

A revision of the genus Leucobryum (Musci) in Asia

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To be published in  
the Journal of the Hattori Botanical Laboratory  
No. 72, 1992

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## I. Introduction

The genus Leucobryum is a group of whitish mosses as indicated by Latin epithet. Some species of Leucobryum form beautiful whitish green colonies and they are used for horticultural purposes in Japan (Inoue 1980, Ando & Matsuo 1984). Because of characteristic color of colonies, Leucobrya easily catch a collector's eye and numerous collections have been made in the world. According to Wijk et al. (1959-1969) and some additional literature, 189 species and 25 varieties have been described throughout the world.

The basic taxonomical characters of Leucobryum are the leaf structure with its peculiar combination of leucocysts (empty cells) and chlorocysts (chlorophyllose cells), and the dicranoid sporophyte. However, a large part of the leaf is occupied by a costa with multilayered cells, and the surface view of leaf cells is almost identical among all members of the genus. The characters of surface view of leaf cells (except for apical cells of the leaf) of Leucobryum are not useful for diagnostic characters, unlike most of the moss groups, and taxonomic distinction among the species of this genus have been unclear.

To date, 71 species and 7 varieties have been known

from Asia. The region of Asia in this study (Fig. I) corresponds with the locality abbreviations As 2-4 in Wijk et al. (1959-1969).

The purpose of this study is to revise all the known taxa of Asian Leucobryum, and secondly to find general taxonomic characters which reflect the phylogeny of the genus. In the course of this study, I examined ca. 3000 specimens deposited in various herbaria in addition to my own collections. The type specimens of 69 taxa deposited in 13 herbaria were also carefully examined. I also examined the specimens collected from Europe, America and Oceania to compare with Asian taxa. As a result, I recognized 19 taxa of Leucobryum in Asia.

## II. Acknowledgements

I wish to express my sincere gratitude to Prof. Z. Iwatsuki of Hiroshima University for introducing me to this field of work, and for constant guidance and encouragement during my study. I also wish to express my thanks to Dr. N. Nishimura for his valuable advice and kind help for literature. I am indebted to Dr. K. Une of Okayama Hakuryo High School for his kind cooperation in carrying out a study of sexuality and geographical distribution of Japanese Leucobryum. Many thanks are also due to Assoc. Prof. T.

Seki, Dr. G. Toyohara, Dr. T. Nakano, Dr. M. Higuchi and the colleagues of the Botanical Institute of Hiroshima University for their kind consideration and encouragement during this study.

Sincere thanks are extended to the directors and curators of the herbaria of the following institutions for their kind arrangements of the loan of type and other important specimens: Botanisches Museum, Berlin (B); Natural History Museum, London (BM); Royal Botanical Garden, Edinburgh (E); Farlow Herbarium, Harvard University, Cambridge (FH); Herbarium Universitatis Florentinae, Firenze (FI); Conservatoire et Jardin botaniques, Genève (G); Botanical Museum, University of Helsinki, Helsinki (H); Herbarium Haussknecht, Friedrich-Schiller-Universität, Jena (JE); Kanazawa University, Kanazawa (KANA); Kochi University, Kochi (KOCHI); Kyoto University Herbarium, Kyoto (KYO); Rijksherbarium, Leiden (L); Makino Herbarium, Tokyo Metropolitan University, Tokyo (MAK); Hattori Botanical Laboratory, Nichinan (NICH); National Herbarium of New South Wales, Sydney (NSW); New York Botanical Garden, New York (NY); Herbier du Laboratoire de Cryptogamie du Muséum National d'Histoire Naturelle, Paris (PC), and National Science Museum, Tokyo (TNS).

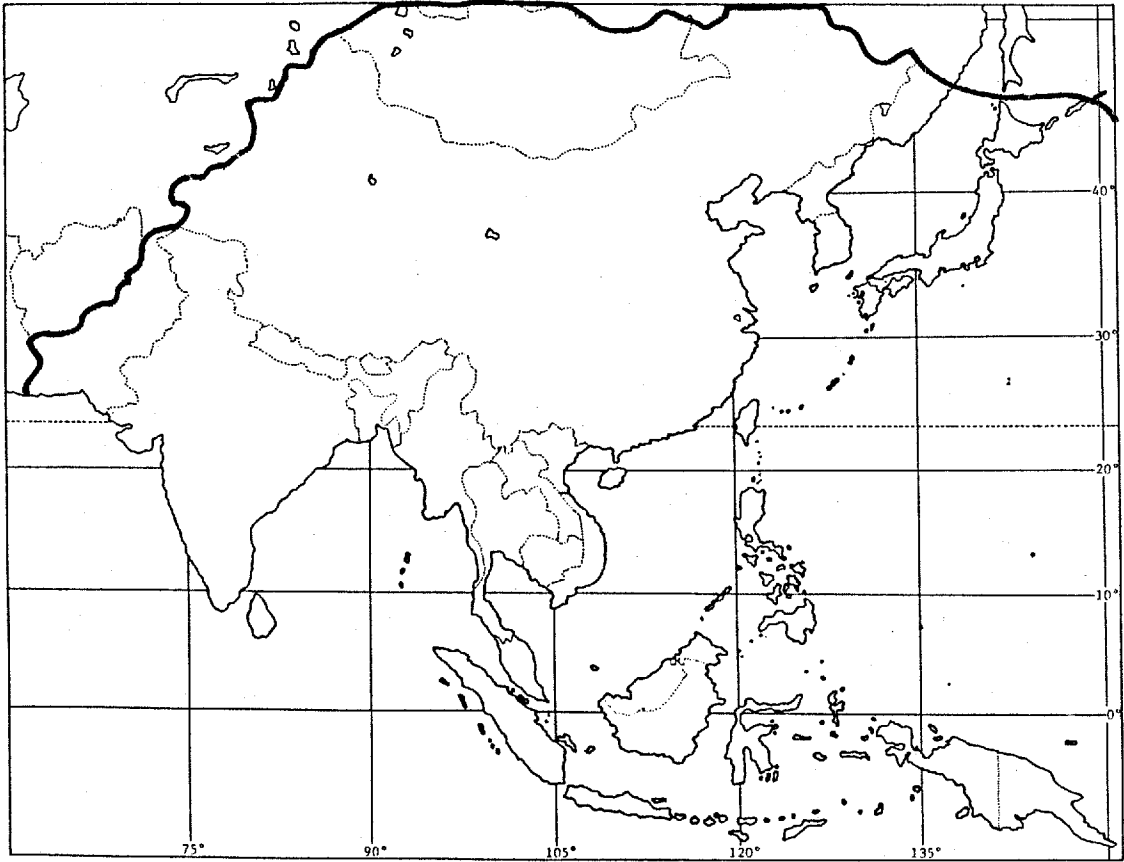


Figure 1. Map showing the study area.

### III. History

#### 1. Classification systems of leucobryoid genera

The genus Leucobryum was validly described by Hampe (1839). Before Hampe (1939), the taxa of Leucobryum were included in Dicranum, Bryum or Sphagnum because of their dicranoid sporophyte and whitish habits like Sphagnum. Leucobryum is characterized by its unique structure of leaves which are composed of leucocysts and chlorocysts. Schimper (1856) proposed Leucobryaceae which comprises Leucophanes, Octoblepharum and Arthrocorumus together with Leucobryum, all of them have leucobryoid leaves.

Eleven genera are currently known as leucobryoid mosses which belong to Leucobryaceae in a wide sense. However, the classification systems of leucobryoid genera are very variable by each taxonomists (Table 1). Cardot (1899) classified Leucobryaceae into four tribus: Leucobryeae, Leucophaneae, Octoblephareae and Arthrocormeae. Brotherus (1901) adopted Cardot's sense of Leucobryaceae with four tribus. Brotherus (1924) promoted each tribus to subfamilies, namely, Leucobryoideae, Leucophanoideae, Octoblepharoideae and Arthrocomoideae, and he placed Leucobryaceae (sensu Cardot) in Dicranales. The classification systems of Leucobryaceae by Cardot and



Table 1. Summary of various classification of genera with leucobryoid leaves

Cardot (1899)	Fleischer (1904)	Herzog (1926)	Andrews (1947)	Vitt (1984)	Robinson (1985, 1990)	Eddy (1990)	Yamaguchi (1992)
LEUCOBRYACEAE	LEUCOBRYACEAE	LEUCOBRYACEAE	DICRANACEAE (syn. Leucobryaceae)	LEUCOBRYACEAE	LEUCOBRYACEAE	LEUCOBRYACEAE	LEUCOBRYACEAE
Leucobryeae	Eu-leucobryeae	Leucobryoideae	Leucobryum	Leucobryum	Leucobryum	Leucobryum	Leucobryum
Leucobryum	Leucobryum	Leucobryum	(Syn. Cardotia)				
Ochrobryum	Schistomitriaceae	Ochrobryum	Ochrobryum	Ochrobryum	Ochrobryum	SCHISTOMITRIACEAE	Ochrobryum
Cladopodanthus	Cladopodanthus	Cladopodanthus	Cladopodanthus	Cladopodanthus	Cladopodanthus	Cladopodanthus	Cladopodanthus
Schistomitrium	Schistomitrium	Schistomitrium	Schistomitrium	Schistomitrium	Schistomitrium	Schistomitrium	Schistomitrium
	LEUCOPHANACEAE		CALYMPERACEAE (syn. Leucophanaceae)	CALYMPERACEAE		CALYMPERACEAE	CALYMPERACEAE
Octoblephareae	Octoblephareae	Octoblepharoideae	Octoblepharum	Octoblepharum	Octoblepharum	OCTOBLEPHARACEAE	Octoblepharum
Octoblepharum	Octoblepharum	Octoblepharum	Octoblepharum	Octoblepharum	Octoblepharum	Octoblepharum	Octoblepharum
Cardotia							
Arthrocormeae	Arthrocormeae	Arthrocormoideae	Arthrocormus	Arthrocormus	Arthrocormus	CALYMPERACEAE	Arthrocormus
Arthrocormus	Arthrocormus	Arthrocormus	Arthrocormus	Arthrocormus	Arthrocormus	Arthrocormus	Arthrocormus
Exodictyon	Exodictyon	Exodictyon	Exodictyon	Exodictyon	Exodictyon <sup>3</sup>	Exodictyon	Exodictyon
						Exostratum	
Leucophaneae	Leucophaneae	LEUCOPHANACEAE					
Leucophanes	Leucophanes	Leucophanes	Leucophanes	Leucophanes	Leucophanes	Leucophanes	Leucophanes
				Carinafolium <sup>1</sup>			

<sup>1</sup> Carinafolium was described by Williams (1931) as monotypic genus including only Carinafolium tatsi Williams. Bartram (1960) recombined C. tatsi with Octoblepharum as Q. tatsi (Williams) Bartr.

<sup>2</sup> Holomitriopsis and Steyermarkiella were described by Robinson (1965b) as monotypic genera.

<sup>3</sup> Ellis (1985) divided Exodictyon (sensu lato) into Exodictyon (sensu stricto) and Exostratum.

Brotherus were based on gametophytic characters, especially on cross-sectional features of leaves.

Fleischer (1904), considering peristome structure, divided Leucobryaceae (sensu Cardot) into two families, Leucobryaceae and Leucophanaceae. Fleischer (1904) placed Leucobryaceae (sensu Fleischer) with dicranoid peristome in Reihe Dicranoideae together with Dicranaceae and Fissidentaceae. At the same time, he placed Leucophanaceae with hyophiloid peristome in Reihe Hyophiloideae together with Syrrhopodontaceae and Calymperaceae.

Although Fleischer (1923) rearranged both Leucophanaceae and Leucobryaceae (sensu Fleischer) in Unterreich Leucobryineae (Reihe Dicranales), his principal consideration in which the Leucobryaceae (sensu Cardot) was divided into two groups was accepted by Andrews (1947), Vitt (1984) and others. Andrews (1947) included Leucobryaceae (sensu Fleischer) and Leucophanaceae in Dicranaceae and Calymperaceae respectively. Crosby and Magill (1981) compiled a list of genera including familial disposition based on the Andrew's system concerning leucobryoid genera. Vitt (1984) revived Leucobryaceae (sensu Fleischer) and disposed it in Dicranineae, and placed other leucobryoid genera in Calymperaceae (Pottineae). Ellis (1985) emended Leucophanoideae (Card.) Broth. and described Calymperaceae subfamily Leucophanoideae which includes Leucophanes,

Octoblepharum, Arthrocnemum, Exostratum and Exodictyon. I agree with classification of Vitt (1984) and Ellis (1985). Yamaguchi and Iwatsuki (1991) used subfamily Leucophanoideae in the study of New Caledonian moss flora.

## 2. History of the taxonomic studies of Asian Leucobryum

The first species of Leucobryum was described by Bridel (1798) as Sphagnum javense. The name Sphagnum javense became nomenclaturally valid by the publication of Schwägrichen (1823), and S. javense was combined with Leucobryum by Mitten (1859), namely, L. javense (Brid. ex Schwägr.) Mitt.

After that, a large number of taxa were described from Asia mainly by European bryologists. Main authorities who contributed to the descriptions of new taxa from Asia (cf. Fig. I for area of Asia in this study) were Dozy and Molkenboer (1845, 1854, 1855), Fleischer (1899, 1904), Bescherelle (1898) and Renauld and Cardot (1905). Dozy, Molkenboer and Fleischer made great contributions to taxonomic study of Leucobryum and related genera of Java, Sumatra and Borneo. Bescherelle, Cardot and Renauld described many taxa from Japan, China, India and neighboring regions. Seventy one species with seven varieties are currently known from Asia as shown in Table 2.

Iwatsuki (1966, 1977) and Iwatsuki and Noguchi (1979) reduced many species to the synonymy, and proved the

Table 2. Historical review of Asian Leucobryum<sup>1</sup>

- 
- Leucobryum glaucum (Hedw.) Ångström in Fries (1846)  
[Europe, N. America and Jamaica. Basionym: Dicranum glaucum Hedwig (1801). Also reported from China and Japan]
- L. javense (Brid. ex Schwägr.) Mitten (1859) [Java, Réunion. Basionym: Sphagnum javense Bridel ex Schwägrichen (1823)]
- L. candidum (Bridel ex P. Beauv.) Wilson (1854)  
[Australia. Basionym: Dicranum candidum Bridel ex Palisot de Beauvois (1805). Also reported from S. E. Asia]
- L. juniperoideum (Brid.) C. Müller (1845) [Tenerife and Réunion. Basionym: Dicranum juniperoideum Bridel (1826). Also reported from Japan, Taiwan, China and India]
- L. sanctum (Brid.) Hampe (1839) [Java. Basionym: Dicranum glaucum var. sanctum Bridel (1827)]
- L. piliferum (Dozy & Molk.) Jaeger (1873) [Java. Basionym: Cladopodanthus pilifer Dozy & Molkenboer (1845)]
- L. chlorophyllosum C. Müller (1851) [Sumbawa]
- L. mucronifolium Braun in C. Müller (1851) [Java]
- L. neilgherrense C. Müller (1854) [India]
- L. aduncum Dozy & Molkenboer (1854) [Java]
- L. pentastichum Dozy & Molkenboer (1854) [Java]
- L. holleanum Dozy & Molkenboer (1855) [Java]
- L. teysmannianum Dozy & Molkenboer (1855) [Java]
- L. boninense Sullivant & Lesquereux (1859) [Japan]
- L. bowringii Mitten (1859) [India, Sri Lanka and China]
- L. scabrum Sande Lacoste (1866) [Japan]
- L. triviale C. Müller (1869) [India]
- L. stenophyllum Bescherelle (1873) [New Caledonia. Also reported from New Guinea]
- L. naumannii C. Müller (1884) [New Guinea]
- L. auriculatum C. Müller in Geheeb (1889) [New Guinea]
- L. retractum Bescherelle (1893) [Japan]
- 

<sup>1</sup>Type locality is represented in square brackets.

Table 2. Continued

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<u>L. pachyphyllum</u>	C. Müller (1896)	[Hawaii. Also reported from New Guinea]
<u>L. papuense</u>	Paris (1896)	[New Guinea]
<u>L. ceylanicum</u>	(Besch.) Cardot (1901)	[Sri Lanka. Basionym: <u>Ochrobryum ceylanicum</u> Bescherelle (1897)]
<u>L. humillimum</u>	Cardot (1901)	[India. Basionym: <u>Ochrobryum wightii</u> Bescherelle (1897)]
<u>L. japonicum</u>	(Besch.) Cardot in Brotherus (1901)	[Japan. Basionym: <u>Ochrobryum japonicum</u> Bescherelle (1897)]
<u>L. arfakianum</u>	C. Müller ex Geheeb (1898)	[New Guinea]
<u>L. sericeum</u>	Brotherus ex Geheeb (1898)	[New Guinea]
<u>L. altiusculum</u>	Bescherelle (1898)	[Japan]
<u>L. brevicaule</u>	Bescherelle (1898)	[Japan]
<u>L. galeatum</u>	Bescherelle (1898)	[China]
<u>L. humile</u>	Brotherus ex Bescherelle (1898)	[Japan]
<u>L. lacteorum</u>	Bescherelle (1898)	[Japan]
<u>L. mittenii</u>	Bescherelle (1898)	[India]
<u>L. textorii</u>	Bescherelle (1898)	[Japan]
<u>L. wichurae</u>	Brotherus ex Bescherelle (1898)	[Japan]
<u>L. yamatense</u>	Bescherelle (1898)	[Japan]
<u>L. holleanum</u>	var. <u>fragilifolium</u> Fleischer (1899)	[Java]
<u>L. imbricatum</u>	Brotherus (1899a)	[India]
<u>L. nagasakense</u>	Brotherus (1899b)	[Japan]
<u>L. cuculliphyllum</u>	Fleischer (1904)	[Sri Lanka]
<u>L. scalare</u>	C. Müller ex Fleischer (1904)	[Java, Sumbawa, Singapore and Philippines]
<u>L. scalare</u>	var. <u>marschmeyeri</u> Fleischer (1904)	[Java]
<u>L. scalare</u>	var. <u>tjibodense</u> Fleischer (1904)	[Java]
<u>L. sumatranum</u>	Brotherus ex Fleischer (1904)	[Sumatra]
<u>L. uncinatum</u>	Fleischer (1904)	[Borneo]
<u>L. cucullifolium</u>	Cardot in Renauld & Cardot (1905)	[India and Nepal]
<u>L. deciduum</u>	Cardot in Renauld & Cardot (1905)	[Vietnam]

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Table 2. Continued

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<u>L. brotheri</u> Cardot in Renauld & Cardot (1905)	[Sumatra, Sulawesi, Sri Lanka and Japan]
<u>L. ferriei</u> Cardot in Renauld & Cardot (1905)	[Japan]
<u>L. flavulum</u> Cardot in Renauld & Cardot (1905)	[Sri Lanka]
<u>L. salmonii</u> Cardot in Renauld & Cardot (1905)	[China]
<u>L. scaberulum</u> Cardot in Renauld & Cardot (1905)	[China]
<u>L. siamicum</u> Bescherelle in Renauld & Cardot (1905)	[Siam]
<u>L. stenobasis</u> Cardot in Renauld & Cardot (1905)	[Himalaya, Sri Lanka]
<u>L. neilgherrense</u> var. <u>minus</u> Cardot (1905)	[Taiwan]
<u>L. confine</u> Cardot (1905)	[Taiwan]
<u>L. subsanctum</u> Brotherus (1907)	[Philippines]
<u>L. rhizophyllum</u> Warnstorff (1915)	[Japan]
<u>L. subscalare</u> Brotherus ex Potier de la Varde (1917)	[Cambodia]
<u>L. krempfii</u> Thériot (1919)	[Vietnam]
<u>L. cyathifolium</u> Dixon (1922)	[New Guinea]
<u>L. pulchrum</u> Brotherus (1928)	[Borneo]
<u>L. angustissimum</u> Brotherus (1929)	[China]
<u>L. armatum</u> Brotherus (1929)	[China]
<u>L. poilanei</u> Thériot (1929)	[Cambodia]
<u>L. perichaetiale</u> Dixon (1932a)	[Siam]
<u>L. scaberulum</u> var. <u>divaricatum</u> Dixon (1933)	[China]
<u>L. subsericeum</u> Dixon (1933)	[China]
<u>L. nakaii</u> Horikawa (1935)	[Japan]
<u>L. aduncum</u> var. <u>arnottii</u> Thériot (1936)	[Indes orientales]
<u>L. propaguliferum</u> (Dix.) Robinson (1965a)	[Sri Lanka and India. Basionym: <u>Ochrobryum propaguliferum</u> Dixon (1938)]
<u>L. novae-guineae</u> Bartram (1953)	[New Guinea]
<u>L. brassii</u> Bartram (1957)	[New Guinea]
<u>L. antarense</u> Zanten (1964)	[New Guinea]
<u>L. papuense</u> var. <u>pendulum</u> Zanten (1964)	[New Guinea]

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Table 2. Continued

---

<u>L. byssaceum</u>	C. Müller ex Johnson (1964)	[New Guinea]
<u>L. microleucophanoides</u>	Dixon ex Johnson (1964)	[Malay Penin.]

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Table 3. Taxonomic treatments of Japanese Leucobryum by Iwatsuki (1966, 1977) and Iwatsuki and Noguchi (1979)

---

Leucobryum bowringii Mitt.

Syn. L. confine Card.

L. nagasakense Broth.

L. yamatense Besch.

L. glaucum (Hedw.) Ångstr. in Fries

L. javense (Brid. ex Schwägr.) Mitt.

L. neilgherrense C. Müll.

Syn. L. altiusculum Besch.

L. boninense Sull. & Lesq.

L. brevicaule Besch.

L. ferriei Card. in Ren. & Card.

L. humile Broth. ex Besch.

L. japonicum (Besch.) Card. in Broth.

L. lacteorum Besch.

L. nakaii Hor.

L. retractum Besch.

L. rhizophyllum Warnst.

L. scaberulum Card. in Ren. & Card.

L. scabrum Lac.

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Table 4. Taxonomic treatment of Leucobryum juniperoideum of Japan by Yamaguchi and Iwatsuki (1988)

---

Leucobryum juniperoideum (Brid.) C. Müll.

Syn. L. altiusculum Besch.

L. brevicaule Besch.

L. ferriei Card. in Ren. & Card.

L. humile Broth. ex Besch.

L. japonicum (Besch.) Card. in Broth.

L. lacteorum Besch.

L. neilgherrense C. Müll. (specimens reported from Japan)

L. rhizophyllum Warnst.

L. textorii Besch.

---

Table 5. Taxonomic treatment of Malesian Leucobryum by Enroth (1989, 1990)

---

Leucobryum aduncum Dozy & Molk.

Syn. L. scalare C. Müll. ex Fl.

L. scalare var. marschmeyeri Fl.

L. scalare var. tjibodense Fl.

L. subscalare Broth. ex Vard.

L. bowringii Mitt.

Syn. L. brotheri Card. in Ren. & Card.

L. confine Card.

L. sericeum Broth. ex Geh. — L. bowringii var. sericeum (Broth. ex Geh.) Dix.

L. chlorophyllosum C. Müll.

L. javense (Brid. ex Schwägr.) Mitt.

Syn. L. brassii Bartr.

L. candidum (Brid. ex P. Beauv.) Wils.

L. cyathifolium Dix.

L. novae-guineae Bartr.

L. pentastichum Dozy & Molk. — L. candidum var. pentastichum (Dozy & Molk.) Dix.

L. teysmannianum Dozy & Molk.

L. uncinatum Fl.

L. neilgherrense C. Müll.

Syn. L. holleanum Dozy & Molk.

L. triviale C. Müll.

L. pulchrum Broth.

L. sanctum (Brid.) Hampe

Syn. L. arfakianum C. Müll. ex Geh.

L. papuense Par.

L. subsanctum Broth.

L. stenophyllum Besch.

Syn. L. byssaceum C. Müll. ex Johnson

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Table 6. Taxonomic treatment of Malesian Leucobryum by Eddy (1990)

---

Leucobryum aduncum Dozy & Molk. var. aduncum

L. aduncum var. scalare (Dozy & Molk.) A. Eddy

Basionym L. scalare C. Müll. ex Fl.

Syn. L. scalare var. marschmeyeri Fl.

L. scalare var. tjibodense Fl.

L. bowringii Mitt.

Syn. L. brotheri Card. in Ren. & Card.

L. sericeum Broth. ex Geh. — L. bowringii var. sericeum (Broth. ex Geh.) Dix.

L. candidum (Brid. ex P. Beauv.) Wils.

Syn. L. pentastichum Dozy & Molk. — L. candidum var. pentastichum (Dozy & Molk.) Dix.

L. teysmannianum Dozy & Molk.

L. javense (Brid. ex Schwägr.) Mitt.

Syn. L. antarense Zant.

L. brassii Bartr.

L. candidum (P. Beauv.) Wils.

L. cyathifolium Dix.

L. novae-guineae Bartr.

L. uncinatum Fl.

L. juniperoideum (Brid.) C. Müll.

Syn. L. holleanum Dozy & Molk.

L. neilgherrense C. Müll.

L. microleucophanoides Dix. ex Johnson

L. papuense Par.

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Table 6. Continued

- 
- L. sanctum (Brid.) Hampe var. sanctum  
Syn. L. auriculatum C. Müll. in Geh.
- L. sanctum var. arfakianum (C. Müll. ex Geh.) A. Eddy  
Basionym L. arfakianum C. Müll. ex Geh.  
Syn. L. papuense Par.  
L. subsanctum Broth.
- L. scabrum Lac.
- L. sumatranum Broth. ex Fl.  
Syn. L. pulchrum Broth.
-

occurrence of six species of Leucobryum in Japan (Table 3). Yamaguchi and Iwatsuki (1988) proposed that Leucobryum neilgherrense C. Müll. reported from Japan was identical with L. juniperoideum (Brid.) C. Müll. described from Canary Islands and Réunion Island (Table 4).

Enroth (1989, 1990) and Eddy (1990) re-examined Malesian taxa of Leucobryum. However, there are some difference of taxonomic treatments between them (Table 5, 6). As mentioned by Eddy (1990), taxonomic status of Asian Leucobrya is not settled. It is necessary to critically re-examine the type specimens and to clarify the taxonomic status of Leucobryum in Asia where the genus is one of the main constituents of bryoflora.

