia, Kuala Lumpur. Pp. 103-123.

Zander, R.H. (1993). Genera of Pottiaceae: Mosses of harsh environments. *Bull. Buffalo Soc. Nat. Sci.* 32: 1-378.

Zander, R.H. (1997). On mounting delicate bryophytes in glycerol. *Bryologist* 100(3): 380-382.

Zander, R.H. & Vitt, D.H. (1979). Gametophytic distinctions of *Zygodon* (Orthotrichaceae) and *Anoectangium* and *Leptodontium* (Pottiaceae) and the status of *Anoectangium rubrigemmium* of Hawaii. *Can. J. Bot.* 57: 292-296.