#### IV. Morphology

General morphology of Leucobryum species is described below and each character is discussed in view of its taxonomic value in the genus.

##### 1. Habit

Color of plants is yellowish- or whitish-green when moist and whitish when dry. Some taxa, such as L. bowringii and L. sumatranum, have more or less glossy appearances.

Most taxa of Leucobryum grow on soil and humus, and form colonies like cushions. Some taxa also grow on tree

trunks (e. g. Leucobryum arfakianum C. Müll. ex Geh.) or wet rocks (e. g. Leucobryum scabrum Lac.). The habitats and the growth habits are important characters for taxonomy of Leucobryum.

Figs. II-IV show plants of 19 taxa of Leucobryum in Asia. Each taxon differs in plant size, leaf arrangement.

Most species of perennial acrocarpous mosses continuously grow by innovations. However, the maximum size of plant is limited and variable among taxa. The variation of plant size seems to be depending on the branching pattern, amount of annual growth and habitat. Taxa with perichaetia terminal on lateral short branches, which continuously grow by elongation of main stems and without subfloral innovations, tend to be robust. They are L. javense and its varieties, L. scabrum and L. sumatranum. The plants growing in wet habitats tend to elongate. They are plants of L. scabrum growing on vertical rock faces splashed with water in streams, and plants of L. glaucum growing on wet humus in damp sites.

Leaf arrangement and posture are classified by manner of spreading, secundness and shape when dry. Leaves of some taxa, such as L. aduncum var. aduncum, L. aduncum var. teysmannianum and L. boninense, are arranged in five rows on stem. However, sometimes the pentastichous leaf arrangement

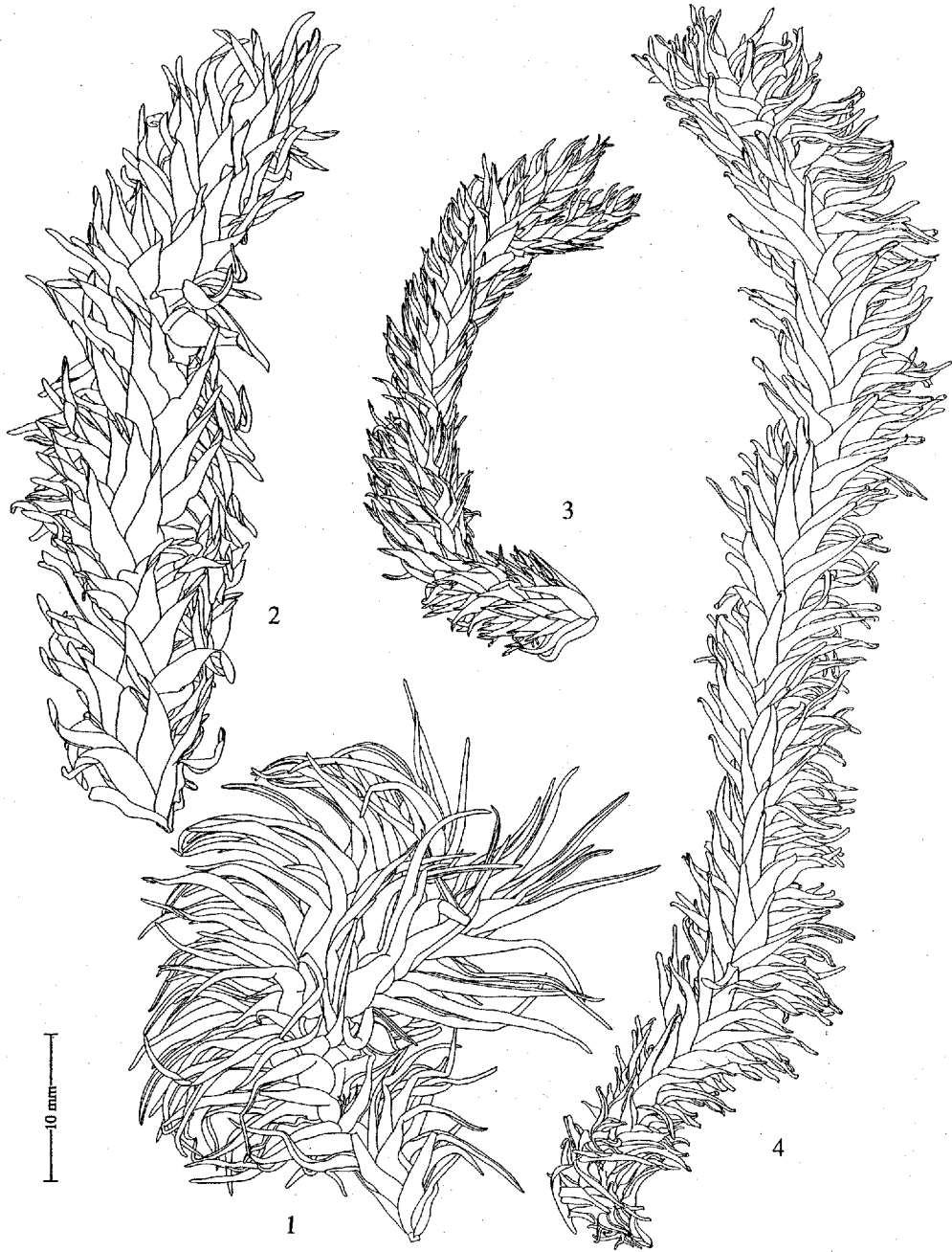


Figure II. Habits of 4 taxa of *Leucobryum*. 1. *L. javense* (Brid. ex Schwägr.) Mitt. 2. *L. javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 3. *L. javense* var. *novae-guineae* (Barr.) T. Yamaguchi. 4. *L. javense* var. *uncinatum* (Fl.) T. Yamaguchi. Fig. 1 was drawn from Joncheere 1621 (L); 2, from holotype of *L. cyathifolium* (BM); 3, from holotype of *L. novae-guineae* (FH); 4, from holotype of *L. uncinatum* (FH).



Figure III. Habits of 10 taxa of *Leucobryum*. 1. *L. scabrum* Lac. 2. *L. aduncum* Dozy & Molk. var. *aduncum*. 3. *L. aduncum* var. *teysmannianum* (Dozy & Molk.) T. Yamaguchi. 4. *L. aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 5. *L. chlorophyllosum* C. Müll. 6. *L. boninense* Sull. & Lesq. 7. *L. juniperoideum* (Brid.) C. Müll. 8. *L. humillimum* Card. 9. *L. imbricatum* Broth. 10. *L. glaucum* (Hedw.) Ångstr. in Fries. Fig. 1 was drawn from holotype of *L. scabrum* (L); 2, from lectotype of *L. aduncum* (L); 3, from holotype of *L. teysmannianum* (L); 4, from lectotype of *L. scalare* var. *marschmeyeri* (FH); 5, from isotype of *L. chlorophyllosum* (L); 6, from holotype of *L. boninense* (FH); 7, from syntype (Teneriffa) of *Dicranum juniperoideum* (B); 8, from isotype of *L. galeatum* (BM); 9, from lectotype of *L. imbricatum* (H); 10, from Europe, Sept. 1797, s. n. (B).



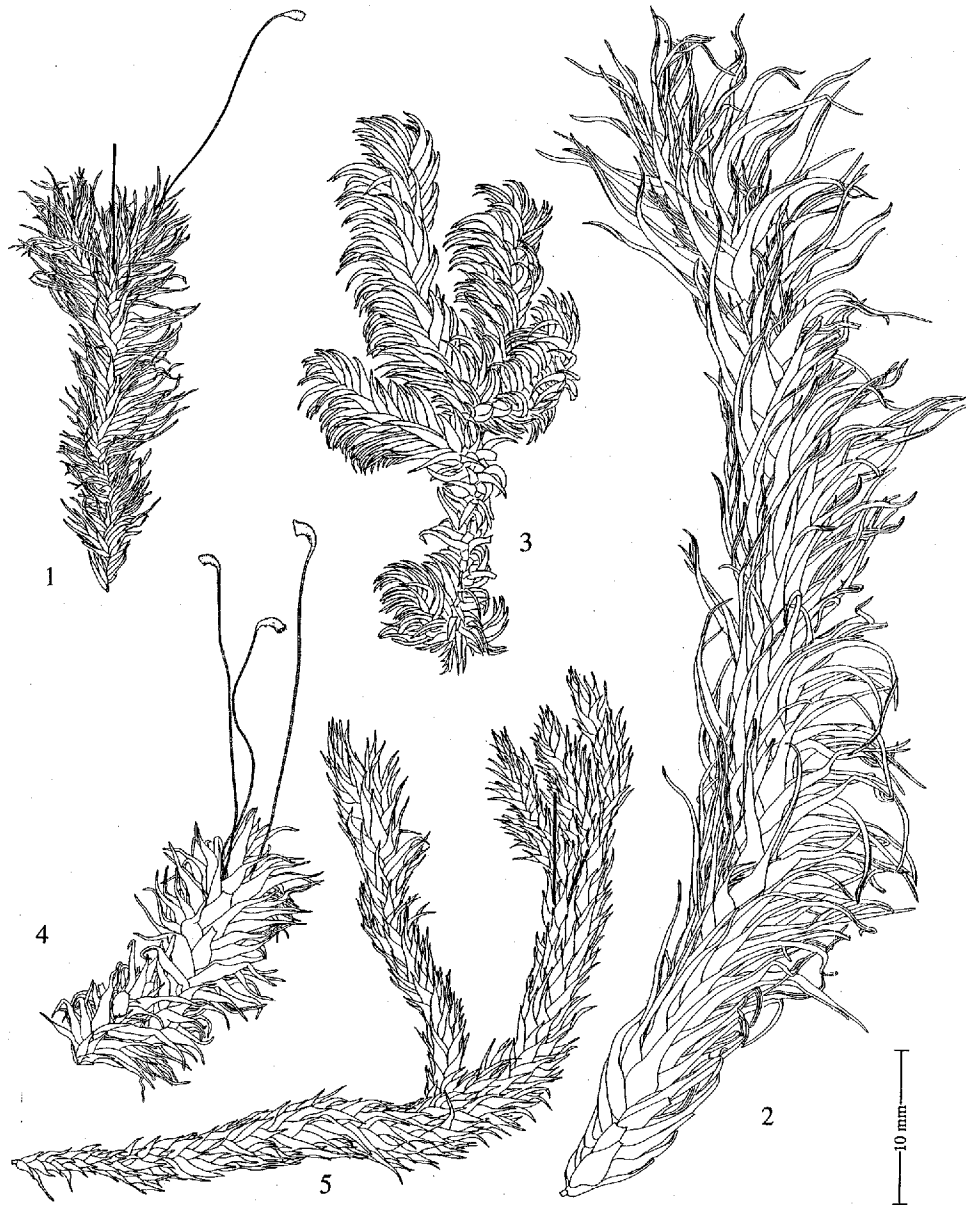


Figure IV. Habits of 5 taxa of *Leucobryum*. 1. *L. bowringii* Mitt. 2. *L. sumatranum* Broth. ex Fl. 3. *L. sericeum* Broth. ex Geh. 4. *L. sanctum* (Brid.) Hampe. 5. *L. arfakianum* C. Müll. ex Geh. Fig. 1 was drawn from lectotype of *L. bowringii* (NY); 2, from holotype of *L. sumatranum* (FH); 3, from holotype of *L. sericeum* (H); 4, from holotype of *Dicranum glaucum* var. *sanctum* (B); 5, from isolectotype of *L. arfakianum* (F).

is not clear. Leaf arrangement and posture are variable to a certain extent owing to growing habitat or maturity.

## 2. Stems

Kawai (1980) studied detailed anatomical characters of stems in five species of Japanese Leucobryum by staining methods. He distinguished two different types of stem anatomy in Leucobryum as follows:

1 (type III in Kawai 1980). Stem differentiates into an epidermis, cortex, leptome and a hadrome. L. scabrum, L. javense and L. textorii (= L. juniperoideum) were included in this type.

2 (type IV in Kawai 1980). Stem differentiates into an epidermis, cortex, leptome, hydrome sheath and a hadrome. L. neilgherrense (= L. juniperoideum) and L. bowringii were included in this type.

However, according to my observations of stem anatomy, differentiation between epidermis and cortex, that between cortex and leptome, and that between cortex and central tissue are indistinct. My observations also show a certain variability within a species. Therefore, in this study, I distinguished three parts in the cross-section of a stem, which are epidermal layer, cortical layer and central strand. In my classification, the epidermal layer includes a part of cortex which defined by Kawai (1980), and the cortical layer includes leptome and a part of cortex. The

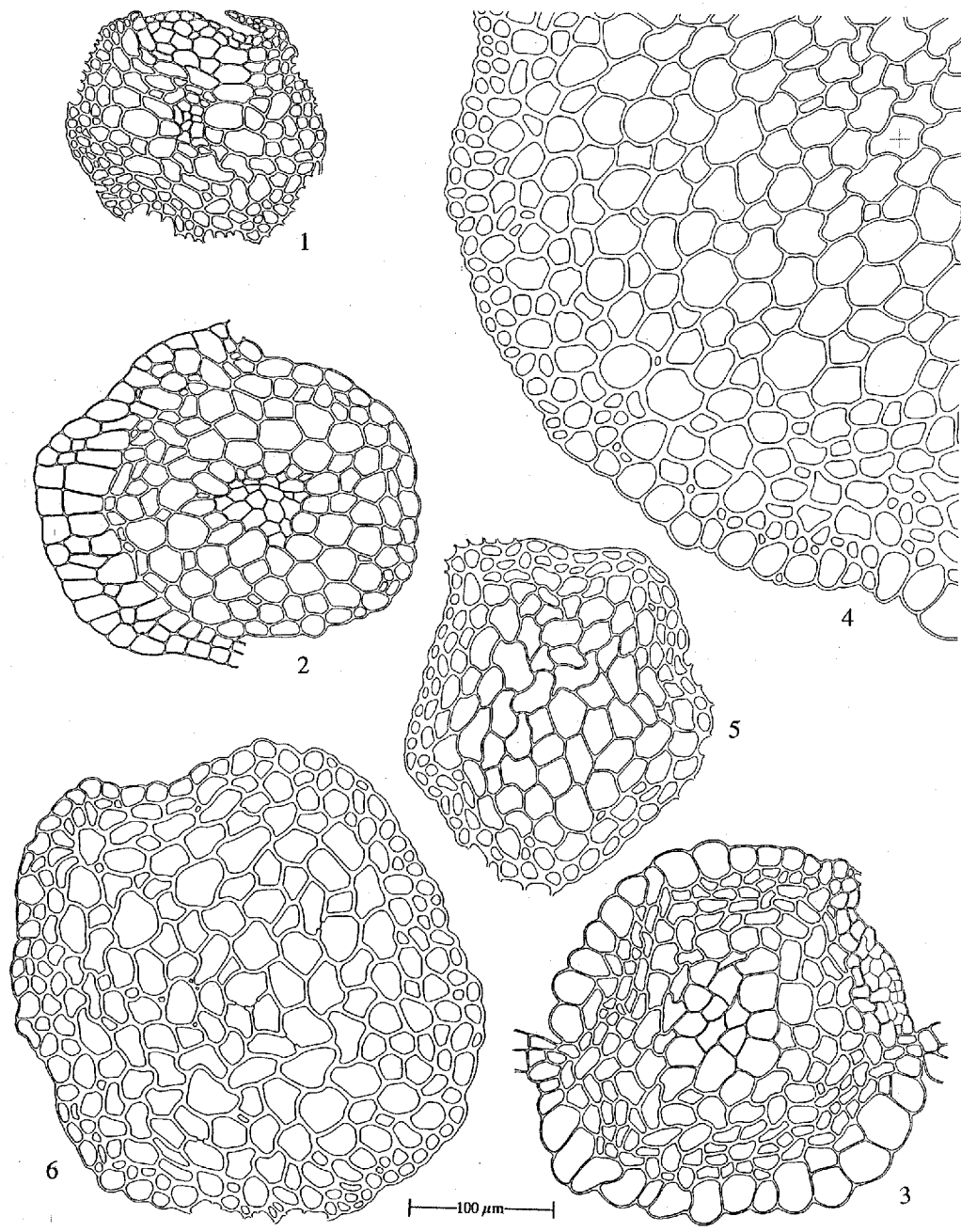


Figure V. Cross-sections of stems of 6 taxa of *Leucobryum*. 1. *L. bowringii* Mitt. 2. *L. imbricatum* Broth. 3. *L. arfakianum* C. Müll. ex Geh. 4. *L. javense* (Brid. ex Schwägr.) Mitt. 5. *L. aduncum* Dozy & Molk. 6. *L. glaucum* (Hedw.) Ångstr. in Fries. Fig. 1 was drawn from lectotype of *L. bowringii* (NY); 2, from lectotype of *L. imbricatum* (H); 3, from isolectotype of *L. arfakianum* (FI); 4, from Joncheere (L); 5, from lectotype of *L. aduncum* (L); 6, from Europe, Sept. 1797, s. n. (B).

central strand by my definition corresponds to the hydrom sheath and the hadrom by Kawai (1980). My classification is not anatomically distinct, but it is reasonable judging from the variability within a species, and it is effective concerning for systematic study of Leucobryum.

Based on the three parts of stem tissues mentioned above, I recognize here three principal types of stem structure.

Type A. The differentiation between the epidermal and the cortical layers is distinct, but the central strand is indistinct (Fig. V: 4-6). This type is nearly equivalent to type III by Kawai (1980). Taxa which belong to this type are L. javense and its varieties, L. scabrum, L. aduncum and its varieties, L. chlorophyllosum, L. boninense, L. juniperoideum and L. glaucum. The cortical layer of this type is usually composed of nearly uniform cells. However, the cortical layer cells of some robust taxa, such as L. javense and its varieties, are getting gradually smaller and the walls are thinner inward. In this case, however, the central strand is not differentiated. Sometimes the stems of L. juniperoideum have weakly differentiated central areas. The area is composed of smaller and thin-walled cells, but the cell walls are colored with light brown and different from the true central strand which is composed of small cells with colorless very thin walls. Because of the

structural variability of stems of L. juniperoideum, Kawai (1980) classified the species into type III (as L. textorii) and type IV (as L. neilgherrense). My observations prove that the materials of L. neilgherrense used by Kawai (1980) had weakly differentiated central area, but the cell walls were tinged with light brown. In conclusion, I determined that the stems of L. juniperoideum (syn. L. textorii and L. neilgherrense) belong to type A.

Type B. The differentiation between the epidermal and the cortical layers is distinct, and the central strand is clearly differentiated (Fig. V: 1, 3). The central strand is composed of small cells with colorless very thin walls. This type is nearly equivalent to type IV by Kawai (1980). Among the taxa treated in this study, L. humillimum, L. bowringii, L. sumatranum, L. sericeum, L. sanctum and L. arfakianum belong to type B. Among them, the central strands of L. sanctum and L. arfakianum are different from those of other taxa. In L. sanctum and L. arfakianum, the central strand is surrounded by one to three layers of large and thin walled cells (Fig. V: 3). The taxa which belong to type B are easily distinguished from type A by distinct central strand. However, the central strands of juvenile plants of type B are sometimes undifferentiated.

Type C. The central strand is distinctly differentiated, but the differentiation between the

epidermal and the cortical layers is not clear because of their nearly uniform cells (Fig. V: 2). Among the taxa treated in this study, only L. imbricatum belongs to type C.

In some cases, the abaxial leucocysts of leaves decurrent on stems and look like outer layers of stems in cross-sections. However, the leucocysts on stems are large and thin-walled, so that they are distinguished from the epidermis.

### 3. Leaves

#### (a) General morphology

The leaves of this genus are composed of leucocysts and chlorocysts (Fig. VI, VII). The leucocysts are hyaline empty cells which are devoid of any protoplasmic contents. The chlorocysts are green living cells which are enclosed by leucocysts in a single central layer and form a reticulum. The leaves of this genus are composed mainly of costa which is composed of a single layered chlorocyst sandwiched by two to several layers of leucocysts. The laminal areas are restricted to small narrow areas at the both margins of leaf base, and are composed of single layer of leucocysts. The most of laminal cells are quadrate or rectangular, but they are linear at margin (Fig. VI: 4, 5). These border cells are characterized by oblique cross and often pored walls, but the differentiation between the border cells and the

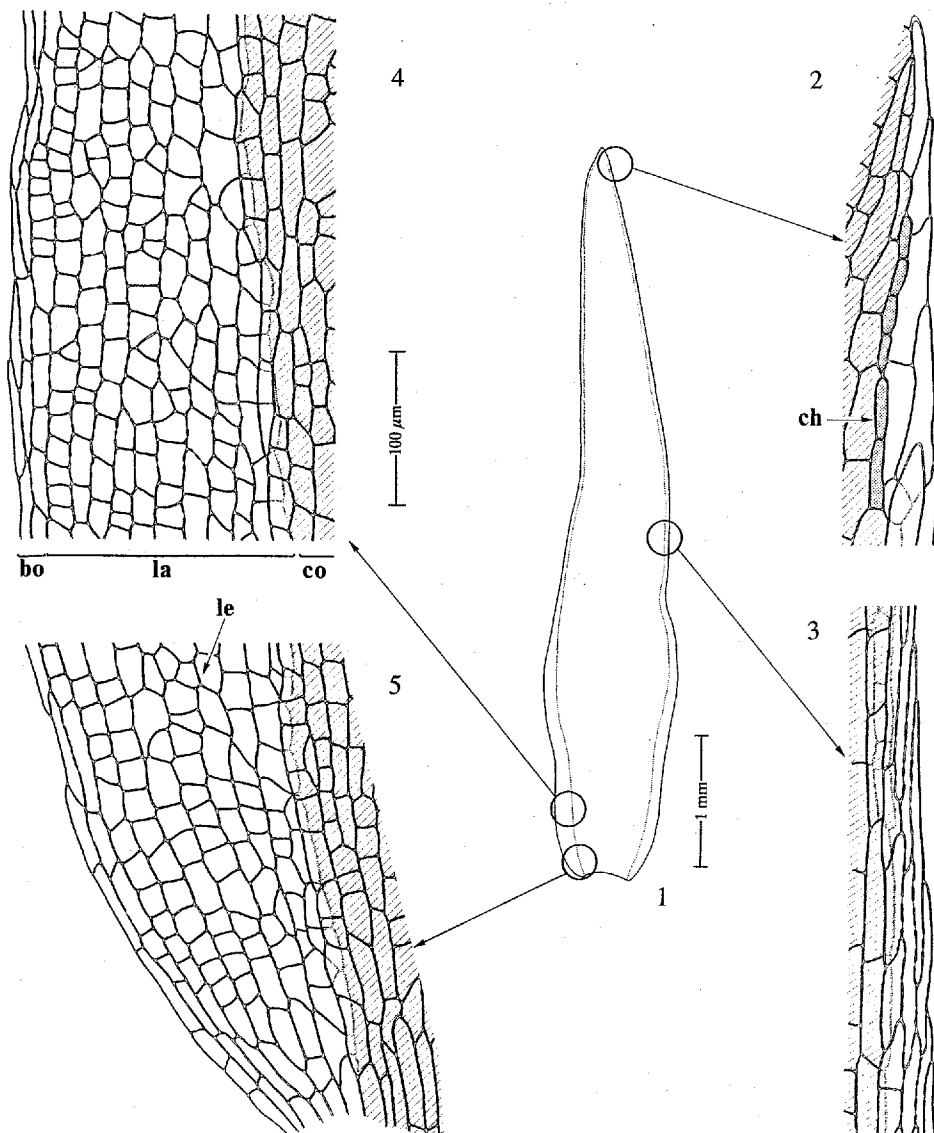


Figure VI. General morphology of leaf of *Leucobryum*. 1. Leaf (expanded). 2. Cells near leaf apex (adaxial view). 3. Median cells of leaf (abaxial view). 4. Basal cells of leaf (abaxial view). 5. Alar cells of leaf (abaxial view). bo shows border; ch, chlorocyst; co, costa; la, lamina; le, leucocyst. All figures were drawn from isotype of *L. textorii* (= *L. juniperoideum*; L).

laminal cells is often indistinct. The margin of upper part of leaf is usually composed of a few rows of linear cells (Fig. VI: 2, 3).

Castaldo et al. (1979), Ligrone (1985), Robinson (1985) and Yamaguchi and Iwatsuki (1987) studied the structure of leaves of Leucobryum using SEM or TEM. According to them, the chlorocysts are arranged in longitudinal rows interconnected by numerous anastomoses, and communicate each other by plasmodesmata that cross their transverse cell walls. The cell walls of leucocysts are thin and unipored both on the inner transverse and longitudinal faces. The leucocysts usually have external pores on the abaxial surfaces of cells at the apical and basal regions of leaves. The structure of leucocysts is effective in reducing water stress by either enhancing water absorption and storage or by lowering water loss (Héban 1977, Proctor 1979, 1982, Ligrone 1985). Robinson (1985) also suggested that the leucocysts enhanced photosynthesis by having air bubbles mixed with the water in the cells.

In cross-sections of leaves the chlorocysts, except for the chlorocyst at the center, are rhombic and generally surrounded by four leucocysts (two on abaxial side and two on adaxial side; Fig. VII). The central chlorocyst in cross-section of leaf (Fig. VII: cch) is trapezoid and surrounded by one leucocyst on the adaxial side and three on



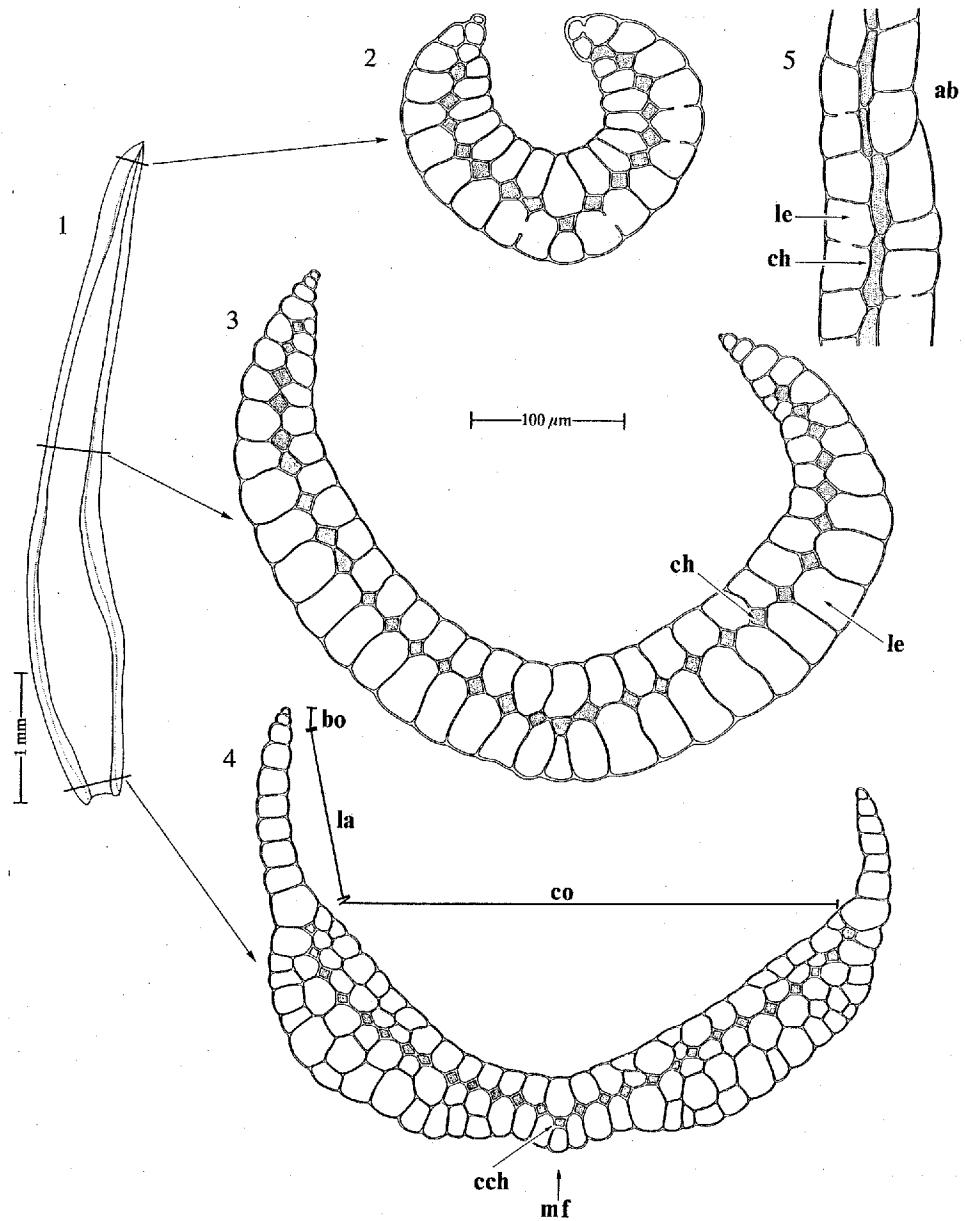


Figure VII. General morphology of leaf of *Leucobryum*. 1. Leaf. 2–4. Cross-sections of leaf (2, apical; 3, median; 4, basal portions). 5. Longitudinal section of leaf (apical portion). ab shows abaxial side; bo, border; cch, central chlorocyst; ch, chlorocyst; co, costa; la, lamina; le, leucocyst; mf, median furrow. Figs. 1–4 were drawn from isotype of *L. textorii* (= *L. juniperoideum*; L); 5, from holotype of *L. holleanum* (= *L. juniperoideum*; L).

the abaxial side. In cross-sections of leaf base show median furrow around the central chlorocyst (Fig. VII: 4). The median furrow regions are usually composed of two layered leucocysts. At the leaf base, the leucocysts are usually subdivided and becoming two or more layered on either side of the median furrow. The side part is more or less convex in cross-sections.

The anatomical study of leaves in cross-sections had been reported by Cardot (1901). He classified the relative position of the chlorocysts, as centric, hypocentric or hypercentric according to whether they are median in vertical position or nearer to the abaxial or adaxial leaf face. He also defined homostrosic in which the leucocysts were arranged in two layers, and heterostrosic in which the leucocysts were arranged in more than two layers.

Cardot's system is not so effective in taxonomy of Leucobryum treated in this study, because most taxa are heterostrosic and centric at leaf bases (Fig. VIII). Moreover, each taxon shows a certain variability in the structure of leaf base. However, the leaves of L. sericeum, L. sanctum and L. arfakianum enhance a tendency to be homostrosic at bases. The leaves of L. sanctum and L. arfakianum are clearly hypocentric at bases, and this character is taxonomically important.

(b) Shape

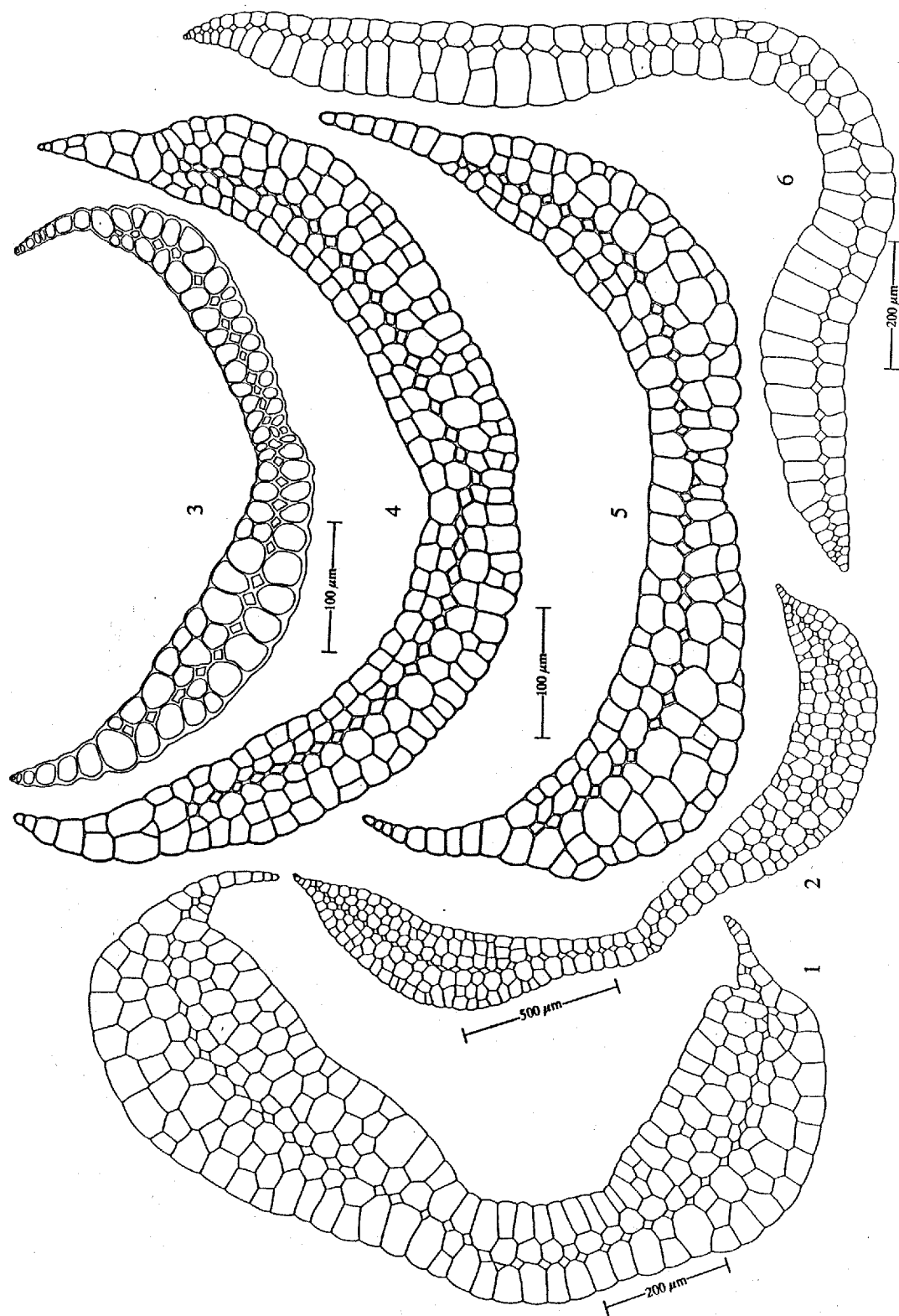


Figure VIII. Cross-sections of leaves. 1. *Leucobryum scabrum* Lac. 2. *L. javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 3. *L. glaucum* (Hedw.) Angstr. 5. *L. juniperoides* (Brid.) C. Müll. 6. *L. sanctum* (Brid.) Hampe. Figure 1 was drawn from holotype of *L. scabrum* (L.); 2, from holotype of *L. cyathifolium* (BM); 3, from lectotype of *L. bowringii* (NY); 4, from Europe, Sept. 1797, s. n. (B); 5, from syntype (Teneriffa) of *Dicranum juniperoides* (B); 6, from holotype of *D. glaucum* var. *sanctum* (B)

In wet conditions, leaves of most taxa treated in this study are lanceolate from an oblong base. When leaves are pressed and expanded, the ratio of length to width become available, and the exact leaf shapes, such as lanceolate (Fig. IX: 10) or linear lanceolate (Fig. IX: 8), are determined. Moreover, when leaf apices are pressed and expanded, shape of leaf apices can be used as taxonomic characters, such as acuminate (Fig. IX: 8) or broadly acute (Fig. IX: 6). Most of the taxa treated in this study have straight leaves, but some taxa, such as L. javense var. javense, L. aduncum var. aduncum and L. sericeum, have falcate leaves. The leaves of L. javense var. cyathifolium and L. sanctum are somewhat squarrose.

(c) Proration of abaxial leucocysts

Most taxa treated in this study have projecting cell ends at leaf tips. While, some taxa have abaxially scabrous leaf surface at least to 1/10 from apex (Fig. X). They are caused by proration or undulation of abaxial leucocysts. The proration on the abaxial surface of apical parts of leaves is one of the important taxonomic characters, and it is classified into four types as follows: 1. smooth, 2. papillosely prorate, 3. undulate and 4. undulate and spinosely prorate (Fig. XI).

(d) Decurrence of abaxial leucocysts on stem

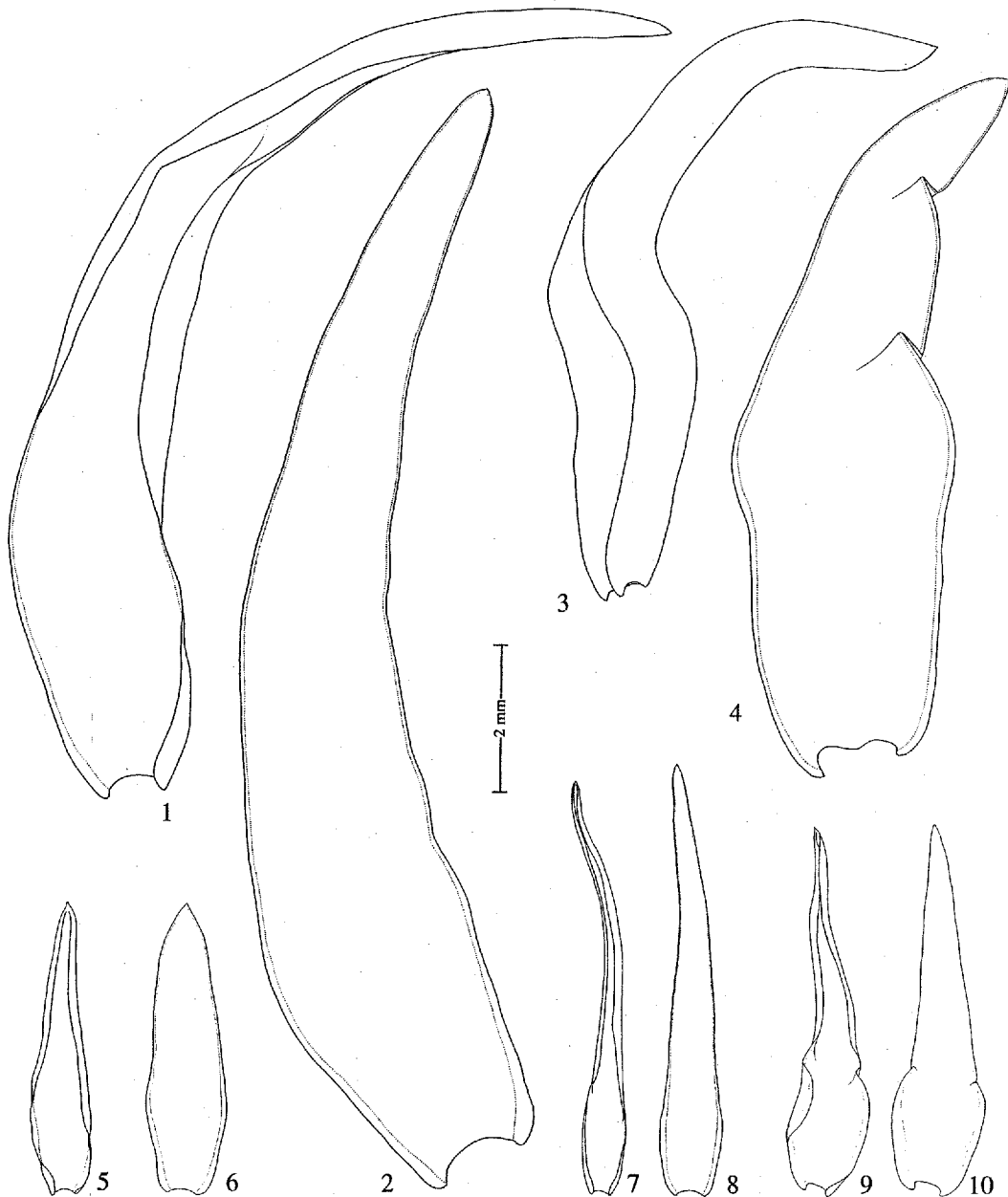


Figure IX. Leaves of 5 taxa of *Leucobryum*. 1, 2. *L. javense* (Brid. ex Schwägr.) Mitt. 3, 4. *L. javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 5, 6. *L. humillimum* Card. 7, 8. *L. bowringii* Mitt. 9, 10. *L. juniperoideum* (Brid.) C. Müll. 2, 4, 6, 8, 10, expanded. Figs. 1, 2 were drawn from Joncheere 1621 (L); 3, 4, from holotype of *L. cyathifolium* (BM); 5, 6, from isotype of *L. galeatum* (BM); 7, 8, from holotype of *L. deciduum* (PC); 9, 10, from isoelectotype of *L. humile* (KYO).

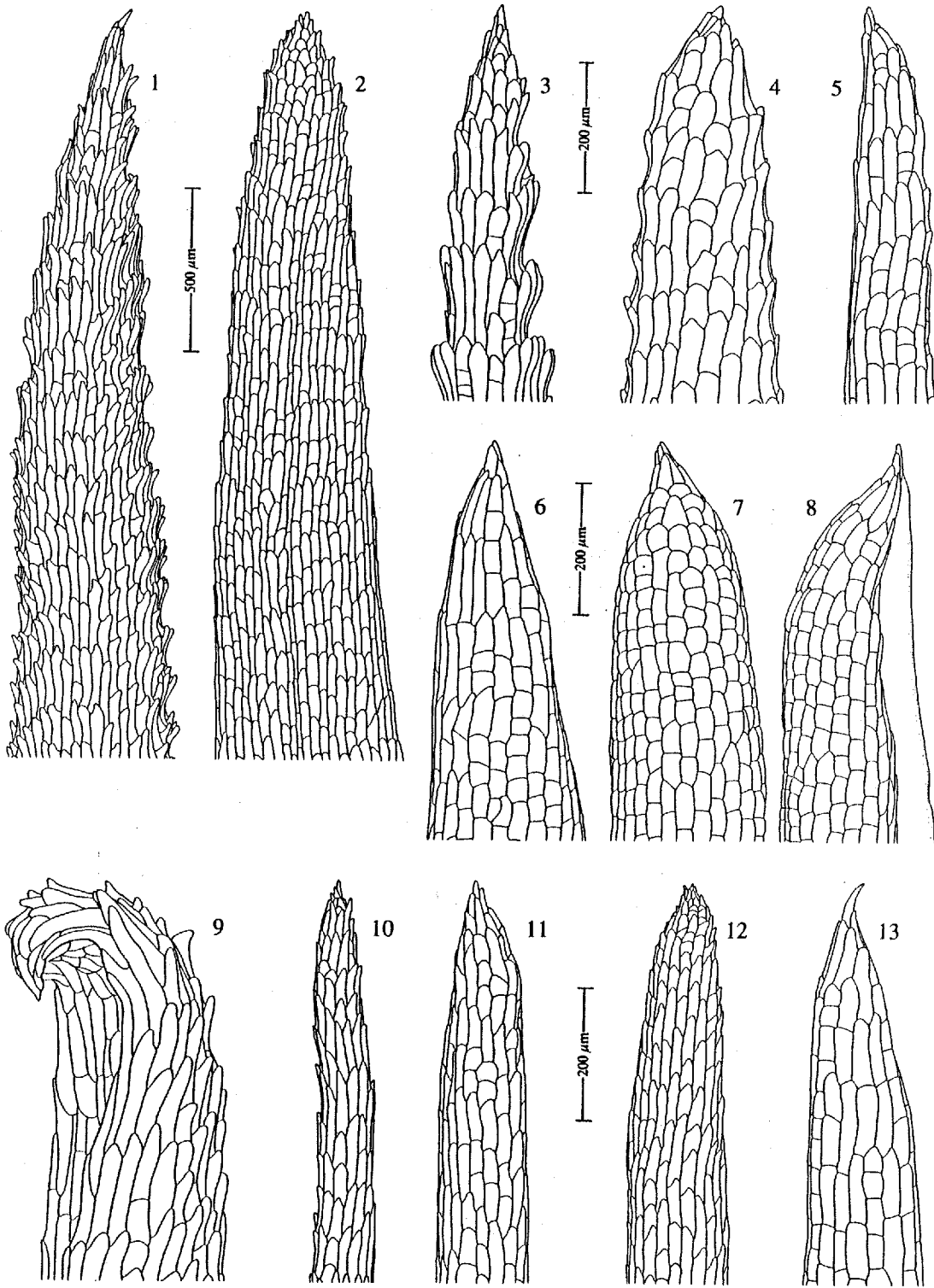


Figure X. Leaf apices of 12 taxa of *Leucobryum*. 1. *L. scabrum* Lac. 2. *L. javense* (Brid. ex Schwägr.) Mitt. 3. *L. aduncum* Dozy & Molk. 4. *L. boninense* Sull. & Lesq. 5. *L. chlorophyllosum* C. Müll. 6. *L. juniperoideum* (Brid.) C. Müll. 7, 8. *L. humillimum* Card. 9. *L. javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 10. *L. sericeum* Broth. ex Geh. 11. *L. bowringii* Mitt. 12. *L. sanctum* (Brid.) Hampe. 13. *L. arfakianum* C. Müll. ex Geh. Fig. 1 was drawn from Yamaguchi 7188 (HIRO); 2, from Joncheere 1621 (L); 3, from lectotype of *L. aduncum* (L); 4, from holotype of *L. boninense* (FH); 5, from isotype of *L. chlorophyllosum* (L); 6, from syntype (Teneriffa) of *Dicranum juniperoideum* (B); 7, 8, from isotype of *L. mittenii* (BM); 9, from holotype of *L. uncinatum* (FH); 10, from holotype of *L. sericeum* (H); 11, from Faurie 62 labeled as *L. bowringii* f. *brevifolium* (KYO); 12, from holotype of *Dicranum glaucum* var. *sanctum* (B); 13, from holotype of *L. papuense* var. *pendulum* (L).

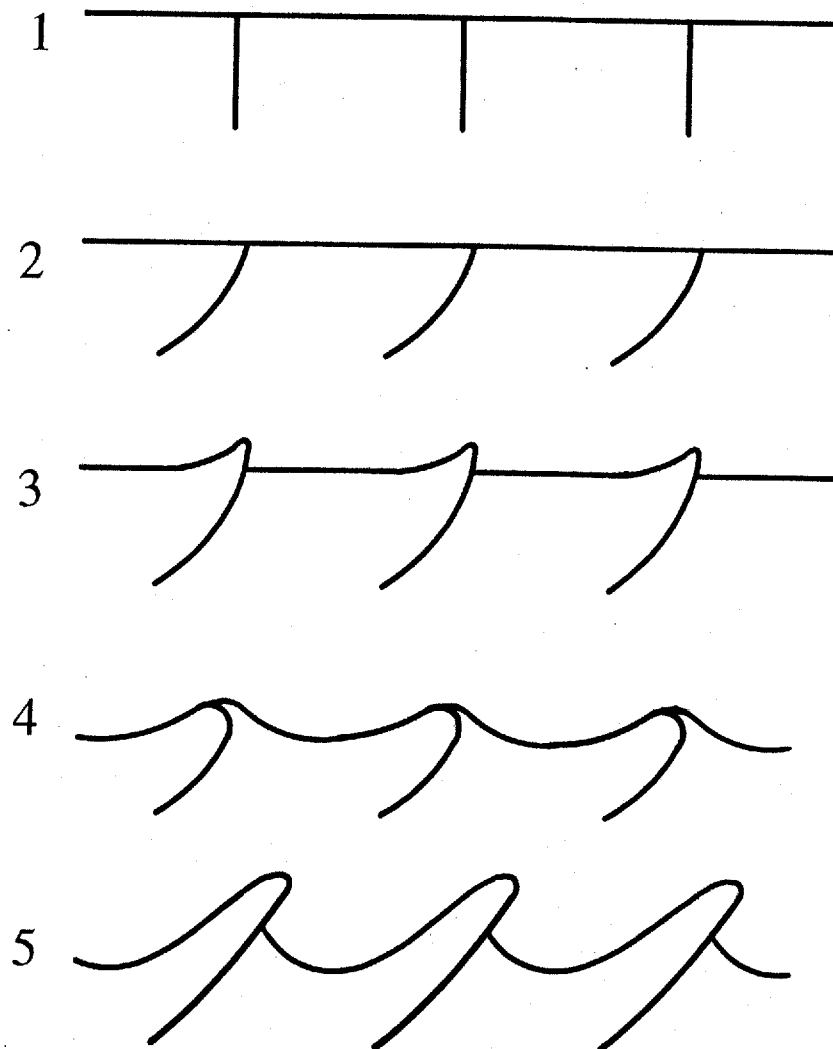


Figure XI. Schematic representation of proration on abaxial side of apical part of leaf. 1, 2. Smooth. 3. Papillosely prorate. 4. Undulate. 5. Undulate and spinosely prorate.

The abaxial leucocysts of extremely basal parts of leaves more or less overlap on cortical cells of stems. In some cases, such as in L. javense var. cyathifolium, L. javense var. novae-guineae, L. javense var. uncinatum, L. sanctum and L. arfakianum, the overlapped construction is recognized as a distinct decurrency. The decurrent part of these taxa, except for L. arfakianum, is composed of multilayered leucocysts. In L. sanctum and L. arfakianum, the abaxial leucocysts are long decurrent and reach to the insertional part of the next lower leaf, and consequently overlap the whole stem. According to Yamaguchi and Iwatsuki (1987), the anatomy of leaves and stems of L. neo-caledonicum is similar to L. sanctum and L. arfakianum. Considering the anatomical affinities, a phylogenetic relationship between L. sanctum, L. arfakianum and L. neo-caledonicum can be recognized.

#### 4. Rhizoids

In Leucobryum the bases of stems and branches bear rhizoids like other mosses. However, characteristic rhizoids at the leaf apex are also found (Correns 1899, Cardot 1901, Burrell 1907, Plitt 1909, Williams 1913, Crundwell 1979, Fig. XIII: 1, 3). The formation of rhizoids at the leaf apex has been considered as a mode of asexual reproduction (Correns 1899, Burrell 1907, Plitt 1909). Buds with rhizoids at leaf apices were also observed (Burrell



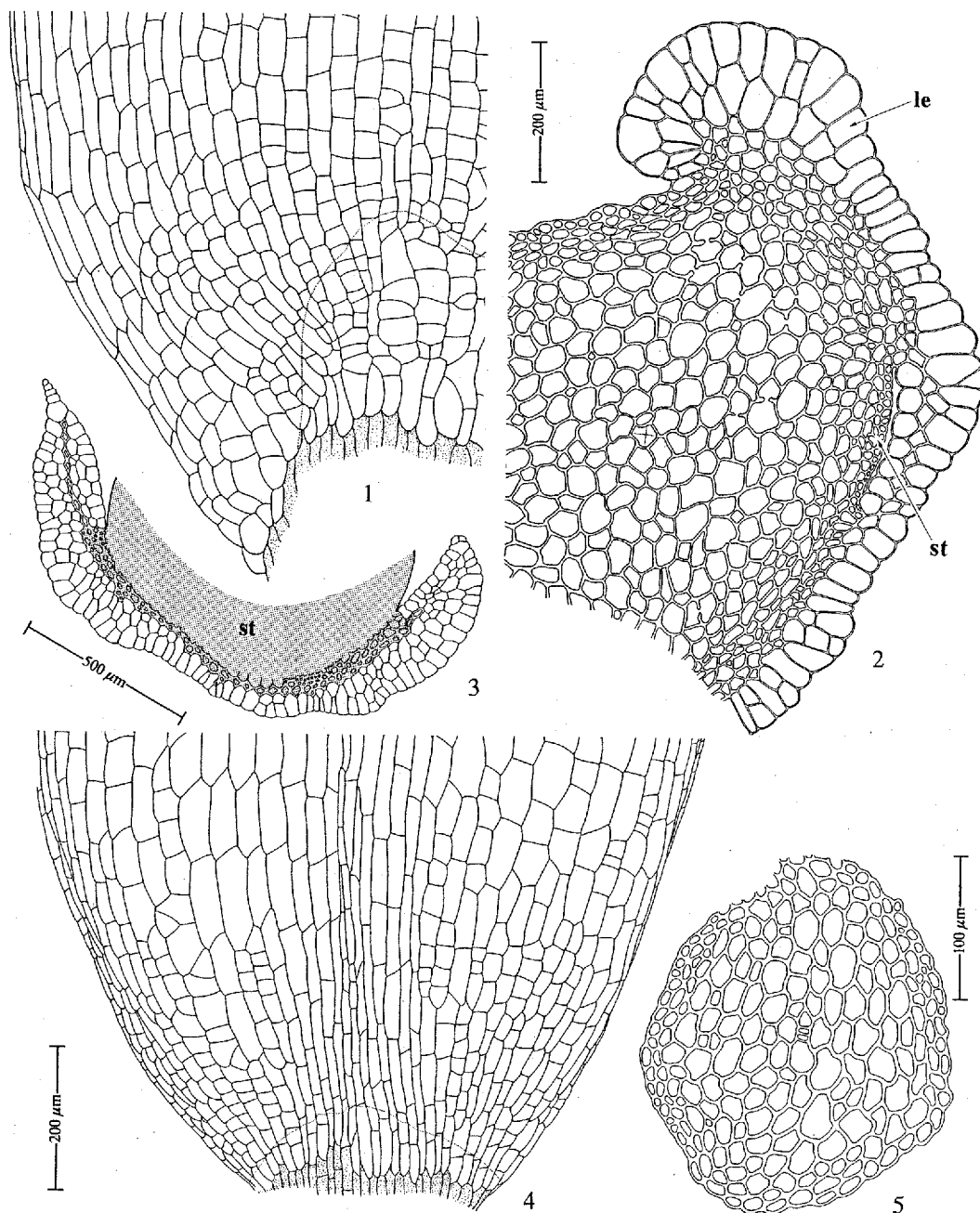


Figure XII. Decurrence of abaxial leucocysts of leaf on stem. 1-3. Distinctly decurrent type. 1. Leaf base (abaxial view). 2. Cross-section of stem. le shows abaxial leucocyst of leaf which decurrent on stem; st, stem. 3. cross-section of leaf at decurrent portion. 4, 5. Indistinctly decurrent type. 4. Leaf base (abaxial view). 5. Cross-section of stem. Figs. 1-3 were drawn from holotype of *L. cyathifolium* (BM); 4, 5, from holotype of *L. armatum* (H).

1907, Fig. XIII: 4). The rhizoids at the leaf apex are born from the adaxially exposed chlorocysts (Correns 1899, Cardot 1901, Fig. XIII: 2). The chlorocysts are usually covered by the leucocysts, but exposed chlorocysts are mainly found at adaxial side of apex (rarely at basal margins on adaxial side and lower central parts on abaxial side). These exposed chlorocysts often bear the rhizoids. I observed the leaves of L. javense var. novae-guineae (holotype specimen) frequently form rhizoids at the basal margins of leaves on abaxial side.

The other characteristic rhizoids formation is found at the lower abaxial side of inner perichaetial leaves. The rhizoids found on the inner perichaetial leaves are very fine and densely branched, and form a tometum enclosed by the perichaetial leaves (Bruch et al. 1847, Correns 1899, Plitt 1909, Grout 1905, Williams 1913, Crum 1981, Salazar Allen 1989). The differentiation between the rhizoids on perichaetial leaves and those on ordinary leaves is structurally and functionally distinct. Bruch et al. (1847), Correns (1899), Plitt (1907) and Grout (1905) considered the formation of rhizoids on perichaetial leaves as a mode of asexual reproduction, because of the growing of young plant on the tomenta. However, as mentioned later, the young plants growing on the tomenta originate from the germinations of spores dropped onto the tomenta, and some of

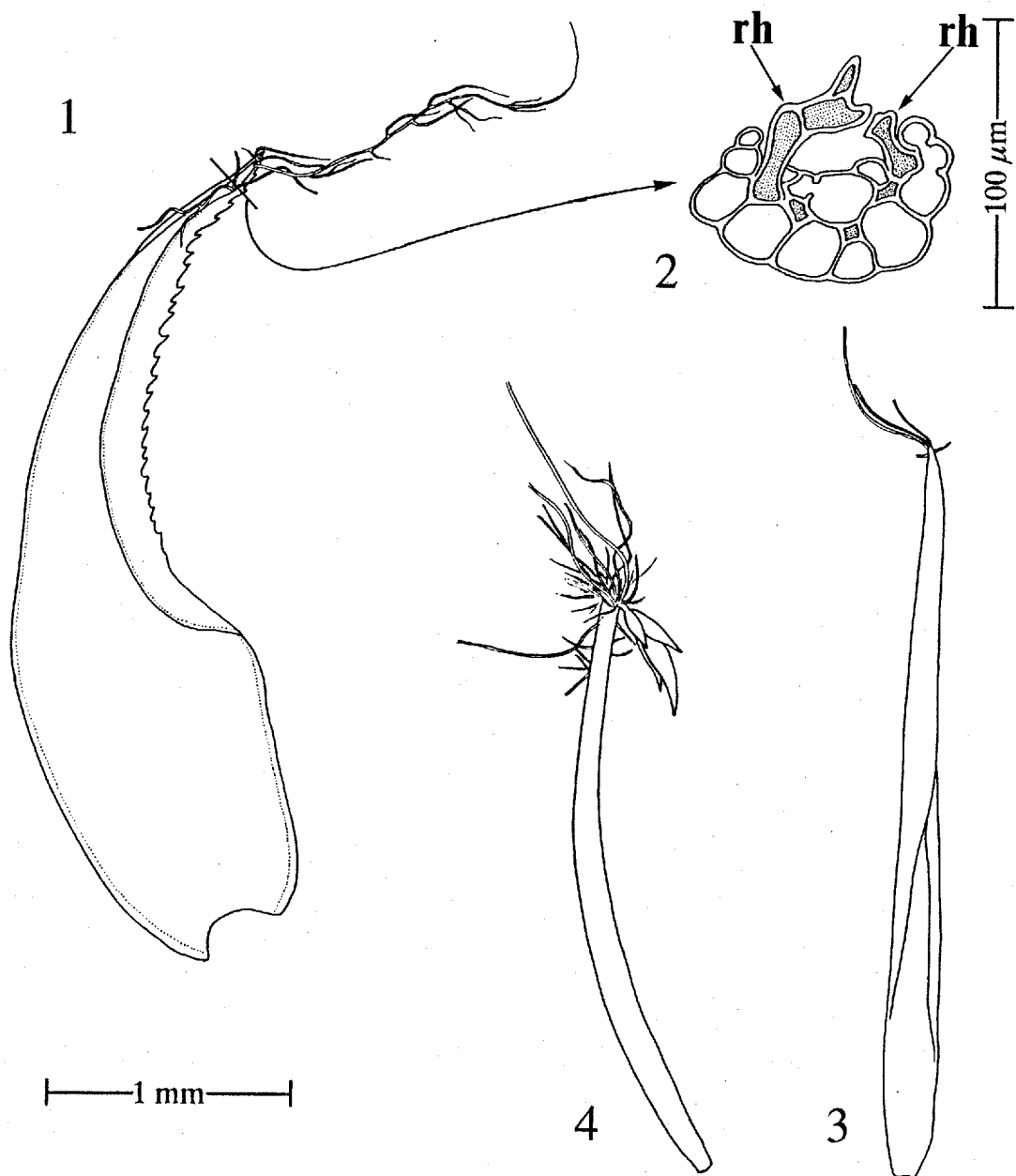


Figure XIII. Rhizoids at leaf apex. 1. Ordinary leaf. 2. Cross-section of leaf 1 at apex. rh shows rhizoid. 3, 4. Deciduous leaves (fig. 4 shows bud formation at apex). Figs. 1, 2 were drawn from lectotype of *L. aduncum* (L); 3, 4, from holotype of *L. holleanum* (= *L. juniperoideum*; L).

which grow to dwarf male plants (Williams 1913, Grout 1937, Florschütz 1964, Blackstock 1987, Yamaguchi & Iwatsuki 1987). Therefore, the formation of rhizoids on the perichaetial leaves is related to the sexual reproduction.

## 5. Sexual organs

Most taxonomists, with the exceptions of Fleischer (1904) and Yamaguchi and Iwatsuki (1987), did not describe any sexual organs of Leucobryum in detail. However, in the course of this study, I recognized that the characters of sexual organs were extremely important for classification of the genus Leucobryum.

### (a) Position of perichaetia and perigonia

In acrocarpous mosses, the branching pattern related to distribution of sexual organs is principally classified into the two types (Meusel 1935). In the first type, the sexual organs are terminal on the specialized short lateral branches, and the main stem continuously grows upward. This type of branching is defined as monopodial. In the second type, the sexual organs are terminal on the main stems, and the subfloral innovations are changed into the main stems. Therefore, the growth of stems is regulated by the formation of sexual organs. This type of branching is defined as sympodial.

The branching in acrocarpous mosses is mostly

sympodial. However, there are some cases that both types of branchings exist in a single family, e. g., Pottiaceae (cf. Saito 1975) and Bryaceae (cf. Ochi 1959), while both two types exist in a single genus, e. g., Fissidens (cf. Iwatsuki & Suzuki 1982) and Grimmia (cf. Deguchi 1979).

In the taxa of Leucobryum treated in this study, two branching types, sympodial and monopodial are found, but is mixed types mentioned above are also recognized. These types are represented by the female plants because the normal male plants are found only in a few species.

Type A. Perichaetia are terminal on the main stems (sympodial branching; Fig. XIV: 1, XV: 2, XVI: A). Fig. XVI(A): 1 shows the typical form of this type. However, this type includes some modifications as follows: (1) The sexual branches look like lateral branches because of the unformed perichaetia at stem apices (Fig. XV: 2, XVI: 2). (2) The subfloral innovations are relatively short, so that the sexual branches look like short lateral branches (Fig. XVI: 3, 4). Among the taxa treated in the present study, L. juniperoideum, L. humillimum, L. glaucum and L. bowringii belong to this type.

Type B. Perichaetia are terminal on the short lateral branches (never terminal on the main stems; monopodial branching; Fig. XIV: 2, Fig. XV: 4, Fig. XVI: B). The taxa belong to this type are often relatively robust, such as L.



Figure XIV. Branching showing position of perichaetia of 3 taxa of *Leucobryum*. 1. *L. glaucum* (Hedw.) Ångstr. in Fries. 2. *L. javense* (Brid. ex Schwägr.) Mitt. 3-7. *L. aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. Fig. 1 was drawn from Zanten 3319 (NICH); 2, from Joncheere 1621 (L); 3, from isotype of *L. scalare* var. *tjibodense* (HIRO); 4, 5, from Touw 10733 (L); 6, from holotype of *L. perichaetiale* (BM); 7, from isolectotype of *L. scalare* var. *marschmeyeri* (HIRO).



Figure XV. Branching showing position of perichaetia of 3 taxa of *Leucobryum*. 1, 3, 5. Female plants. 2, 4, 6. Branching showing position of perichaetia. 1, 2. *L. bowringii* Mitt. 3, 4. *L. sumatranum* Broth. ex Fl. 5, 6. *L. sericeum* Broth. ex Geh. Figs 1, 2 were drawn from Yamaguchi 9313 (HIRO); 3, from holotype of *L. sumatranum* (FH); 4, from Wilde & Wilde-Duyfjes 15066A (L); 5, 6, from Deguchi 22292 (KOCHI).

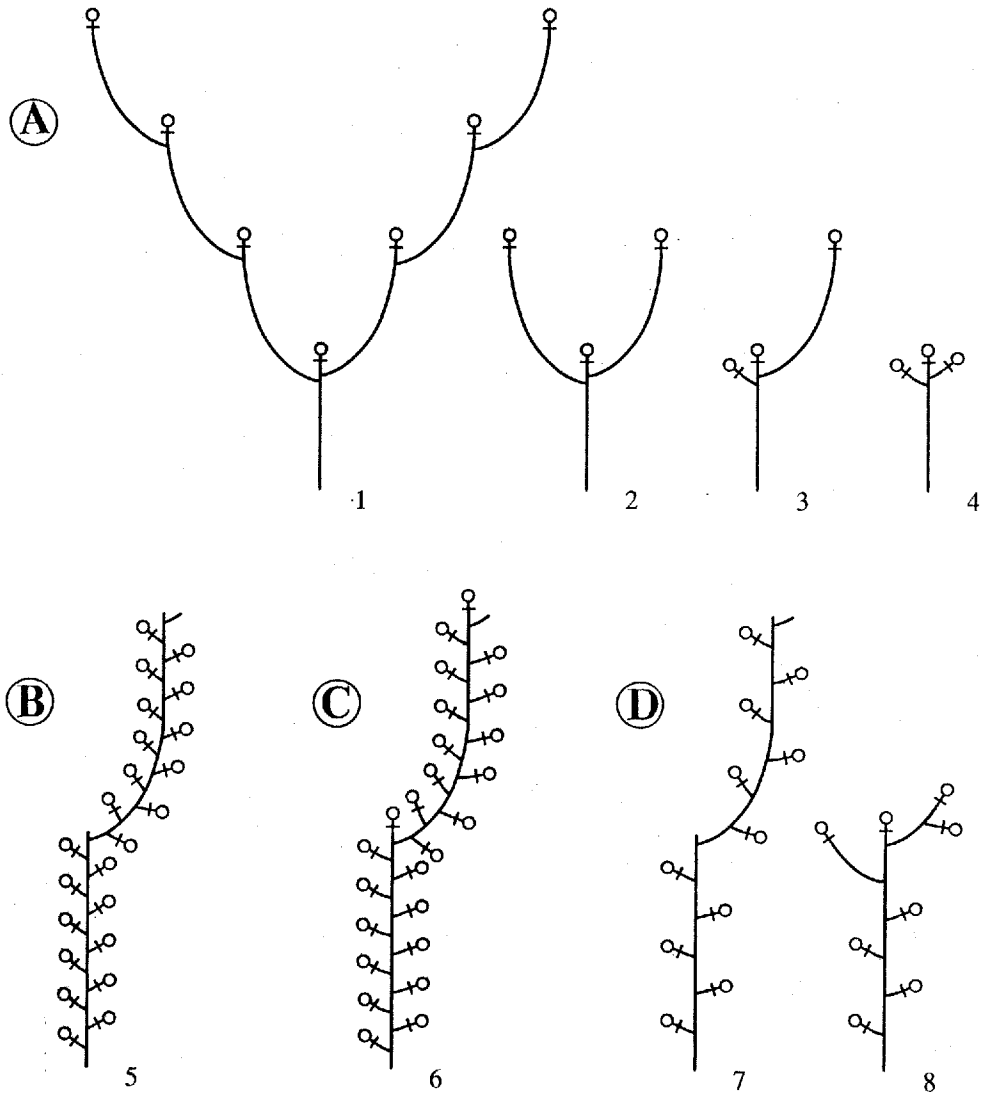


Figure XVI. Schematic representation of branching and distribution of perichaetia. ♀ represents perichaetium.



javense and its varieties, L. aduncum var. aduncum, L. aduncum var. teysmannianum, L. boninense, L. sumatranum, L. sanctum and L. arfakianum. The sexual branches are usually much shorter than those of type A (Table 7). Therefore I consider that the distribution of perichaetia and the length of sexual branches are useful for classification of Leucobryum.

Type C. Perichaetia are mainly terminal on the short lateral branches, but rarely terminal on the main stems (Fig. XV: 6, XVI: C). This type seems to be formed by a slight modification of type B. Among the taxa treated in this study, L. sericeum belongs to this type.

Type D. Perichaetia are terminal on short or elongate lateral branches, on subfloral innovations, or on main stems (Fig. XIV: 3-7, XVI: D). The taxa of this type include L. aduncum var. scalare and L. chlorophyllosum.

The branching and the distributional patterns of the perigonia of the normal male plants are similar to the female plants of the same taxa, although I could not examine adequate number of samples.

#### (b) Archegonia and antheridia

The length of archegonia seem to be correlated with the position of perichaetia, type A-D mentioned above, and no relation to the plant size. The archegonia of the taxa belong to type A are 1.2-1.8 mm long, and longer than those

Table 7. Length of female branches of three species of Leucobryum in Japan

Species	Min. (mm)	Mean (mm)	Max. (mm)	Standard deviation	Number of specimens examined	Number of materials
<u>L. juniperoides</u>	0.8	2.0	12.0	1.7	19	55
<u>L. bowringii</u>	1.0	4.3	16.2	3.0	20	50
<u>L. scabrum</u>	0.2	0.5	1.0	0.1	19	43

belong to type B, C and D (Fig. XVII: 1-16). The archegonia of the taxa belong to type B, C and D are shorter, 0.5-1.2 mm in length, except for L. sumatranum (about 1.5 mm long).

The size of antheridia is variable within a taxon or even in a specimen, because of the variety of the size of male plants. The antheridia of dwarf male plants are much smaller than those of normal male plants (Fig. XVII, 20-23).

(c) Perichaetial and perigonial leaves

Large part of the perichaetial leaves is composed of the basal part with relatively broad lamina. The apical part of perichaetial leaves is narrowed, short and almost filled with costa. Size and shape of perichaetial leaves of Leucobryum are more or less differentiated from ordinary leaves. The perichaetial leaves around unfertilized archegonia are not well developed, especially for the inner leaves (Fig. XVIII: A, XIX: A, XXI: A, XXII: A, XXIV: A). When the sporophytes matured, the perichaetial leaves reach maximum size and show the characters for the taxon (Fig. XVIII: B, XIX: B, XX, XXI: B, XXII: B, XXIII: B, XXIV: B). Therefore, the differentiation of the perichaetial leaves is examined using those around mature sporophytes. They are classified into three types as follows:

Type A. The inner perichaetial leaves (1.0-) 1.4-1.8 times longer than the stem leaves near the perichaetium.

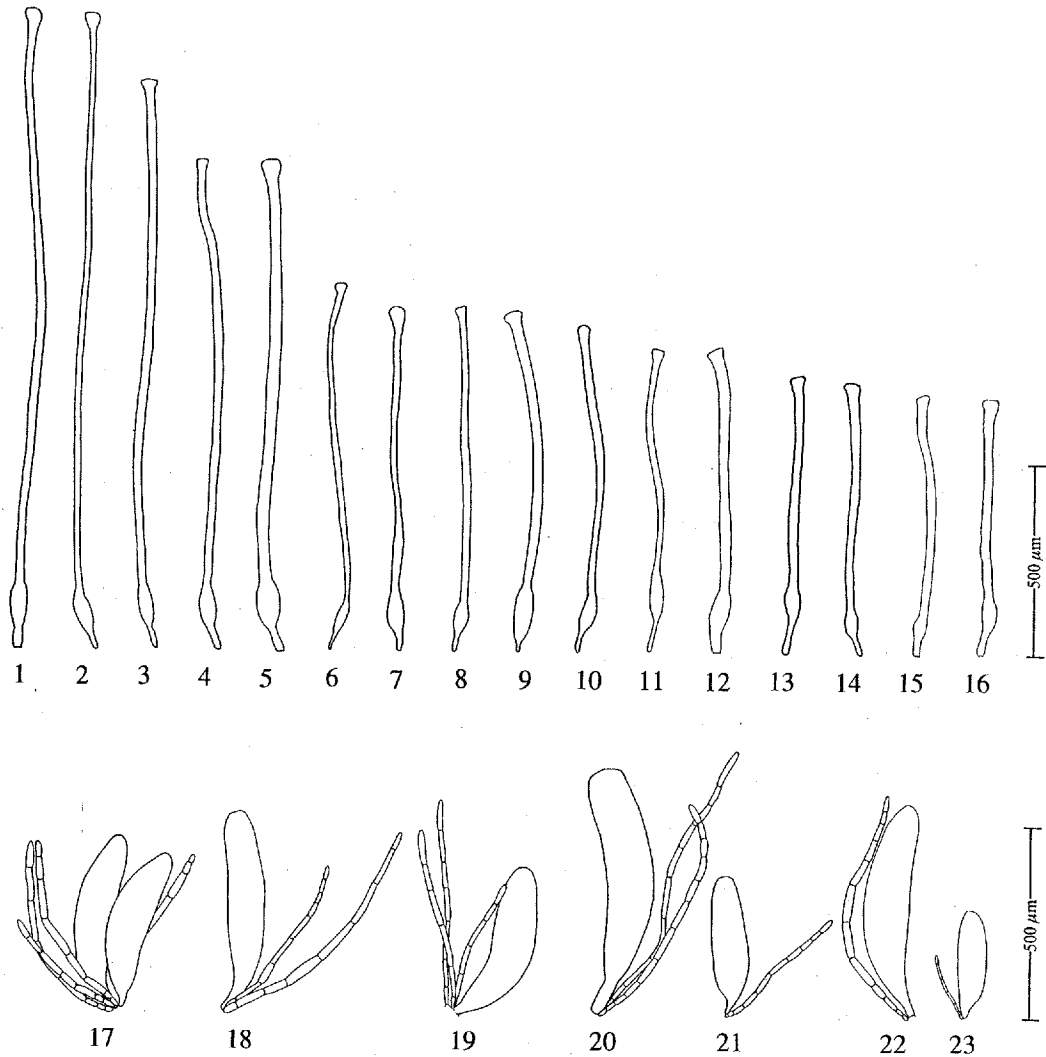


Figure XVII. 1–16. Archegonia. 17–23. Antheridia (19, 21, 23 from dwarf male plants). 1, 20, 21. *L. bowringii* Mitt. 2. *L. glaucum* (Hedw.) Ångstr. in Fries. 3. *L. sumatranum* Broth. ex Fl. 4, 22, 23. *L. juniperoideum* (Brid.) C. Müll. 5. *L. humillimum* Card. 6. *L. arfakianum* C. Müll. ex Geh. 7. *L. sericeum* Broth. ex Geh. 8, 17. *L. aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 9. *L. javense* (Brid. ex Schwägr.) Mitt. var. *javense*. 10. *L. javense* var. *novae-guineae* (Bartr.) T. Yamaguchi. 11. *L. aduncum* Dozy & Molk. var. *aduncum*. 12, 19. *L. scabrum* Lac. 13. *L. chlorophyllum* C. Müll. 14. *L. sanctum* (Brid.) Hampe. 15, 18. *L. boninense* Sull. & Lesq. 16. *L. aduncum* var. *teysmannianum* (Dozy & Molk.) T. Yamaguchi. Figs. 1, 20, 21 were drawn from Yamaguchi 9313 (HIRO); 2, from Zanten 3319 (NICH); 3, from Wilde & Wilde-Duyfjes 15066A (L); 4, 22, from Noguchi 16753 (NICH); 5, from Nishimura 1514 (HIRO); 6, from holotype of *L. papuense* var. *pendulum* (L); 7, from holotype of *L. sericeum* (H); 8, from isotype of *L. scalare* var. *tjibodense* (HIRO); 9, from Joncheere 1621 (L); 10, from holotype of *L. antareense* (L); 11, from lectotype of *L. aduncum* (L). 12, 19, from Iwatsuki & Minamidani s. n., Musci Japonici Exsiccati 28: 1378 (NICH); 13, from isotype of *L. chlorophyllum* (L); 14, from lectotype of *L. papuense* (H); 15, 18, from holotype of *L. boninense* (FH); 16, from holotype of *L. teysmannianum* (L); 17, from lectotype of *L. scalare* (FH); 23, from Une 3545 (HIRO).

The taxa belong to this type include L. aduncum var. scalare (Fig. XXI), L. juniperoideum (Fig. XXII) and L. humillimum.

Type B. The inner perichaetial leaves (0.5-) 0.7-1.0 times longer than the stem leaves near the perichaetium. The taxa belong to this type include L. aduncum var. aduncum (Fig. XX), L. chlorophyllosum, L. boninense, L. glaucum (Fig. XXIII) and L. bowringii (Fig. XXIV).

Type C. The inner perichaetial leaves 0.3-0.6 times longer than the stem leaves near the perichaetium. The taxa belong to this type include L. javense var. javense (Fig. XVIII), L. scabrum (Fig. XIX), L. sumatranum, L. sericeum, L. sanctum and L. arfakianum.

The inner perichaetial leaves of the perichaetia terminal on the main stems usually longer than the stem leaves, except for L. glaucum and L. bowringii, while those of the perichaetia terminal on lateral branches are more or less shorter than the stem leaves, except for L. aduncum var. scalare. The specimens with mature sporophytes treated in this study are not so many, so that the further examinations are needed. However, the comparison between the inner perichaetial leaves around mature sporophytes and the stem leaves near the perichaetia seems to be taxonomically important.

I critically examined the perichaetial leaves of more than 19 specimens (with mature sporophytes) each of L.

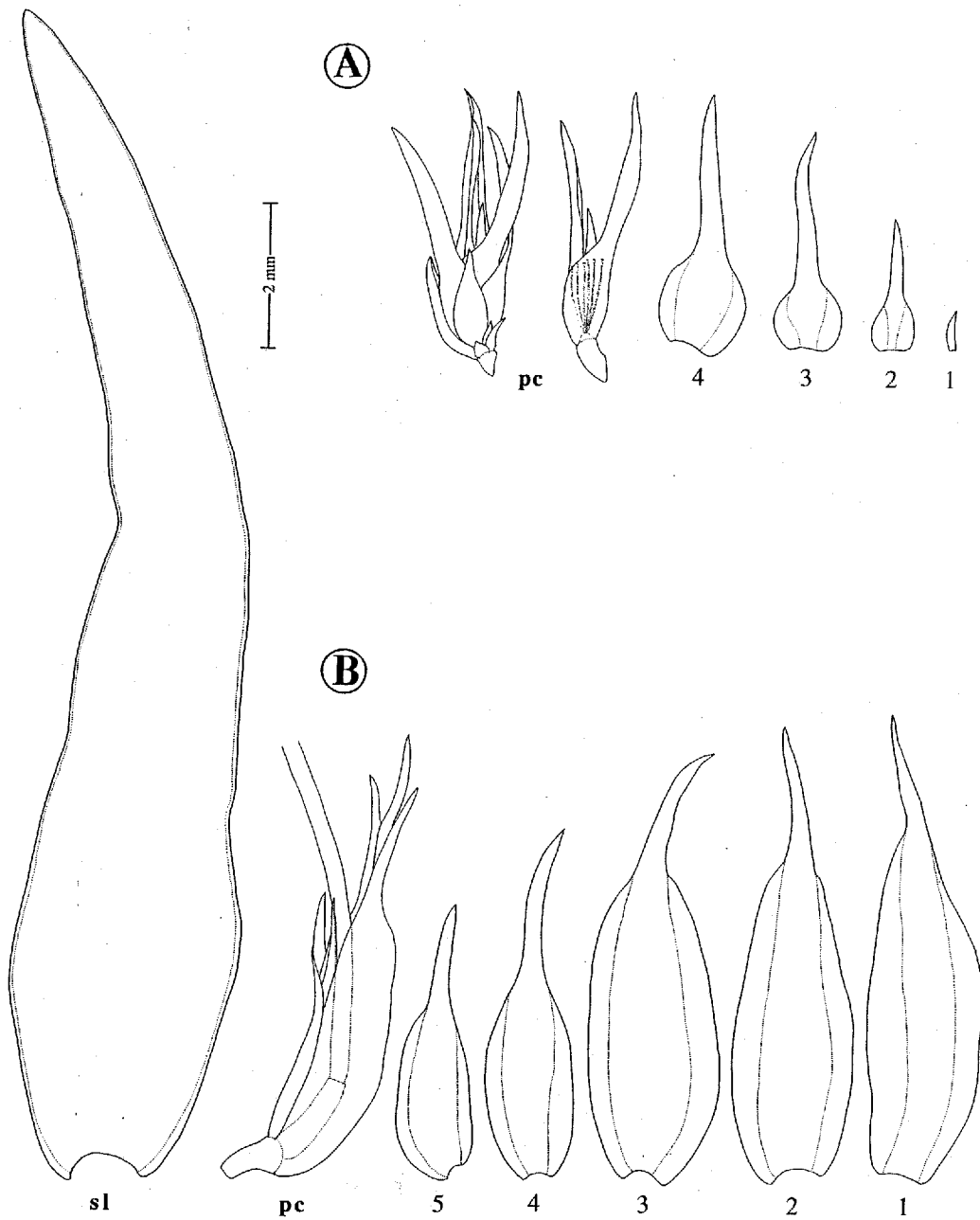


Figure XVIII. Perichaetial leaves of *Leucobryum javense* (Brid. ex Schwägr.) Mitt. var. *javense*. A. Perichaetium and perichaetial leaves (expanded) around unfertilized archegonia. B. Perichaetium and perichaetial leaves (expanded) around mature sporophyte. Numbers show the order of perichaetial leaves from the innermost leaf (number 1); pc, perichaetium; sl, stem leaf (expanded) near perichaetia A and B. All figures were drawn from Joncheere 1621 (L).

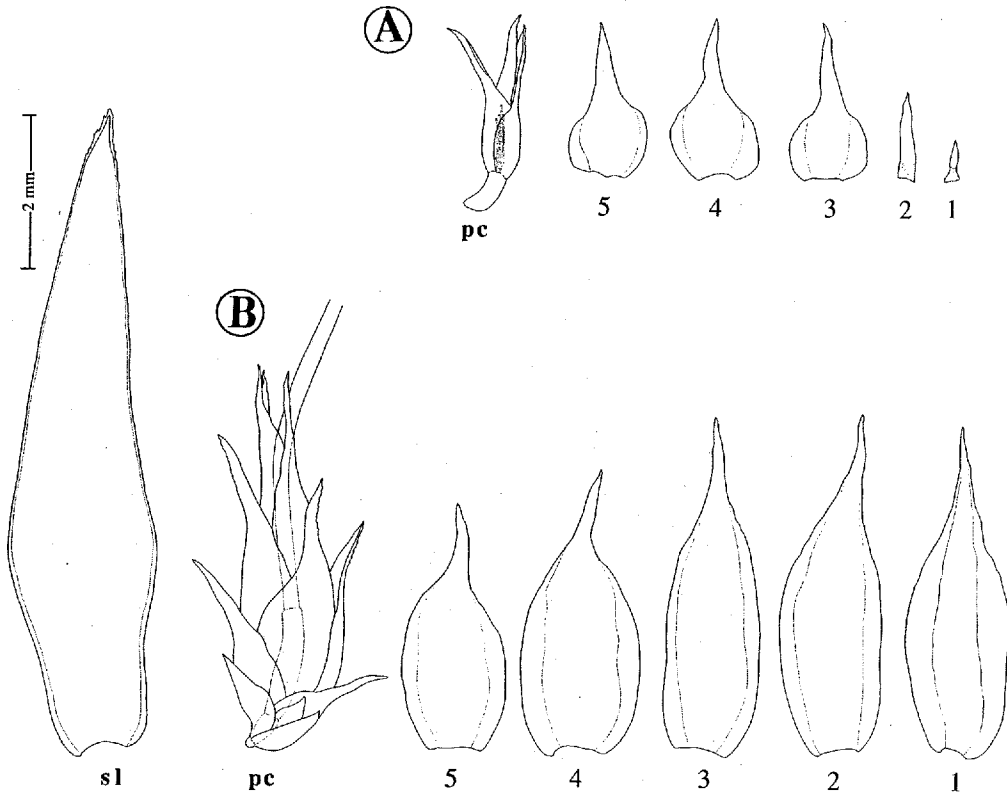


Figure XIX. Perichaetial leaves of *Leucobryum scabrum* Lac. A. Perichaetium and perichaetial leaves (expanded) around unfertilized archegonia. B. Perichaetium and perichaetial leaves (expanded) around mature sporophyte. Numbers show the order of perichaetial leaves from the innermost leaf (number 1); pe, perichaetium; sl, stem leaf (expanded) near perichaetia A and B. All figures were drawn from Iwatsuki & Minamidani s. n., Musci Japonici Exsiccati 28: 1378 (NICH).

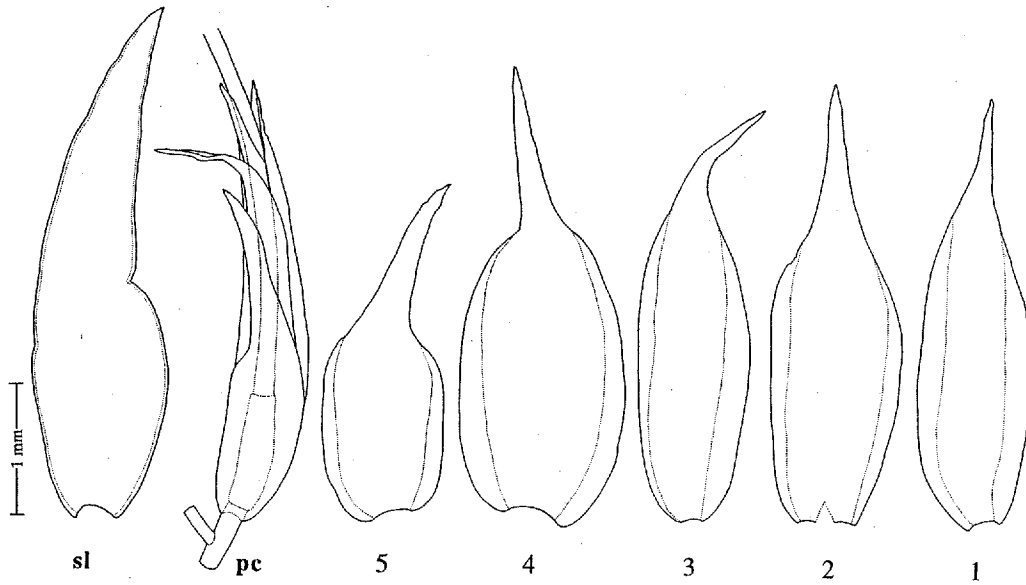


Figure XX. Perichaetium and perichaetial leaves (expanded) around mature sporophyte of Leucobryum aduncum Dozy & Molk. var. aduncum. Numbers show the order of perichaetial leaves from the innermost leaf (number 1); pc, perichaetium; sl, stem leaf (expanded) near perichaetium. All figures were drawn from lectotype of L. aduncum (L).



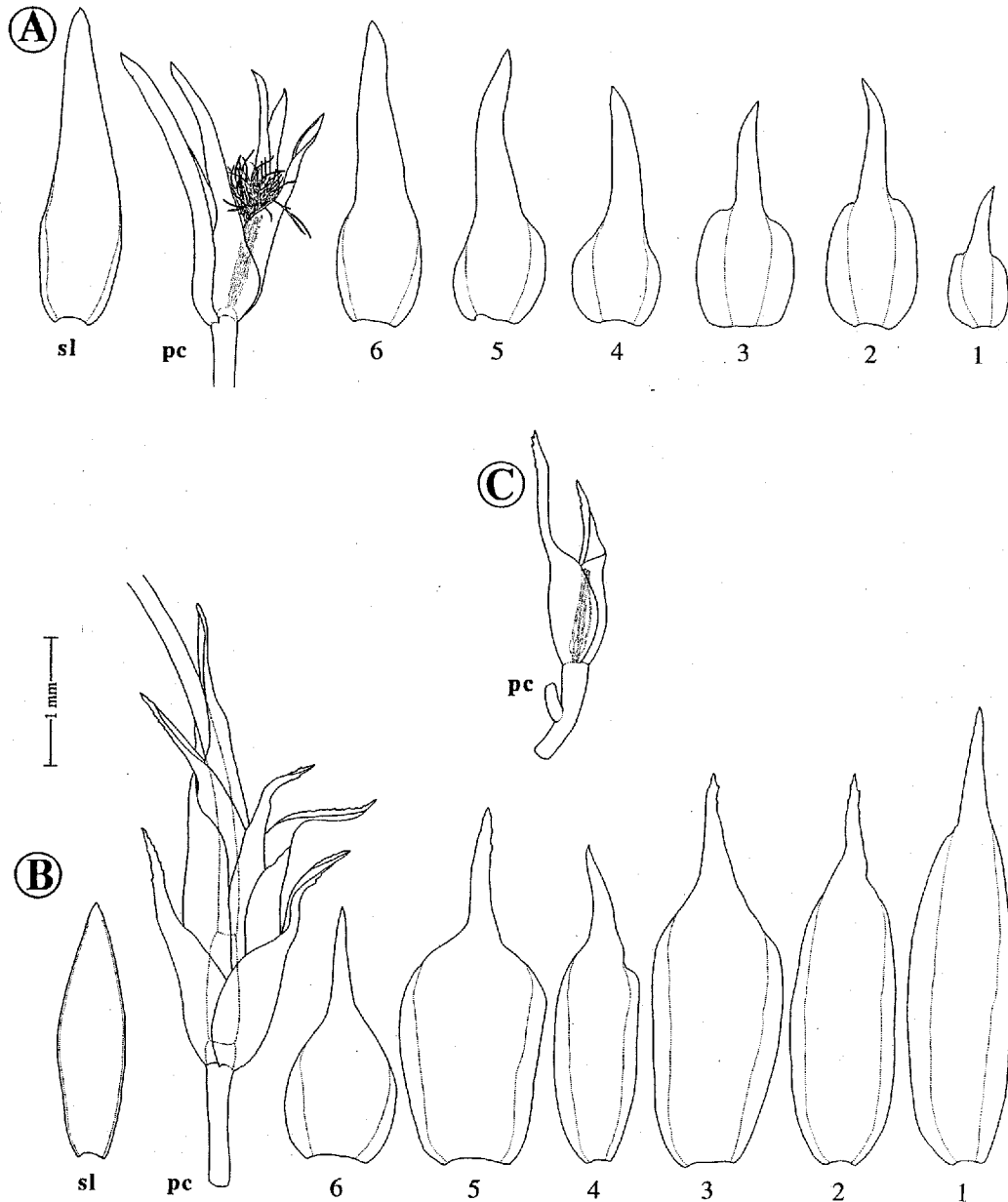


Figure XXI. Perichaetial leaves of *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. A. Perichaetium and perichaetial leaves (expanded) around unfertilized archegonia. B. Perichaetium and perichaetial leaves (expanded) around mature sporophyte. C. Unfertilized perichaetium. Numbers show the order of perichaetial leaves from the innermost leaf (number 1); pc, perichaetium; sl, stem leaves (expanded) near perichaetia A and B respectively. Fig. A was drawn from holotype of *L. krempfii* (PC); B, C, from isoelectotype of *L. scalare* var. *marschmeyerii* (HIRO).

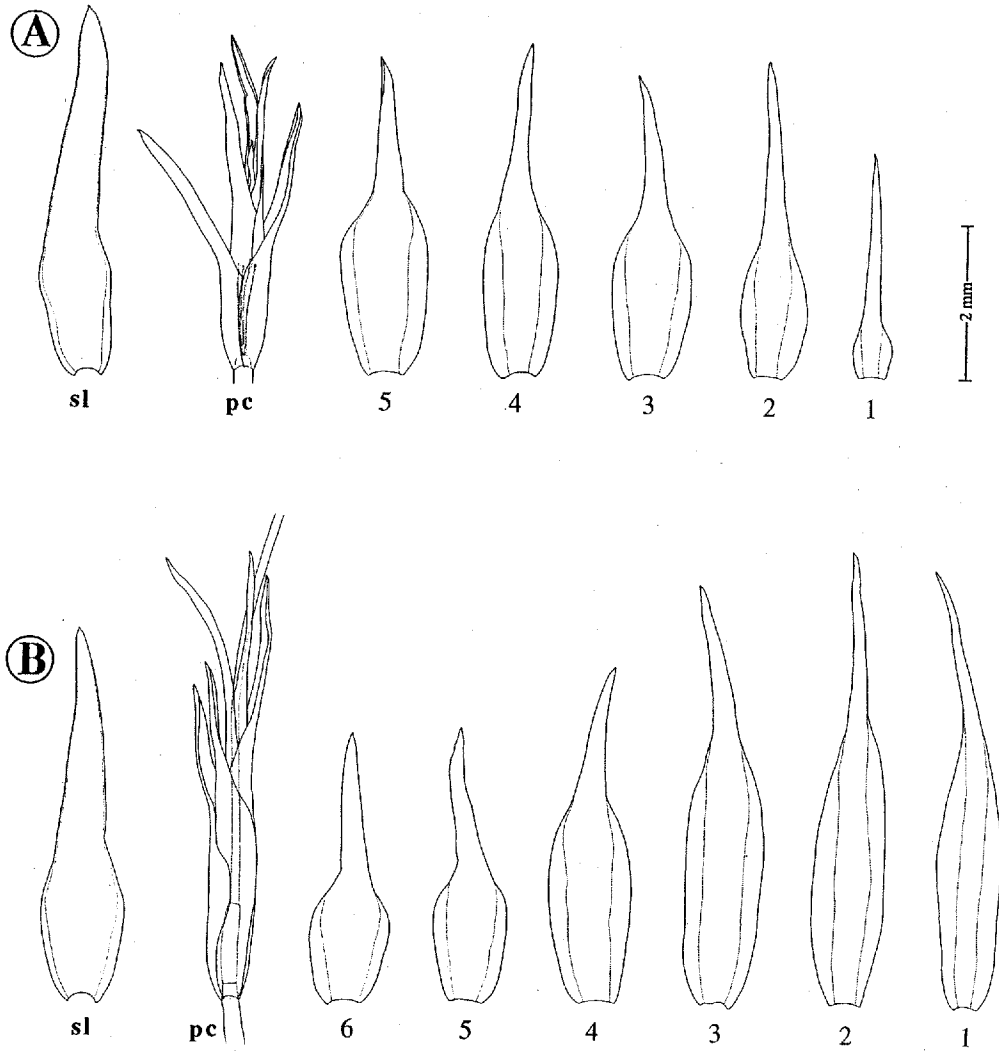


Figure XXII. Perichaetial leaves of *Leucobryum juniperoideum* (Brid.) C. Müll. A. Perichaetium and perichaetial leaves (expanded) around unfertilized archegonia. B. Perichaetium and perichaetial leaves (expanded) around mature sporophyte. Numbers show the order of perichaetial leaves from the innermost leaf (number 1); pe, perichaetium; sl, stem leaves (expanded) near perichaetia A and B respectively. All figures were drawn from Noguchi 16753 (NICH).

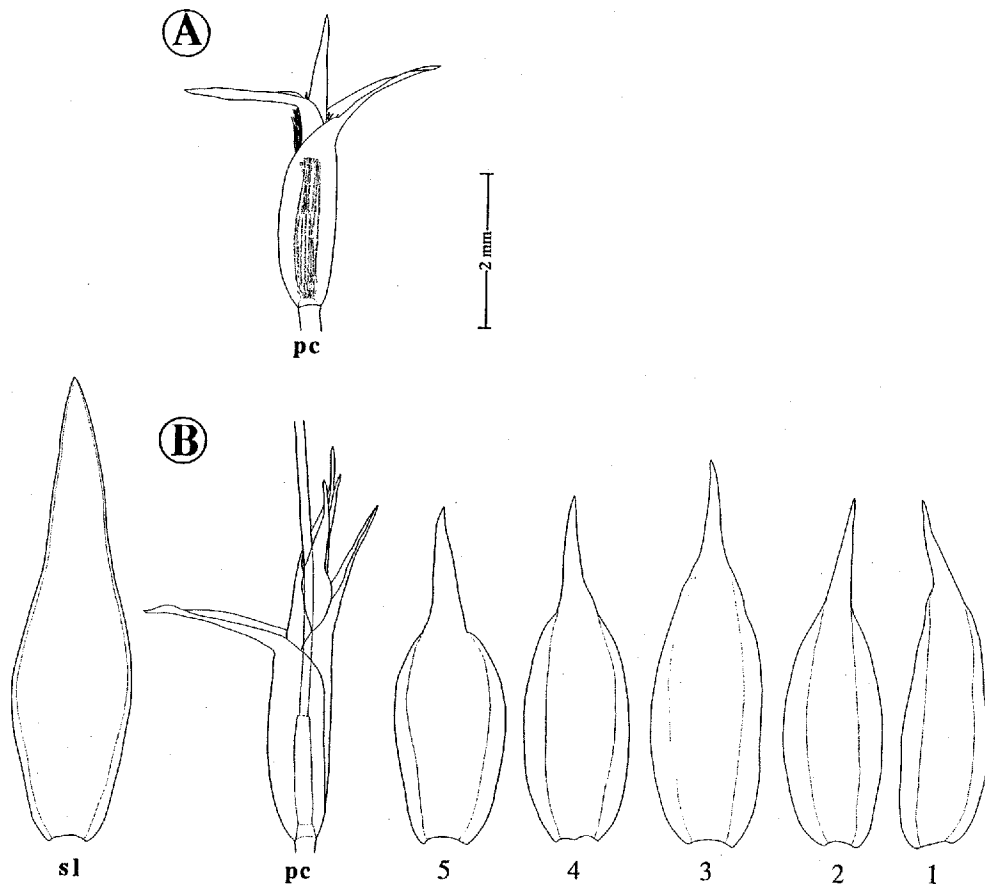


Figure XXIII. Perichaetial leaves of *Leucobryum glaucum* (Hedw.) Ångstr. in Fries. A. Unfertilized perichaetium. B. Perichaetium and perichaetial leaves (expanded) around mature sporophyte. Numbers show the order of perichaetial leaves from the innermost leaf (number 1); pc, perichaetium; sl, stem leaf (expanded) near perichaetia A and B. All figures were drawn from Zanten 3319 (NICH).

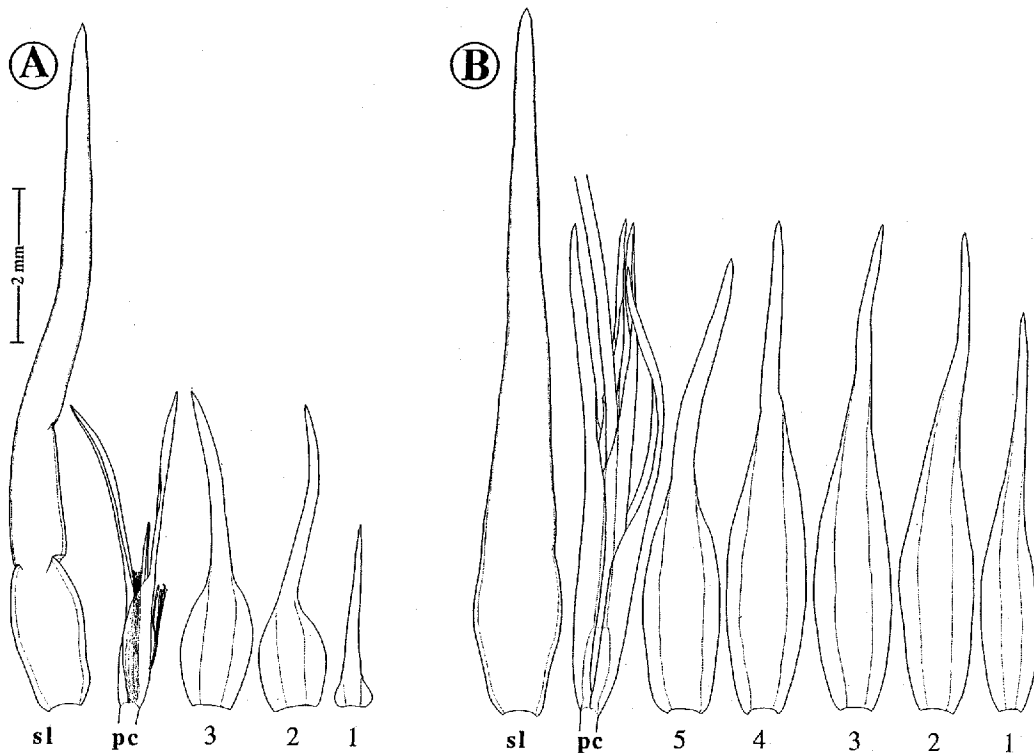


Figure XXIV. Perichaetial leaves of *Leucobryum bowringii* Mitt. A. Perichaetium and perichaetial leaves (expanded) around unfertilized archegonia. B. Perichaetium and perichaetial leaves (expanded) around mature sporophyte. Numbers show the order of perichaetial leaves from the innermost leaf (number 1); pc, perichaetium; sl, stem leaves (expanded) near perichaetia A and B respectively. All figures were drawn from Yamaguchi 9313 (HIRO).

bowringii, L. juniperoideum and L. scabrum from Japan. I found a significant difference between the length of inner perichaetial leaves and that of stem leaves among L. bowringii, L. juniperoideum and L. scabrum (Table 8).

The perigonia are bud-like and very small. The inner perigonial leaves are composed of the round sheathing base which envelops the antheridia (Fig. XXV).

#### 6. Sporophytes

The characters of the sporophytes of Leucobryum are quite similar to those of Dicranum (Fig. XXVI). The genus Leucobryum has a typical dicranoid peristome and this is one of the basic reasons that Leucobryum remains in Dicranales (Fleischer 1904, Edwards 1979). The characters of sporophyte, especially for peristome teeth, are almost same among the taxa treated in this study. For classification of the taxa of Leucobryum, I used the position of sporophytes and the inclination of capsules.

#### V. Sexual reproduction

In the genus Leucobryum, male plants are rare, so that sexual reproduction is infrequent. In this chapter, I discuss sexual reproduction of this genus using data of three species widely distributed in Japan: L. bowringii, L.

Table 8. Ratio of length of inner perichaetial leaves to ordinary leaves near the perichaetium of three species of Leucobryum in Japan<sup>1</sup>

Species	Min. (mm)	Mean (mm)	Max. (mm)	Standard deviation	Number of specimens examined	Number of materials
<u>L. juniperoideum</u>	0.96	1.36	1.79	0.21	19	55
<u>L. bowringii</u>	0.52	0.72	0.93	0.10	20	54
<u>L. scabrum</u>	0.33	0.44	0.57	0.05	19	44

<sup>1</sup>Length of inner perichaetial leaf / Length of ordinary leaf near the perichaetium. The length of inner perichaetial leaf was measured from the longest leaf among inner two leaves. The length of ordinary leaf was average of three longest leaves near the perichaetium.

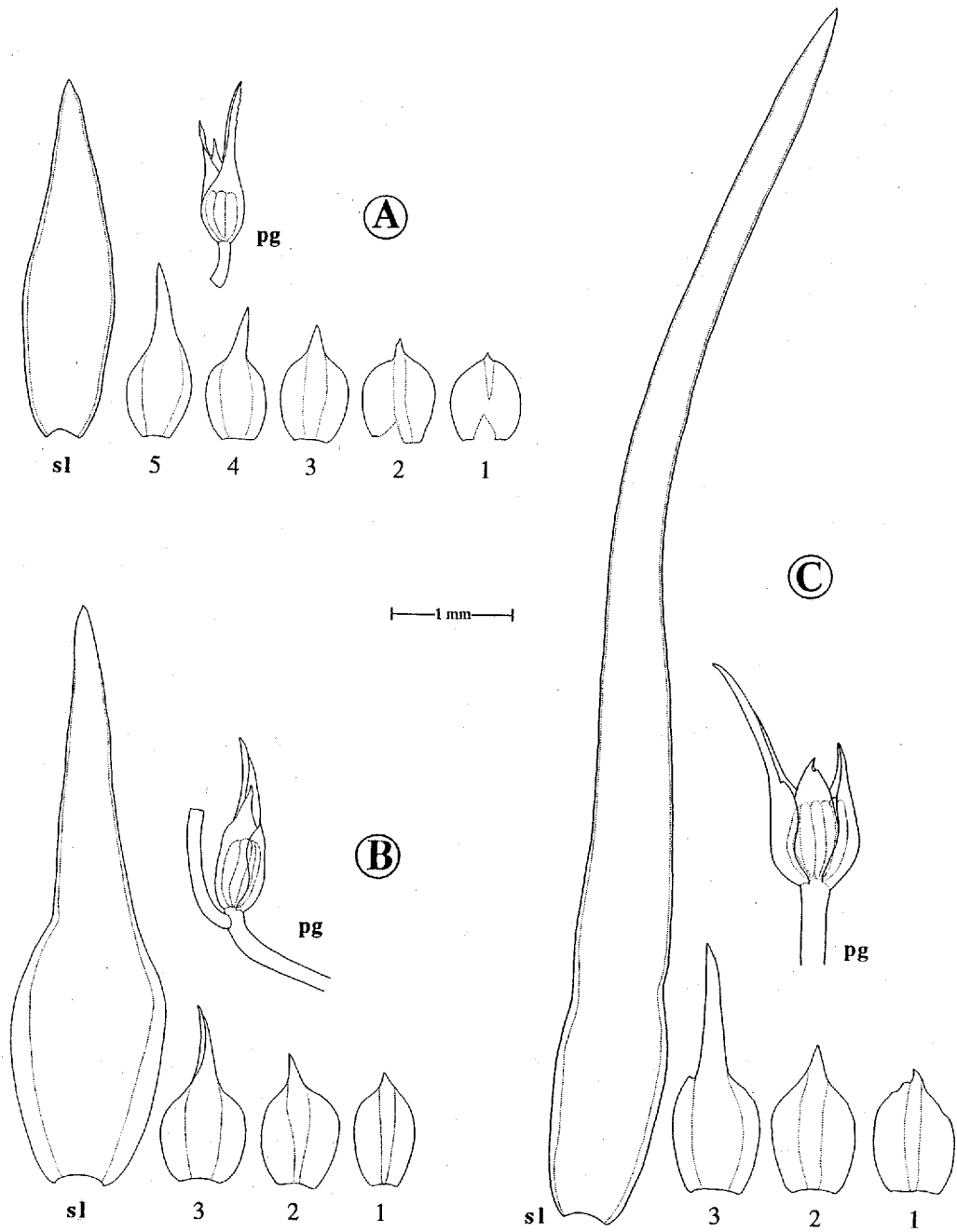


Figure XXV. Perigonal leaves (expanded) of 3 taxa of *Leucobryum*. A. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. B. *L. juniperoideum* (Brid.) C. Müll. C. *L. bowringii* Mitt. Numbers show the order of perigonal leaves from the innermost leaf (number 1); pg, perigonium; sl, stem leaves near perigonia A, B and C respectively. Fig. A was drawn from lectotype of *L. scalare* (FH); B, from Noguchi 16753 (NICH); C, from Yamaguchi 9313 (HIRO).

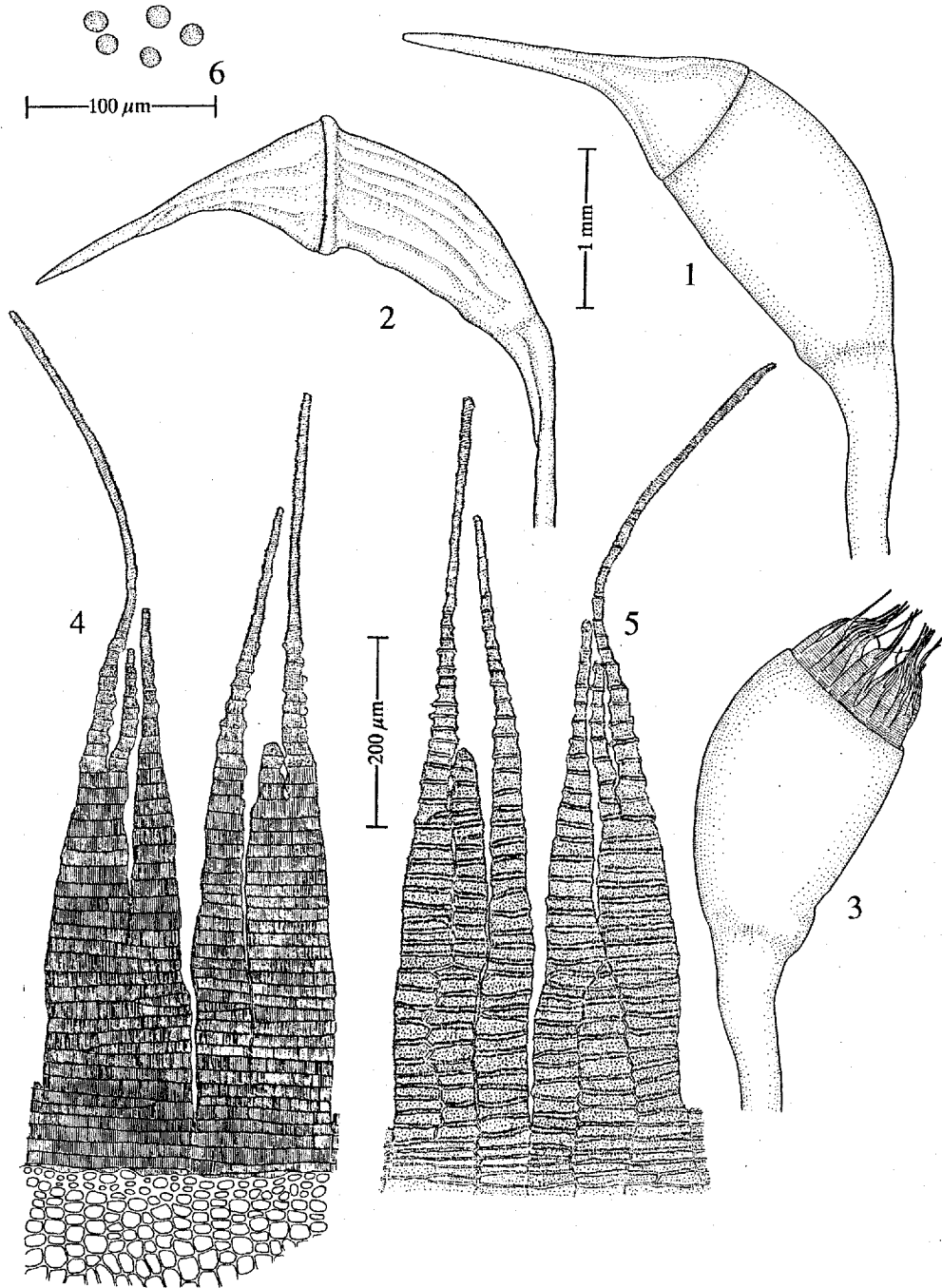


Figure XXVI. Sporophytes of *Leucobryum scabrum* Lac. 1-3. Capsules. 4, 5. peristome teeth (4, dorsal view; 5, ventral view). 6. Spores. All figures were drawn from Iwatsuki & Minamidani s. n., *Musci Japonici Exsiccati* 28: 1378 (NICH).



juniperoideum and L. scabrum. These species produce sporophytes more or less frequently.

### 1. Sexuality

Fleischer (1904), Williams (1913) and Yamaguchi and Iwatsuki (1987) critically described the sexuality of the Leucobryum, but many other authors did not mention this character. Most species of Leucobryum have dioicous inflorescence, but Fleischer (1904) described L. chlorophyllosum as an autoicous species. If Fleischer was right, this is only autoicous species in the genus. My critical examination of the type specimen of L. chlorophyllosum, however, proved that there are female and normal male plants in the packet. Therefore, sexuality of all species of Leucobryum previously examined until now are dioicous.

In the genus Leucobryum, two types of male plants have been reported by many authors. The first type is the normal male plants which are as large as the female plants (Fleischer 1904, Yamaguchi & Iwatsuki 1987), or somewhat smaller than the female plants (Dixon 1924, Blackstock 1987). The second type is the dwarf male plants which are much smaller (usually only a few mm long) than the female plants, and always epiphytic on various parts of the female plants. The dwarf male plants grow on stem leaves of female plants (Crum & Steere 1957, Crum 1976, Scott & Stone 1976,

Yamaguchi & Iwatsuki 1987), or on the tomentum enclosed by the perichaetial leaves (Williams 1913, Woesler 1935, Grout 1937, Florschütz 1964, Blackstock 1987, Yamaguchi & Iwatsuki 1987). These sexual conditions are classified into four types according to Wyatt and Anderson (1984), as follows:

1. Dioicous. The condition with equal sized male and female plants (Fig. XXVII: 1, 2, XXVIII: 1, 2)

2. Heterodioicous. The condition in which the male plants are smaller than female plants, but they are free-living and independent (Fig. XXIX: 3-9).

3. Pseudoautoicous. The condition of male plants that are tiny and bud-like, epiphytic on the stems of female plants, and generally attached to a mass of tomentum (Fig. XXVII: 3-5, XXVIII: 3-6, XXIX: 2).

4. Phyllodioicous. The condition of male plants that are tiny and bud-like, epiphytic on the leaves of female plants (Fig. XXX: 3, 4).

Among these classification (Wyatt & Lewis 1984), the condition of pseudoautoicous is not strictly adapted to the Leucobryum, because the dwarf male plants of Leucobryum attach to a tomentum enclosed by perichaetial leaves and not to that on stems. L. bowringii shows the heterodioicous condition, but the independent small male plants seem to be developed from dwarf male plants.

In the course of this study, I found two types of sexuality in the same species, or even in the same specimen. I critically examined three species of Leucobryum, L. juniperoideum, L. bowringii and L. scabrum to clarify the sexual conditions and the formation of the dwarf male plants. Table 9 shows the sexual conditions and the fertilities of three species. The occurrence of normal male plants is rare (in L. scabrum, no normal male plants are observed). According to Une (unpublished data), however, dwarf male plants of L. scabrum grow into the normal sized plants by trans-plantation onto the soil with the distilled water. Therefore, the dwarf male plants of these isosporous species are not genetically controlled, and the dwarf male plants possibly grow larger if they were removed from the female plants. Une (1985a) defined the term pseudonanandrous as the condition of dioicous which includes nongenetically controlled dwarf male plants.

The growing positions of the dwarf male plants in three species of Leucobryum are shown in Table 10. In L. juniperoideum the dwarf male plants grow mainly on the tomentum enclosed by the perichaetial leaves of the female plants, while in L. scabrum they are restricted on the stem leaves of female plants. In L. scabrum the formation of tomenta were not observed. In L. bowringii the dwarf male plants grow both on the tomenta and on stem leaves of female



Figure XXVII. Sexuality of *Leucobryum juniperoideum* (Brid.) C. Müll. 1a, 1b. Normal male plant and its branching. 2a, 2b. Female plant and its branching. 3. Dwarf male plants growing on tomentum enclosed by perichaetial leaves. 4, 5. Dwarf male plants and their branching. 6a–7b. Perigonia and antheridia from normal male plant (6a, 6b) and dwarf male plant (7a, 7b). 8a, 8b. Perichaetium and archegonium. 9, 10. Inner perichaetial leaves showing formations of tomenta (10, expanded abaxial view). 11–13. Cross-sections of inner perichaetial leaf at basal part. Arrow shows the central position in cross-section. 14. Median cells at sheathing base of inner perichaetial leaf, showing base of rhizoid which forms tomentum. ♂ and ♀ represent perigonium and perichaetium respectively; ch, chlorocyst; le, leucocyst; rh, rhizoid. Figures 1a, 1b, 2a, 2b, 4, 6a, 6b, 8a, 8b were drawn from Noguchi 16753 (NICH); 3, 5, 7a, 7b, 10–14, from Une 3545 (HIRO); 9, from Iwatsuki 12012 (NICH).



Figure XXVIII. Sexuality of *Leucobryum bowringii* Mitt. 1a, 1b. Normal male plant and its branching. 2a, 2b. Female plant and its branching. 3. Dwarf male plants growing on tomentum enclosed by perichaetial leaves. 4a-6b. Dwarf male plants and their branching. 7a-9b. Perigonia and Antheridia from dwarf male plants 7a and 8a, and from normal male plant 9a. 10a, 10b. Perichaetium and archegonium. ♂ and ♀ represent perigonium and perichaetium respectively; rh, rhizoid which forms tomentum. Figs. 1a, 1b, 2a, 2b, 7a, 7b, 9a, 9b, 10a, 10b were drawn from Yamaguchi 9313 (HIRO); 3, 4a-6b, 8a, 8b from Yamada 572 (NICH).

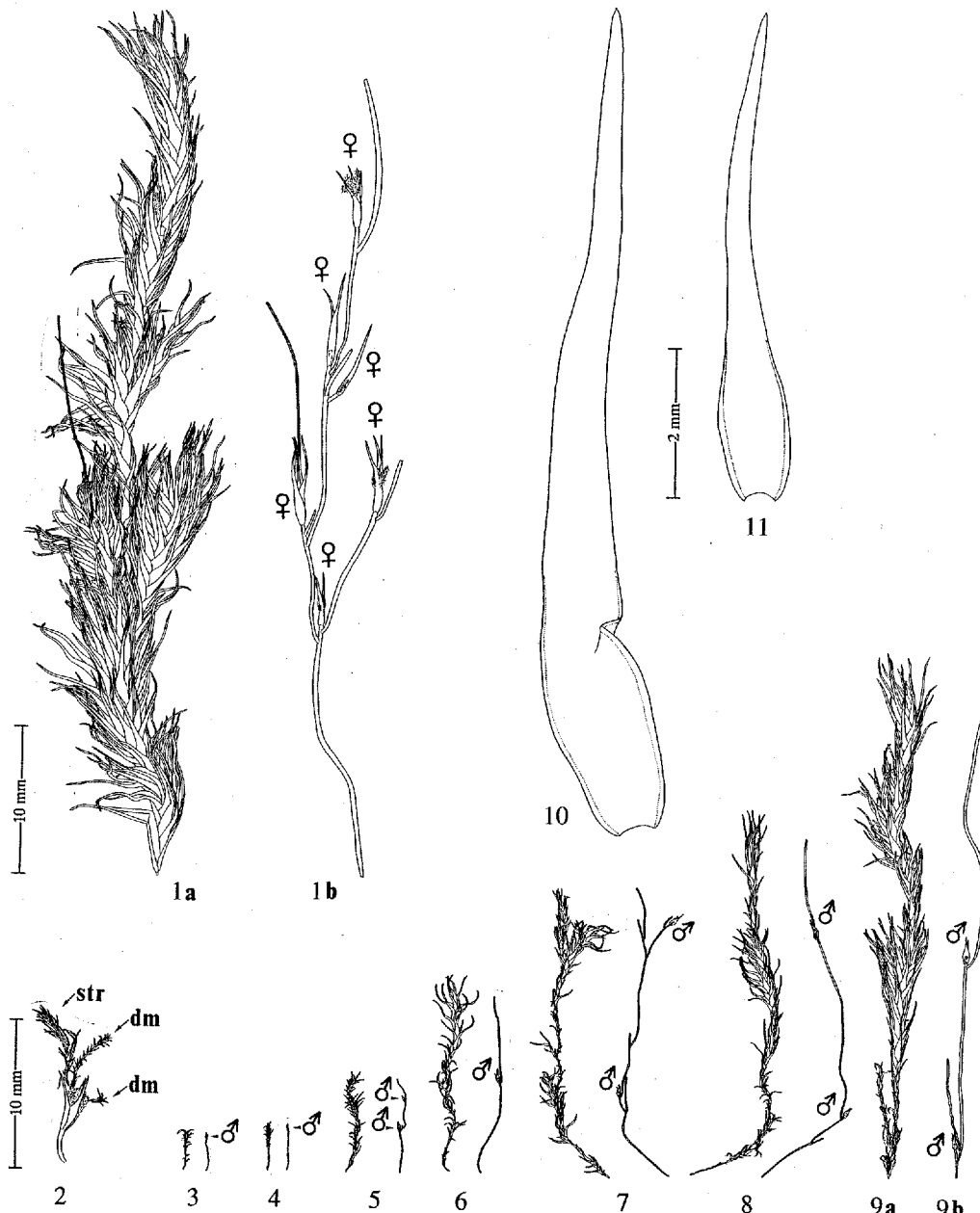


Figure XXIX. Secondary growth of dwarf male plants of *Leucobryum bowringii* Mitt. 1a, 1b. Female plant and its branching. 2. Dwarf male plants growing on tomentum enclosed by perichaetial leaves. 3-9b. Dwarf male plants and their branching. 10, 11. Stem leaves (expanded) of female plant 1a and male plant 9a respectively. ♂ and ♀ represent perigonium and perichaetium respectively; dm, dwarf male plant; str, sterile plant. All figures were drawn from Noguchi 26323 (NICH).

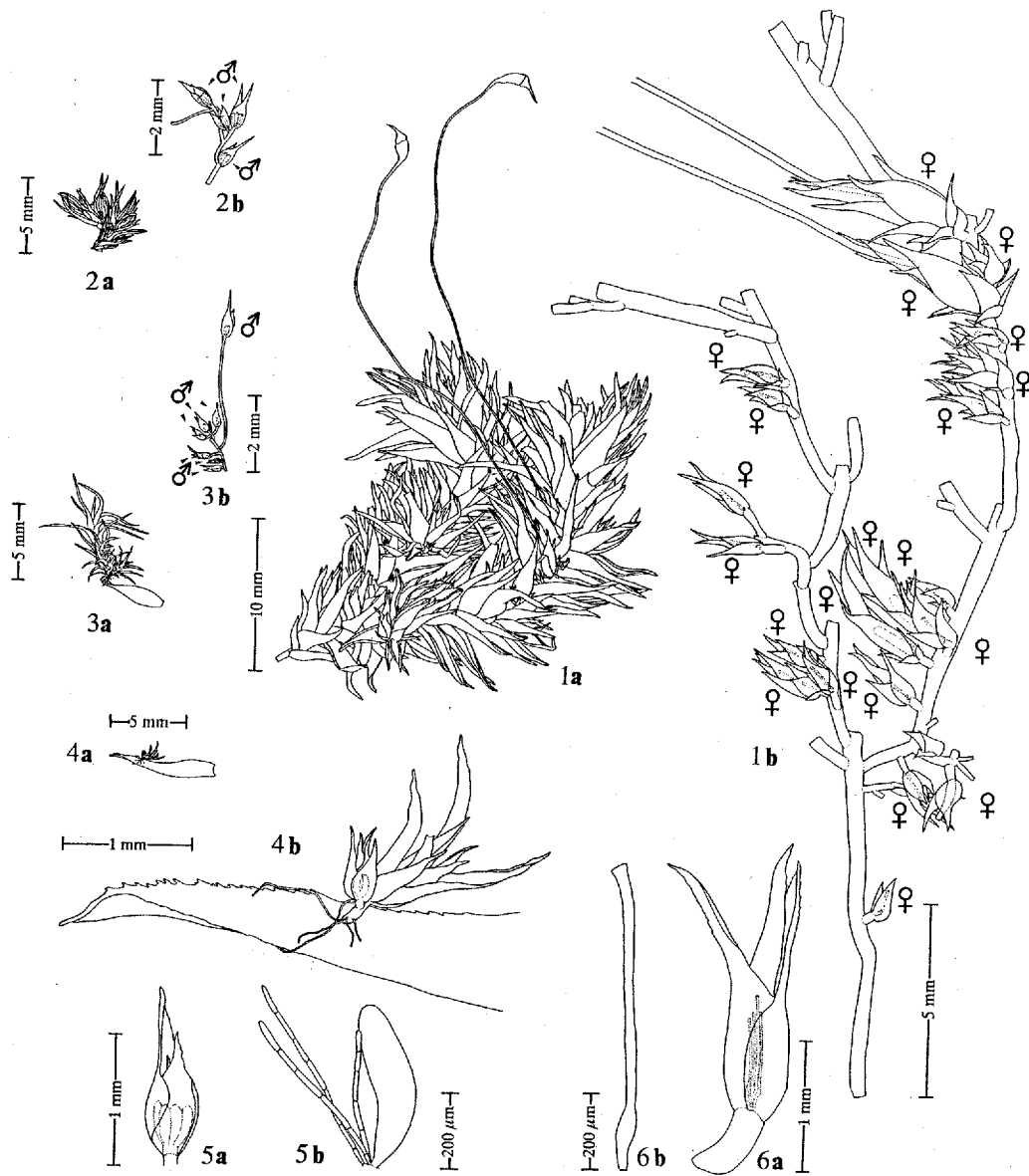


Figure XXX. Sexuality of *Leucobryum scabrum* Lac. 1a, 1b. Female plant and its branching. 2a, 2b. Dwarf male plant and its branching. 3a–4b. Dwarf male plants (3b, showing branching) growing on female stem leaves. 5a, 5b. Perigonium and antheridium from dwarf male plant. 6a, 6b. Perichaetium and archegonium. ♂ and ♀ represent perigonium and perichaetium respectively. Figs. 1a, 1b, 4a–6b. were drawn from Iwatsuki & Minamidani s. n., *Musci Japonici Exsiccati* 28: 1378 (NICH); 2a–3b, from Une 4329 (HIRO).

Table 9. Occurrence of male and female plants, and fertility of three species of Leucobryum in Japan

Species	Number of specimens <sup>1</sup> (Number of fruiting specimens)					Fertility <sup>2</sup> (%)	
	♀	♀+♂	♂	♀♂+♂	♀♂		Total
<u>L. juniperoideum</u>	123 (3)	9 (9)	9 (0)	6 (6)	27 (27)	171 345	13.0
<u>L. bowringii</u>	96 (9)	12 (12)	4 (0)	12 (12)	24 (24)	116 264	21.6
<u>L. scabrum</u>	246 (0)	0 (0)	0 (0)	0 (0)	20 (20)	45 311	6.4

<sup>1</sup>♀: Female plants. ♂: Normal male plants. ♀♂: Dwarf male plants. Sterile: No sex organ.

<sup>2</sup>(Specimens with sporophytes / Total number of specimens examined) x 100.



Table 10. Growing positions of dwarf male plants of three species of Leucobryum in Japan

Species	Growing positions of dwarf male plants		Number of specimens examined
	on tomentum enclosed by perichaetial leaves	on stem leaf of female or among female shoots	
<u>L. juniperoideum</u>	31	2	33
<u>L. bowringii</u>	21	20	36
<u>L. scabrum</u>	0	20	20

plants in almost equal frequency. The dwarf male plants detached from the tomenta often elongate and finally grow independent male plants (Fig. XXIX).

The tomenta in the perichaetia derive from the rhizoids on the abaxial, lower central parts of inner perichaetial leaves which envelop the archegonia (Fig. XXVII: 9, 10, XXVIII: 10). The tomenta are not observed in the perichaetia with mature sporophyte and usually restricted to those with unfertilized archegonia. The rhizoid forming cells are restricted to abaxially exposed chlorocysts which lie usually on the lower median part of perichaetial leaf (Fig. XXVII: 11-14).

This is the first report of presence of the dwarf and the normal male plants in L. bowringii and L. scabrum. Blackstock (1987) studied the male gametophores of L. glaucum and L. juniperoideum. He described the distribution and variation in size of male plants associated with female plants. He concluded that large sized male plants were derived from dwarf male plants, because of the absence of colonies of normal male plants. However, I found the colonies which contain only normal male plants in L. juniperoideum and L. bowringii (Table 9). I consider the male spores of these two species seem to be able to germinate without the influence of female plants and grow independently to the male plants.

2. Geographical distributions of female and male plants of L. juniperoideum, L. bowringii and L. scabrum in Japan

The distributional patterns of female and male plants of three species of Leucobryum in Japan are similar to those of Macromitrium gymnostomum and M. japonicum reported by Une (1985b) (Fig. XXXI-XXXIII). In L. juniperoideum and L. bowringii the occurrence of the normal male plants are rare, and their distribution range is restricted to the relatively low altitude and latitude compared with that of dwarf male plants. The fact seems to suggest that the survival capacity against the low temperature of male plants especially of normal male plants is lower than that of female plants, as mentioned by Une (1985c).

#### VI. Asexual reproduction

In most cases the taxa of Leucobryum form the caducous leaves which have function of asexual reproduction. This type of caducous leaves is defined as gemmae (Imura & Iwatsuki 1990). The ordinary leaves also bear rhizoids at apices and are considered to be related to asexual reproduction. The caducous leaves are formed at stem apices or on the specialized branchlets (Fig. XXXIV: 1). The abaxial leucocysts at the base of caducous leaves are scarcely decurrent on stems or branchlets, so that the

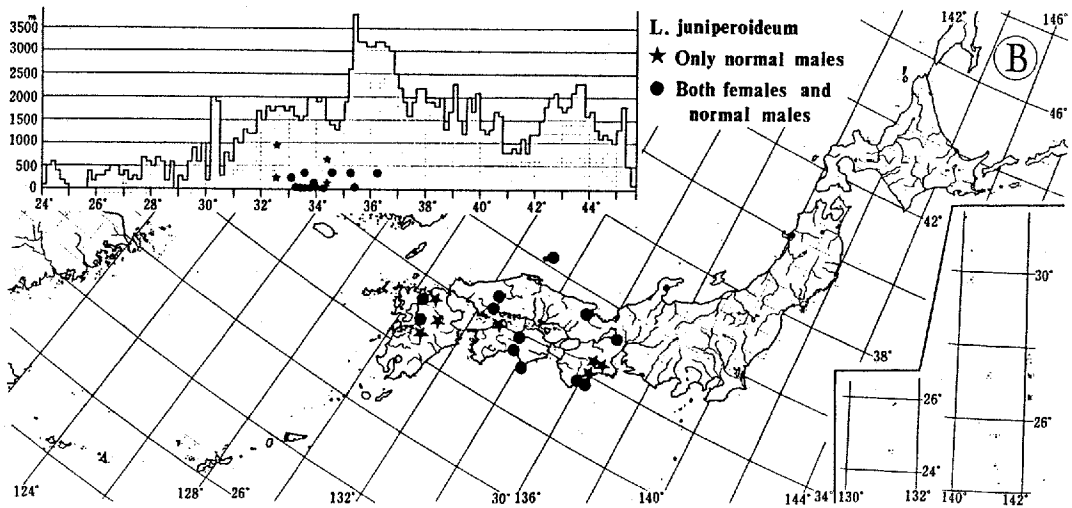
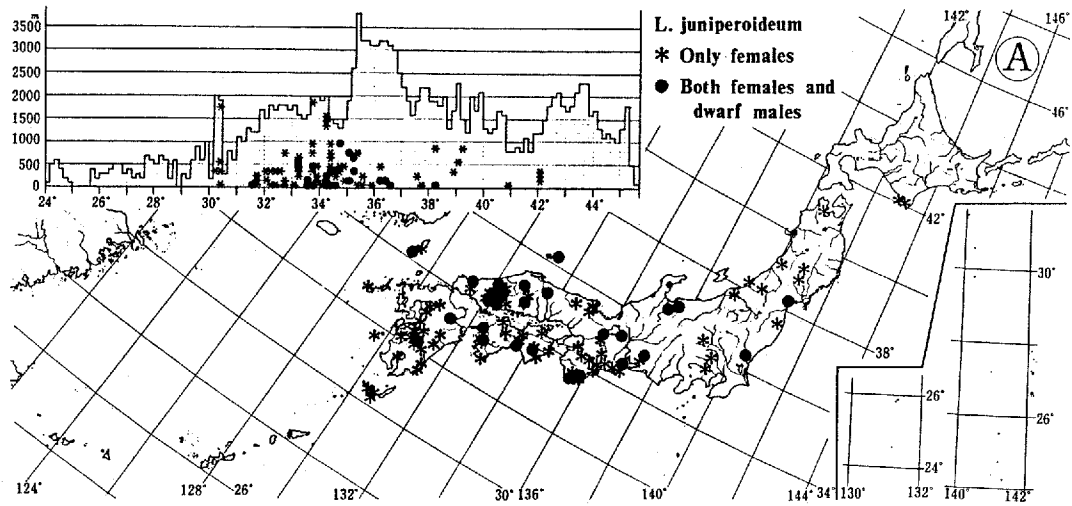


Figure XXXI. Geographical distributions of female and male plants of Leucobryum juniperoideum (Brid.) C. Müll. in Japan.

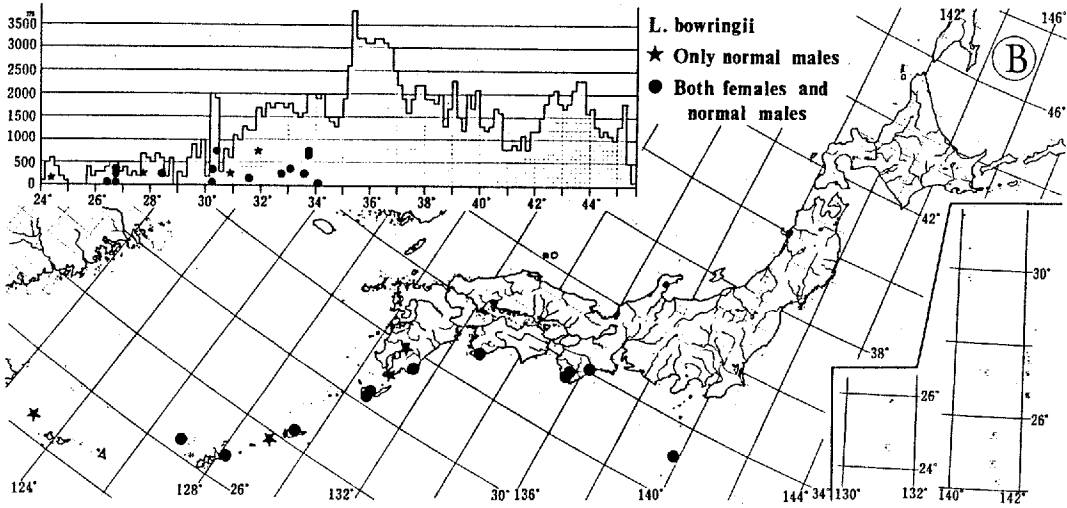
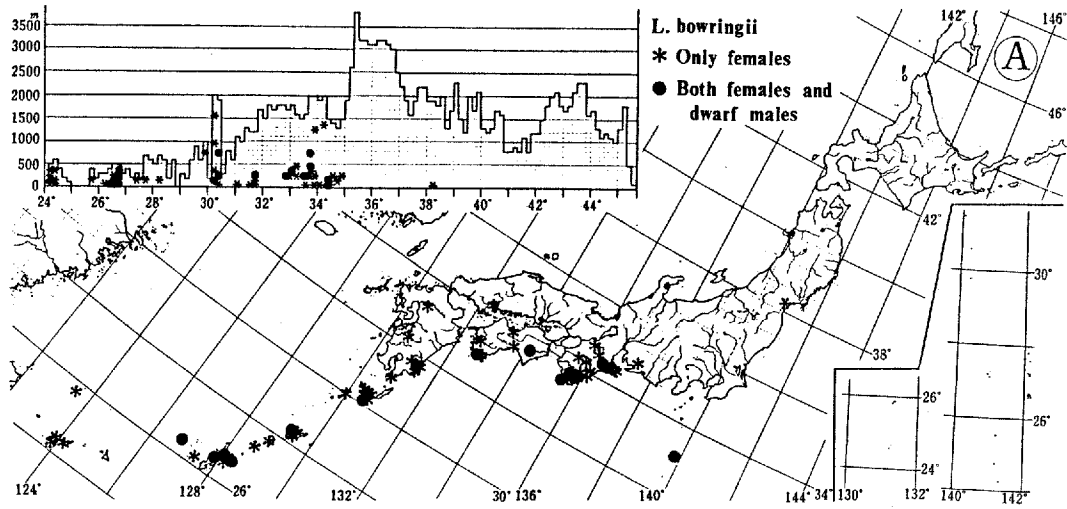


Figure XXXII. Geographical distributions of female and male plants of *Leucobryum bowringii* Mitt. in Japan.

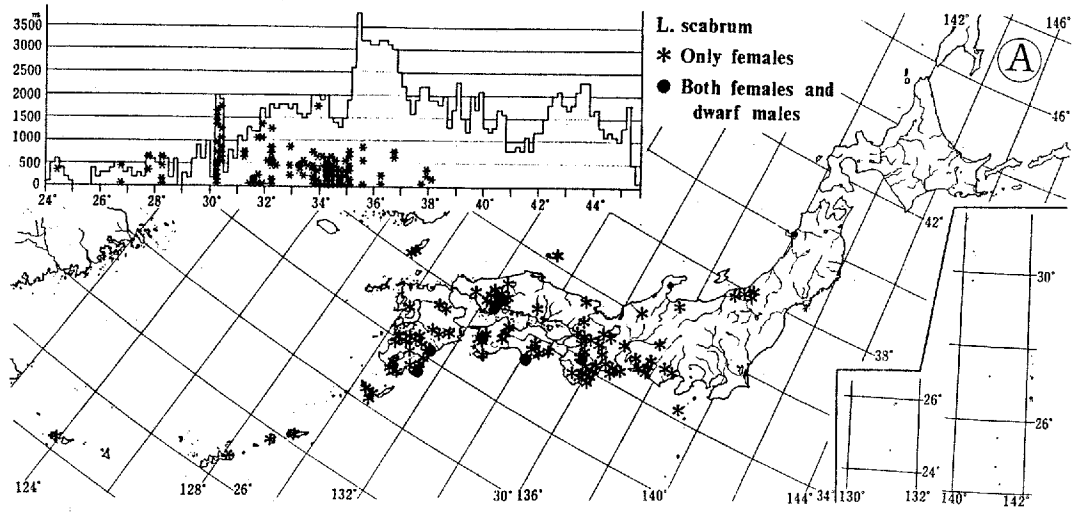


Figure XXXIII. Geographical distributions of female and male plants of *Leucobryum scabrum* Lac. in Japan.

caducous leaves are easily detached from the stems or branchlets (Fig. XXXIV: 6). Moreover, the caducous leaves are much smaller than the ordinary leaves (Fig. XXXIV: 2, 3).

In L. imbricatum extremely specialized gemmae are found at the stem apex enclosed by ordinary leaves (Fig. XXXV). This type gemmae is similar to those of Brothera leana.

#### VII. Synopsis of the genus Leucobryum in Asia

In this study I encountered 17 taxonomic characters (Table 11) and compared each taxon reported in this area.

Among 17 characters, following nine characters are newly adapted to the taxonomical study of Asian Leucobryum: (1) the central strand of stem, (2) the manner of proration of abaxial leucocysts at apical parts of leaves, (3) the decurrency of abaxial leucocysts, (4) the ratio between thickness of the thickest part and thickness of the median furrow in cross-section of leaf, (5) the position of perichaetia, (6) the ratio between length of the mature inner perichaetial leaf and length of the stem leaf near the perichaetium, (7) the length of archegonia, (8) the presence of the normal male plants, and (9) the growing habitat of the dwarf male plants.

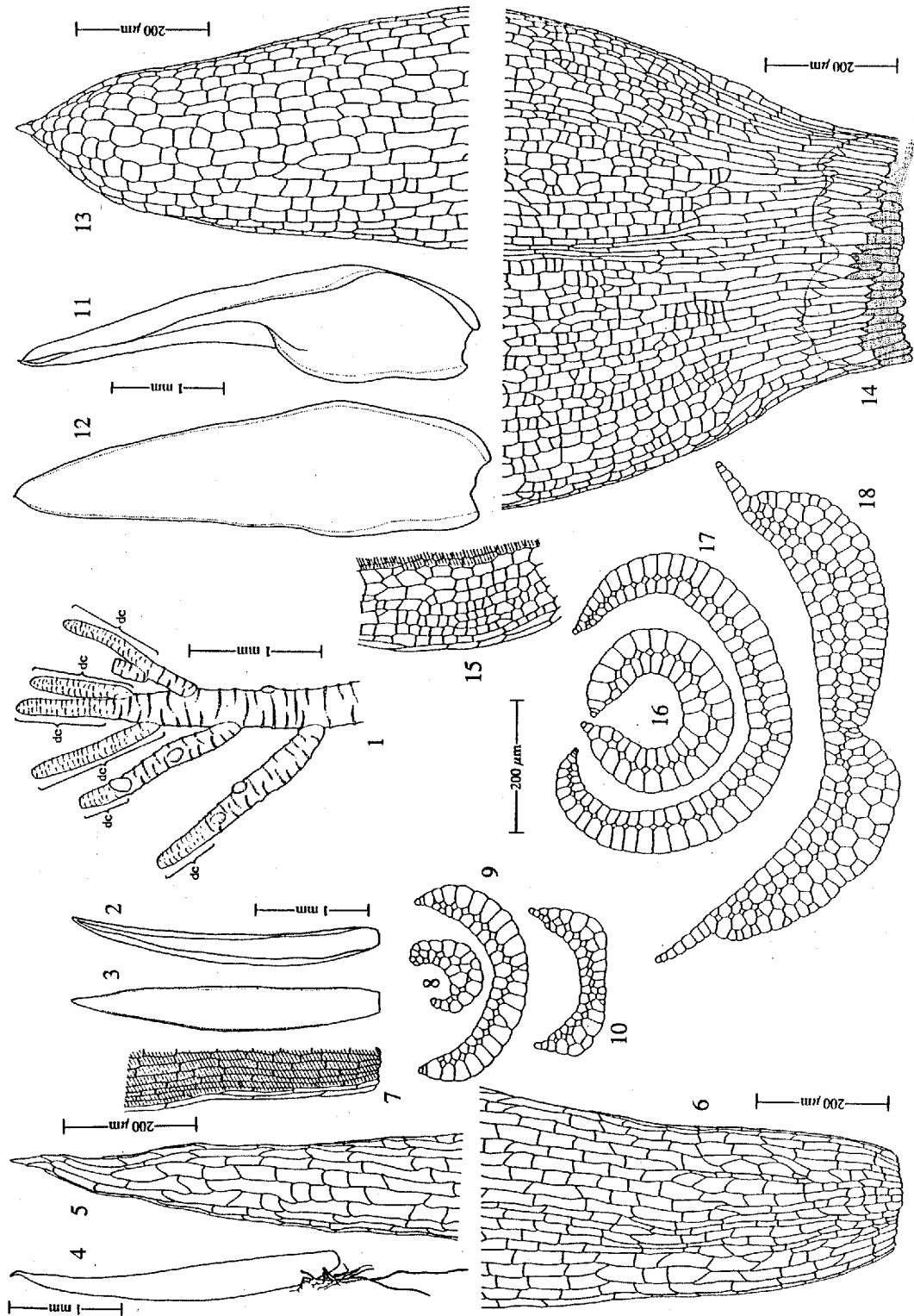


Figure XXXIV. Asexual reproduction of *Leucobryum humillimum* Card. by deciduous leaves. 1. Branching. dc shows portion which produces deciduous leaves. 2-4. Deciduous leaves (3, 4, expanded). 5. Apex of deciduous leaf. 6. Base of deciduous leaf (abaxial view). 7. Basal cells of deciduous leaf (adaxial view). 8-10. Cross-sections of deciduous leaf (8, apical; 9, median; 10, basal portions). 11, 12. Ordinary leaves (12, expanded). 13. Apex of ordinary leaf. 14. Base of ordinary leaf (abaxial view). 15. Basal cells of ordinary leaf (adaxial view). 16-18. Cross-sections of ordinary leaf (16, apical; 17, median; 18, basal portions). All figures were drawn from lectotype of *L. cucullifolium* (PC).



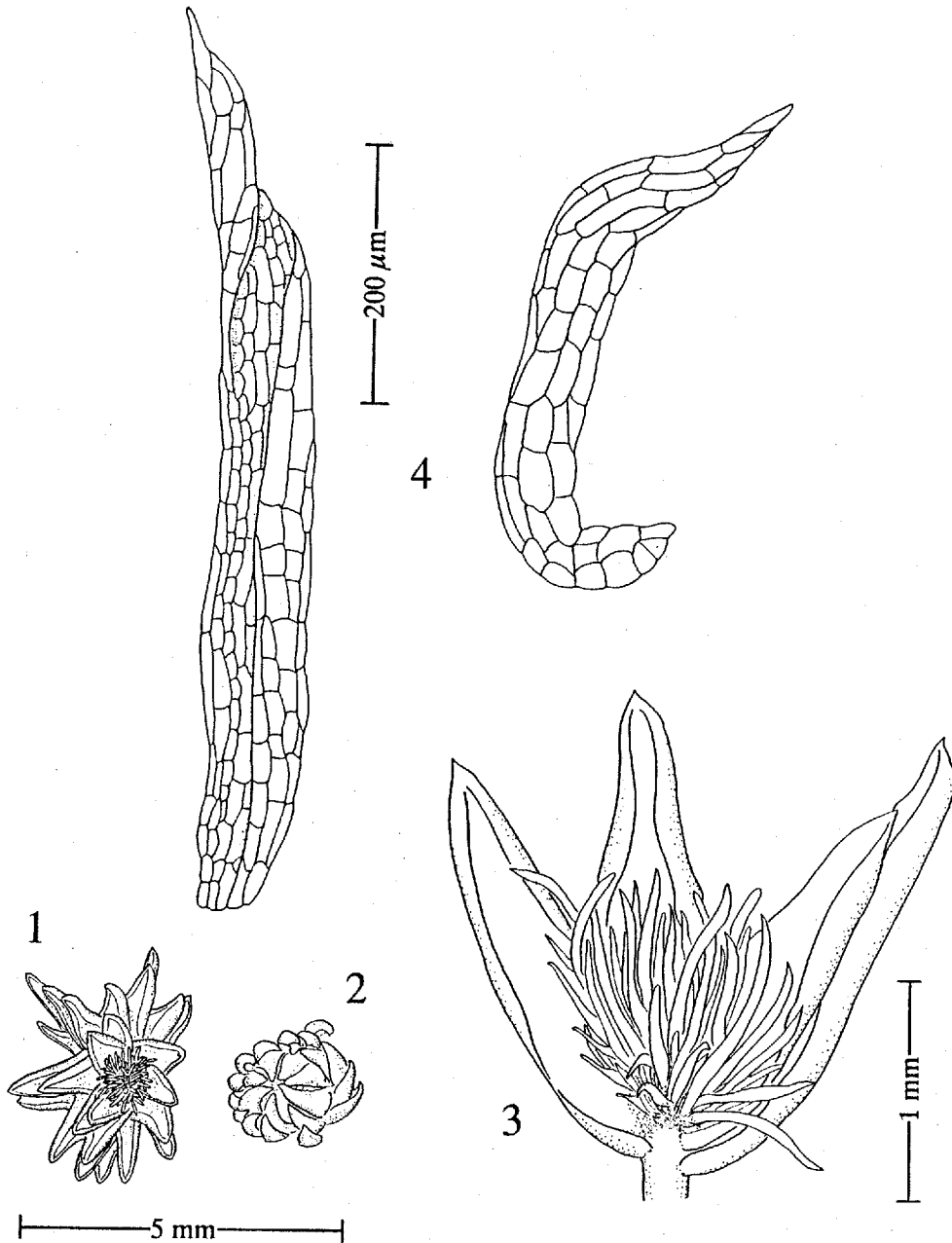


Figure XXXV. Asexual reproduction of Leucobryum imbricatum Broth. by gemmae. 1-3. Shoot apices (1, wet condition; 2, dry condition). 4. Gemmae. All figures were drawn from lectotype of L. imbricatum (H).

Tabele 11. Comparison of some selected characters among the 19 taxa of Asian Leucobryum

Taxa	Maximum length of plant (mm)	Central strand of stem	Leaf arrangement and posture when dry
<u>Leucobryum javense</u>	80	absent	widely spreading, somewhat falcate secund, flexuose above
<u>L. javense</u> var. <u>cyathifolium</u>	80	absent	erect spreading, somewhat falcate secund or squarrose
<u>L. javense</u> var. <u>novae-guineae</u>	150	absent	appressed to erect spreading
<u>L. javense</u> var. <u>uncinatum</u>	80	absent	erect to widely spreading
<u>L. scabrum</u>	60	absent	erect spreading, somewhat falcate secund
<u>L. aduncum</u>	50	absent	falcate secund, somewhat arranged in 5 rows
<u>L. aduncum</u> var. <u>teysmannianum</u>	55	absent	erect spreading, arranged in 5 rows
<u>L. aduncum</u> var. <u>scalare</u>	35	absent	closely imbricate, forming conical point at shoot apex
<u>L. chlorophyllosum</u>	20	absent	erect to widely spreading
<u>L. boninense</u>	50	absent	erect spreading or slightly falcate secund
<u>L. juniperoideum</u>	35	absent	erect spreading
<u>L. humillimum</u>	30	present	imbricate to erect spreading
<u>L. imbricatum</u>	30	present	closely imbricate
<u>L. glaucum</u>	50	absent	erect spreading
<u>L. bowringii</u>	60	present	erect to widely spreading, flexuose and contorted above
<u>L. sumatranum</u>	120	present	erect to widely spreading, somewhat falcate secund, flexuose and contorted above
<u>L. sericeum</u>	35	present	falcate secund
<u>L. sanctum</u>	70	present	widely spreading, somewhat squarrose
<u>L. arfakianum</u>	60	present	appressed to erect spreading

Table 11. Continued

Taxa	Leaf length (mm)	Leaf length / width	Leaf apices	Proration on abaxial side of leaf acumina
<u>Leucobryum javense</u>	8.0-18.0	5.3-5.8	acute to bluntly mucronate	papillosely prorate to 3/10
<u>L. javense</u> var. <u>cyathifolium</u>	9.1-13.0	3.1-4.3	round and apiculate	papillosely prorate to 1/10
<u>L. javense</u> var. <u>novae-guineae</u>	6.6-10.0	3.7-5.0	acute to bluntly mucronate	papillosely prorate to 3/10
<u>L. javense</u> var. <u>uncinatum</u>	8.4-9.7	4.4-5.1	acute and uncinata	papillosely prorate to 4/10
<u>L. scabrum</u>	7.9-8.2	4.3-4.6	acute	undulate and spinosely prorate to 6/10
<u>L. aduncum</u>	3.5-4.1	2.8-4.8	acute	undulate and spinosely prorate to 6/10
<u>L. aduncum</u> var. <u>teysmannianum</u>	3.7-4.3	3.4-4.3	acute	undulate and spinosely prorate to 5/10
<u>L. aduncum</u> var. <u>scalare</u>	2.0-3.5	3.2-4.6	acute	undulate and spinosely or papillosely prorate to 5/10
<u>L. chlorophyllosum</u>	2.5-4.0	5.7-7.8	acute	undulate to 5/10
<u>L. boninense</u>	4.1-7.4	3.7-6.7	acute to bluntly mucronate	papillosely prorate to 6/10
<u>L. juniperoideum</u>	3.1-5.7	3.6-6.0	acute to bluntly mucronate	smooth
<u>L. humillimum</u>	3.0-4.5	3.0-5.3	mucronate	smooth
<u>L. imbricatum</u>	2.4-2.9	2.7-4.7	mucronate	smooth
<u>L. glaucum</u>	5.6-6.8	3.7-4.7	acute to bluntly mucronate	smooth
<u>L. bowringii</u>	4.2-11.0	4.9-13.8	acute	smooth
<u>L. sumatranum</u>	10.0-18.0	6.7-8.0	acute	smooth
<u>L. sericeum</u>	6.5-7.4	9.3-15.0	acute	papillosely prorate to 1/10
<u>L. sanctum</u>	5.3-7.1	4.3-5.3	acute to bluntly mucronate	papillosely prorate to 1/10
<u>L. arfakianum</u>	4.1-6.6	3.5-4.9	acute	smooth

Table 11. Continued

Taxa	Number of cell rows of hyaline lamina and border at leaf base	Decurrency of abaxial leucocysts
<u>Leucobryum javense</u>	6-11	± decurrent on stem
<u>L. javense</u> var. <u>cyathifolium</u>	5-7	distinctly decurrent on stem
<u>L. javense</u> var. <u>novae-guineae</u>	2-7	distinctly decurrent on stem
<u>L. javense</u> var. <u>uncinatum</u>	3-4	distinctly decurrent on stem
<u>L. scabrum</u>	5-7	± decurrent on stem
<u>L. aduncum</u>	3-6	indistinct
<u>L. aduncum</u> var. <u>teysmannianum</u>	4-5	indistinct
<u>L. aduncum</u> var. <u>scalare</u>	3-6	indistinct
<u>L. chlorophyllosum</u>	6-8	indistinct
<u>L. boninense</u>	5-8	indistinct
<u>L. juniperoideum</u>	7-14	indistinct
<u>L. humillimum</u>	4-11	indistinct
<u>L. imbricatum</u>	3-5	indistinct
<u>L. glaucum</u>	5-10	indistinct
<u>L. bowringii</u>	7-12	indistinct
<u>L. sumatranum</u>	7-18	indistinct
<u>L. sericeum</u>	5-8	indistinct
<u>L. sanctum</u>	2-4	distinctly decurrent on stem
<u>L. arfakianum</u>	2-6	distinctly decurrent on stem

Table 11. Continued

Taxa	Structure of leaf bases in cross-sections		
	Thickness of the thickest part / thickness of median furrow	Number of leucocyst layers	vertical position of chlorocysts
<u>Leucobryum javense</u>	2.0-3.5	6-7	centric to hypocentric
<u>L. javense</u> var. <u>cyathifolium</u>	2.5-4.0	6-7	centric to hypocentric
<u>L. javense</u> var. <u>novae-guineae</u>	3.0-3.6	5-6	centric to hypocentric
<u>L. javense</u> var. <u>uncinatum</u>	3.5-4.0	5-6	centric to hypocentric
<u>L. scabrum</u>	1.9-2.2	6-8	centric to hypocentric
<u>L. aduncum</u>	2.3-3.6	5-6	centric
<u>L. aduncum</u> var. <u>teysmannianum</u>	3.0-3.5	4-5	centric
<u>L. aduncum</u> var. <u>scalare</u>	2.0-4.0	3-6	centric to hypercentric
<u>L. chlorophyllosum</u>	1.2-1.7	3-5	centric to hypercentric
<u>L. boninense</u>	2.1-3.1	4-6	centric to hypercentric
<u>L. juniperoideum</u>	1.8-3.0	5-8	centric to hypercentric
<u>L. humillimum</u>	1.6-2.3	4-6	centric to hypercentric
<u>L. imbricatum</u>	1.4-1.7	4	hypercentric
<u>L. glaucum</u>	1.2-1.6	5-6	centric to hypercentric
<u>L. bowringii</u>	1.5-2.5	4-6	centric to hypercentric
<u>L. sumatranum</u>	1.6-1.8	3-4	centric to hypocentric
<u>L. sericeum</u>	1.5-1.6	2-3	centric
<u>L. sanctum</u>	1.5-1.7	2-3	hypocentric
<u>L. arfakianum</u>	1.3-2.0	2	hypocentric

Table 11. Continued

Taxa	Position of perichaetia	Length of mature inner perichaetial leaf / length of ordinary leaf near the perichaetium
<u>Leucobryum javense</u>	terminal on short lateral branches	ca. 0.4
<u>L. javense</u> var. <u>cyathifolium</u>	terminal on short lateral branches	mature perichaetial leaves not seen
<u>L. javense</u> var. <u>novae-guineae</u>	terminal on short lateral branches	mature perichaetial leaves not seen
<u>L. javense</u> var. <u>uncinatum</u>	terminal on short lateral branches	mature perichaetial leaves not seen
<u>L. scabrum</u>	terminal on short lateral branches	0.3-0.6
<u>L. aduncum</u>	terminal on short lateral branches	0.9-1.0
<u>L. aduncum</u> var. <u>teysmannianum</u>	terminal on short lateral branches	mature perichaetial leaves not seen
<u>L. aduncum</u> var. <u>scalare</u>	terminal on short or long lateral branches, sometimes on stems	1.4-1.8
<u>L. chlorophyllosum</u>	terminal on short or long lateral branches, sometimes on stems	ca. 1.0
<u>L. boninense</u>	terminal on short lateral branches	0.7-1.0
<u>L. juniperoideum</u>	terminal on stems and subfloral innovations	1.0-1.8
<u>L. humillimum</u>	terminal on stems and subfloral innovations	1.4-1.6
<u>L. imbricatum</u>	not seen	mature perichaetial leaves not seen
<u>L. glaucum</u>	terminal on stems and subfloral innovations	0.7-0.8
<u>L. bowringii</u>	terminal on stems and subfloral innovations, or on long lateral branches	0.5-0.9
<u>L. sumatranum</u>	terminal on short lateral branches	ca. 0.3
<u>L. sericeum</u>	terminal on short lateral branches, sometimes on stems	ca. 0.5
<u>L. sanctum</u>	terminal on short lateral branches	ca. 0.3
<u>L. arfakianum</u>	terminal on short lateral branches	0.5-0.6

Table 11. Continued

Taxa	Length of archegonia (mm)	Normal male plants	Dwarf male plants
<u>Leucobryum javense</u>	ca. 0.9	not seen	growing on female stem leaves
<u>L. javense</u> var. <u>cyathifolium</u>	ca. 0.7	not seen	not seen
<u>L. javense</u> var. <u>novae-guineae</u>	0.9-1.2	not seen	not seen
<u>L. javense</u> var. <u>uncinatum</u>	not seen	not seen	not seen
<u>L. scabrum</u>	ca. 0.8	not seen	growing on female stem leaves
<u>L. aduncum</u>	0.5-0.8	not seen	growing on perichaetia
<u>L. aduncum</u> var. <u>teysmannianum</u>	ca. 0.7	not seen	not seen
<u>L. aduncum</u> var. <u>scalare</u>	0.7-0.9	present	growing on perichaetia
<u>L. chlorophyllosum</u>	0.7-0.8	present	growing on perichaetia and female stem leaves
<u>L. boninense</u>	0.6-0.8	present	not seen
<u>L. juniperoideum</u>	1.2-1.6	present	growing on perichaetia
<u>L. humillimum</u>	ca. 1.3	present	growing on perichaetia
<u>L. imbricatum</u>	not seen	not seen	not seen
<u>L. glaucum</u>	1.7-1.8	present	growing on perichaetia
<u>L. bowringii</u>	1.2-1.8	present	growing on perichaetia and female stem leaves
<u>L. sumatranum</u>	ca. 1.5	not seen	growing on perichaetia
<u>L. sericeum</u>	0.9-1.0	not seen	growing on perichaetia
<u>L. sanctum</u>	ca. 0.7	not seen	growing on perichaetia
<u>L. arfakianum</u>	1.0-1.2	not seen	growing on perichaetia

Table 12. Synopsis of the genus Leucobryum in Asia

---

Leucobryum Hampe

1. L. javense (Brid. ex Schwägr.) Mitt.  
Basionym: Sphagnum javense Brid. ex Schwägr.
  - 1a. L. javense var. cyathifolium (Dix.) T. Yamaguchi, stat. nov.  
Basionym: L. cyathifolium Dix.  
Synonym: L. brassii Bartr., syn. nov.
  - 1b. L. javense var. novae-guineae (Bartr.) T. Yamaguchi, stat. nov.  
Basionym: L. novae-guineae Bartr.  
Synonym: L. antarensense Zant., syn. nov.
  - 1c. L. javense var. uncinatum (Fl.) T. Yamaguchi, stat. nov.  
Basionym: L. uncinatum Fl.
  2. L. scabrum Lac.
  3. L. aduncum Dozy & Molk.  
Synonym: L. pentastichum Dozy & Molk. = L. candidum (Brid. ex P. Beauv.) Wils. var. pentastichum (Dozy & Molk.) Dix., syn. nov.
  - 3a. L. aduncum var. teysmannianum (Dozy & Molk.) T. Yamaguchi, stat. nov.  
Basionym: L. teysmannianum Dozy & Molk.
  - 3b. L. aduncum var. scalare (C. Müll. ex Fl.) A. Eddy  
Basionym: L. scalare C. Meull. ex Fl.  
Synonym: L. scalare var. marschmeyeri Fl.  
L. scalare var. tjibodense Fl.  
L. flavulum Card. in Ren. & Card., syn. nov.  
L. subscalare Broth. ex Vard., syn. nov.
-



Table 12. Continued

- 
- L. krempfii Thér., syn. nov.  
L. poilanei Thér., syn. nov.  
L. perichaetiale Dix., syn. nov.  
L. aduncum var. arnottii Thér., syn. nov.  
L. microleucophanoides Dix. ex Johnson, syn. nov.
4. L. chlorophyllosum C. Müll.  
Synonym: L. stenophyllum Besch., syn. nov.  
L. byssaceum C. Müll. ex Johnson, syn. nov.
5. L. boninense Sull. & Lesq.  
Synonym: L. salmonii Card. in Ren. & Card., syn. nov.  
L. scaberulum Card. in Ren. & Card., syn. nov.  
L. armatum Broth., syn. nov.  
L. scaberulum var. divaricatum Dix., syn. nov.  
L. nakaii Hor., syn. nov.
6. L. juniperoideum (Brid.) C. Müll.  
Basionym: Dicranum juniperoideum Brid.  
Synonym: L. neilgherrense C. Müll.  
L. holleanum Dozy & Molk.  
L. triviale C. Müll., syn. nov.  
L. retractum Besch., syn. nov.  
L. japonicum (Besch.) Card. in Broth.  
L. altiusculum Besch.  
L. brevicaule Besch.  
L. humile Broth. ex Besch.  
L. lacteorum Besch.
-

Table 12. Continued

- 
- L. textorii Besch.  
L. holleanum var. fragilifolium Fl.,  
syn. nov.  
L. ferriei Card. in Ren. & Card.  
L. neilgherrense var. minus Card., syn.  
nov.  
L. rhizophyllum Warnst.  
L. angustissimum Broth., syn. nov.
7. L. humillimum Card.  
Basionym: Ochrobryum wightii Besch.  
Synonym: L. galeatum Besch. = L. neilgherrense C.  
Müll. var. galeatum (Besch.) Dix.,  
syn. nov.  
L. mittenii Besch., syn. nov.  
L. wichurae Broth. ex Besch., syn. nov.  
L. cuculliphyllum Fl., syn. nov.  
L. cucullifolium Card. in Ren. & Card.,  
syn. nov.  
L. propaguliferum (Dix.) Robinson, syn.  
nov.
8. L. imbricatum Broth.
9. L. glaucum (Hedw.) Ångstr. in Fries  
Basionym: Dicranum glaucum Hedw.
10. L. bowringii Mitt.  
Synonym: L. ceylanicum (Besch.) Card., syn. nov.  
L. yamatense Besch.  
L. nagasakense Broth.  
L. brotheri Card. in Ren. & Card.  
L. deciduum Card. in Ren. & Card., syn.  
nov.
-

Table 12. Continued

- 
- L. stenobasis Card. in Ren. & Card.,  
syn. nov.
- L. confine Card.
- L. subsericeum Dix., syn. nov.
11. L. sumatranum Broth. ex Fl.  
Synonym: L. pulchrum Broth.
12. L. sericeum Broth. ex Geh.  
Synonym: L. bowringii Mitt. var. sericeum (Broth.  
ex Geh.) Dix.
13. L. sanctum (Brid.) Hampe  
Basionym: Dicranum glaucum Hedw. var. sanctum  
Brid.  
Synonym: L. auriculatum C. Müll. in Geh.  
L. papuense Par.
14. L. arfakianum C. Müll. ex Geh.  
Synonym: L. subsanctum Broth.  
L. papuense var. pendulum Zant.  
L. sanctum (Brid.) Hampe var. arfakianum  
(C. Müll. ex Geh.) A. Eddy
-

As a result, I recognized 19 taxa of Leucobryum in Asia (Table 12).

#### VIII. Taxonomic treatment

In the following treatment, the names of herbaria are abbreviated according to Index Herbariorum I, Ed. 8 (Holmgren et al. 1990). Only representative specimens are listed.

Unless otherwise indicated, descriptions of species were based on female plants. The illustrations were mostly based on the type specimens, and, when necessary, additional illustrations were made, based on other appropriate specimens. Synonyms listed in this treatment are restricted to the Asian taxa.

#### Leucobryum Hampe

Linnaea 13: 42 (1839). Type: Leucobryum glaucum (Hedw.) Ångstr. in Fries.

Plants whitish green when moist in field, whitish in dried herbarium specimens, forming cushions or mats. Stems erect, rarely pendulous, sometimes with a central strand. Leaves crowded, thick and fleshy, linear lanceolate to lanceolate, narrowed to subtubulous point from a oblong to ovate base, acute to mucronate, often with rhizoids at apex;

laminae consisting of leucocysts, narrow, usually restricted to basal parts, ± bordered by linear cells, the linear border cells extending to near the leaf apex; costae broad, occupying greater parts of leaves, consisting of 2-8 layer leucocysts and 1 layered of chlorocysts which sandwiched by leucocysts and form reticula; in cross-sections near leaf base ± hollowed at median part. Caducous leaves often differentiated.

Dioicous. Male plants dimorphous; dwarf male plants tiny, growing on tomentum enclosed by perichaetial leaves or on ordinary leaves of female plants; normal male plants as large as female plants, perigonia small, bud-like; perigonial leaves cochleariform, enveloping a whole cluster of antheridia; antheridia oblong with numerous paraphyses. Perichaetia terminal on short lateral branches or on main stems; perichaetial leaves differentiated, the basal parts broader and longer than those of ordinary leaves, the perichaetial leaves around unfertilized archegonia often with rhizoids on lower adaxial surface and forming a mass of tomentum. Sporophytes dicranoid. Setae elongate, erect, sometimes clustered. Capsules inclined to horizontal, rarely erect, ovoid to ellipsoid, ± strumose; opercula long rostrate. Annulus of 1-2 rows of cells when present. Apices of peristome teeth divided to the middle, papillose above, vertically striolate below on the dorsal surface,

densely papillose below on the ventral surface. Spores spherical, minutely papillose. Calyptra cucullate.

Key to the taxa of Leucobryum in Asia

1. Leaves smooth above on abaxial side except extreme leaf tips .....2
1. Leaves scabrous or undulate above on abaxial side .....8
  2. Leaves auriculate, abaxial leucocysts distinctly decurrent on stems .....14. L. arfakianum
  2. Leaves not auriculate, abaxial leucocysts not decurrent on stems .....3
3. Leaves usually lustrous, linear lanceolate, flexuose and contorted above when dry .....4
3. Leaves not lustrous, lanceolate, straight above when dry .....5
  4. Plants medium in size (up to 60 mm long). Leaves 4.2-11.0 mm long. Perichaetia terminal on stems and subfloral innovations, or on long lateral branches ..  
.....10. L. bowringii
  4. Plants robust (up to 120 mm long). Leaves 10.0-18.0 mm long. Perichaetia terminal on short lateral branches .....11. L. sumatranum
5. Stems without a central strand. Leaves erect spreading, acute to bluntly mucronate .....6

- 5. Stems with a central strand. Leaves imbricate to erect spreading, distinctly mucronate .....7
- 6. In cross-sections near leaf bases leucocysts in 2 cell layers at the central parts, the thickest parts 1.8-3.0 times thicker than the central part .....  
.....6. L. juniperoideum
- 6. In cross-sections near leaf bases leucocysts in (2-) 3-4 cell layers at the central parts, the thickest parts 1.2-1.6 times thicker than the central part ...  
.....9. L. glaucum
- 7. Caducous leaves not well differentiated but narrower than ordinary leaves, faintly attached on stems or specialized branches. In cross-sections near leaf apices abaxial leucocysts in 1 cell layer, almost as thick as adaxial leucocysts .....7. L. humillimum
- 7. Caducous leaves highly differentiated, linear, usually helicoid or twisted, forming a cluster at shoot apex enclosed by ordinary leaves. In cross-sections near leaf apices abaxial leucocysts in 1-2 cell layers, distinctly thicker than adaxial leucocysts .....  
.....8. L. imbricatum
- 8. Stems with a central strand .....9
- 8. Stems without a central strand .....10
- 9. Leaves not auriculate, abaxial leucocysts not decurrent on stems .....12. L. sericeum

9. Leaves auriculate, abaxial leucocysts distinctly  
decurrent on stems .....13. L. sanctum
10. Plants small to medium in size. Leaves 2.0-6.0 (-  
7.5) mm long .....11
10. Plants robust. Leaves (6.5-) 8.0-18.0 mm long ...15
11. Plants medium in size. Leaves more than 4.0 mm long,  
papillosely prorate above on abaxial side .....  
.....5. L. boninense
11. Plants usually small. Leaves to 4.3 mm long, undulate  
and spinosely prorate or undulate (not prorate) at upper  
part on abaxial side .....12
12. Leaves narrowly lanceolate, 5.7-7.8 times longer  
than wide, undulate above on abaxial side .....  
.....4. L. chlorophyllum
12. Leaves lanceolate, 2.8-4.8 times longer than wide,  
undulate and spinosely prorate above on abaxial  
side .....13
13. Leaves 2.0-3.5 mm long, spirally arranged, usually  
closely imbricate and forming conical points at shoot  
apices .....3b. L. aduncum var. scalare
13. Leaves 3.5-4.3 mm long, more or less arranged in 5 rows,  
erect spreading or falcate secund, not forming conical  
points at shoot apices .....14
14. Leaves falcate secund, somewhat arranged in 5 rows .  
.....3. L. aduncum var. aduncum



14. Leaves erect spreading, distinctly arranged in 5 rows .....3a. L. aduncum var. teysmannianum
15. Leaves undulate and spinosely prorate to 3/5 above on abaxial side .....2. L. scabrum
15. Leaves papillosely prorate to 2/5 above on abaxial side .....16
16. Abaxial leucocysts weakly decurrent on stems .....1. L. javense var. javense
16. Abaxial leucocysts distinctly decurrent on stems ...17
17. Leaves distinctly uncinata at apex .....1c. L. javense var. uncinatum
17. Leaves not uncinata at apex .....18
18. Leaves erect spreading, somewhat falcate secund or squarrose, rounded and apiculate at apex .....1a. L. javense var. cyathifolium
18. Leaves appressed to erect spreading, acute to bluntly mucronate .....1b. L. javense var. novae-guineae

1. Leucobryum javense (Brid. ex Schwägr.) Mitt. var. javense  
(Fig. XVIII, XXVI, XXXVI-XL, CXLI: 1)

J. Linn. Soc. Bot. Suppl. 1: 25 (1859).

Basionym: Sphagnum javense Brid. ex Schwägr., Spec. Musc. Suppl. 2(1): 4, t. 102 (1823). Type: "In silvis

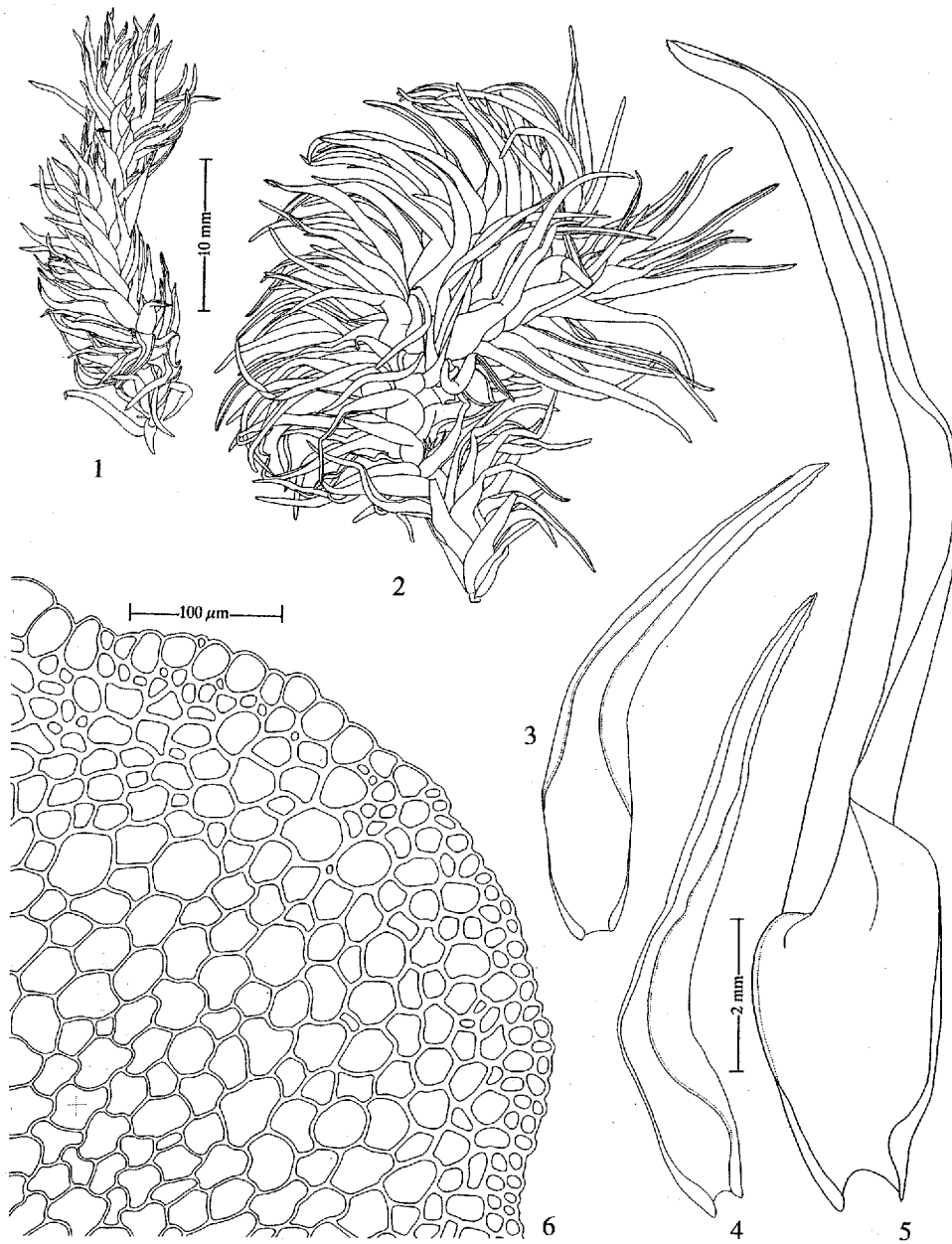


Figure XXXVI. Leucobryum javense (Brid. ex Schwägr.) Mitt. var. javense. 1, 2. Plants. 3–5. Leaves. 6. Cross-section of stem. Figs. 1, 3, 4 were drawn from holotype of Sphagnum javense (B); 2, 5, 6 from Joncheere 1621 (L)..

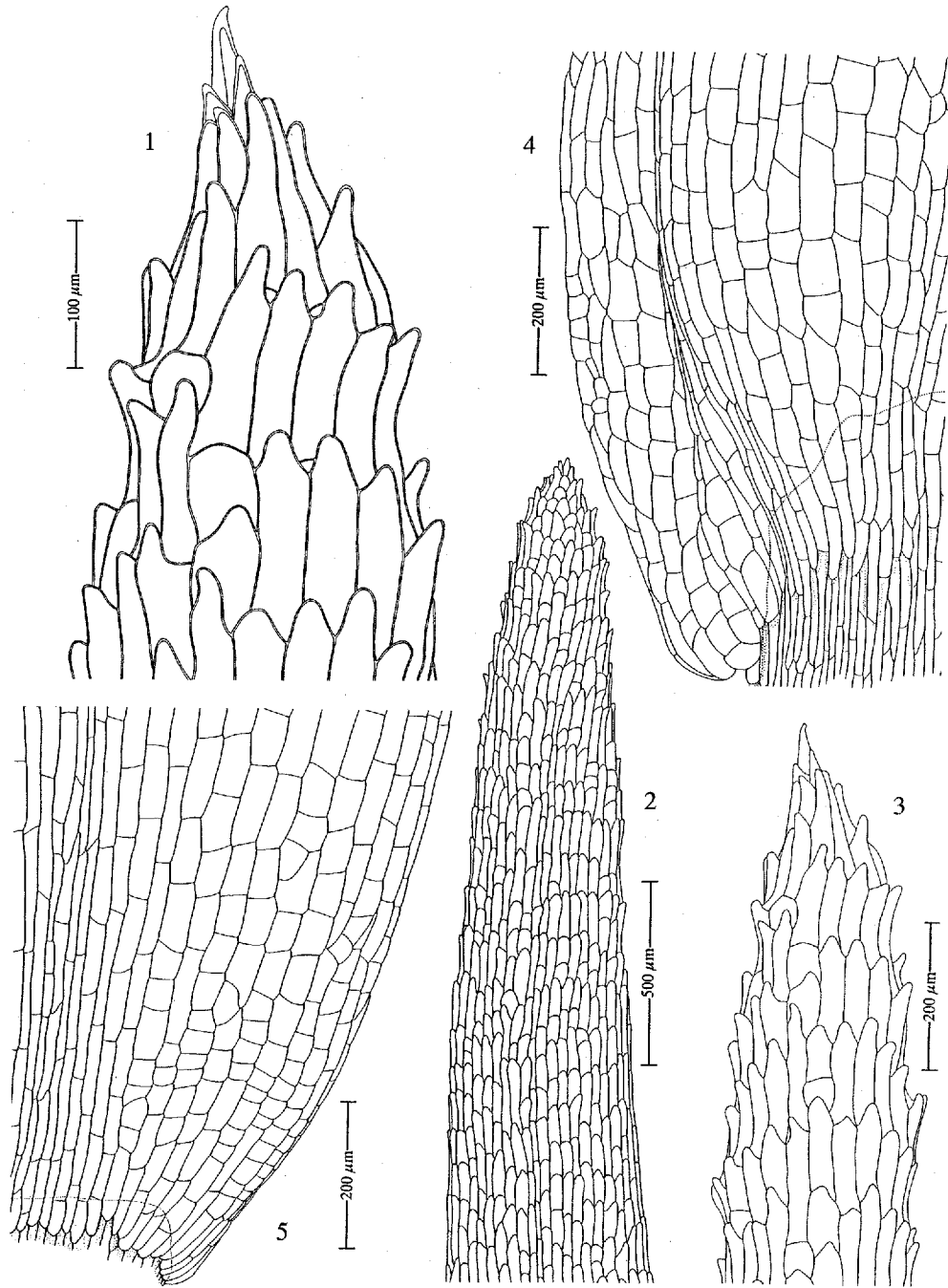


Figure XXXVII. *Leucobryum javense* (Brid. ex Schwägr.) Mitt. var. *javense*. 1-3. Leaf apices. 4, 5. Leaf bases (abaxial view). Figs. 1, 3, 5 were drawn from holotype of *Sphagnum javense* (B); 2, 4, from Joncheere 1621 (L).

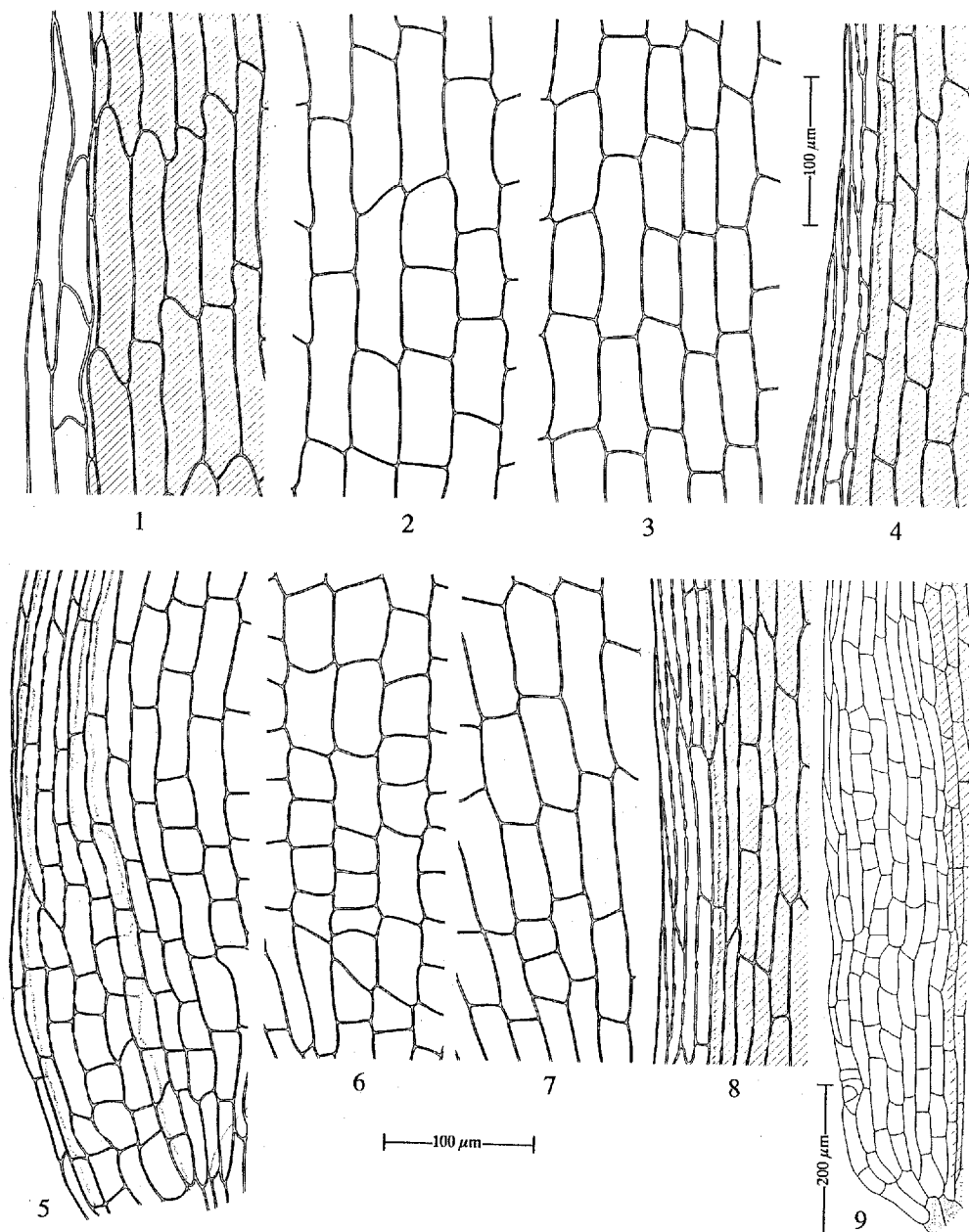


Figure XXXVIII. Leucobryum javense (Brid. ex Schwägr.) Mitt. var. javense. 1. Cells near leaf apex (adaxial view). 2-4. Median cells of leaf (2, abaxial view; 3, 4, adaxial view). 5-9. Basal cells of leaf (5, 6, abaxial view; 7-9, adaxial view). Figs. 1-8 were drawn from holotype of Sphagnum javense (B); 9, from Joncheere 1621 (L).

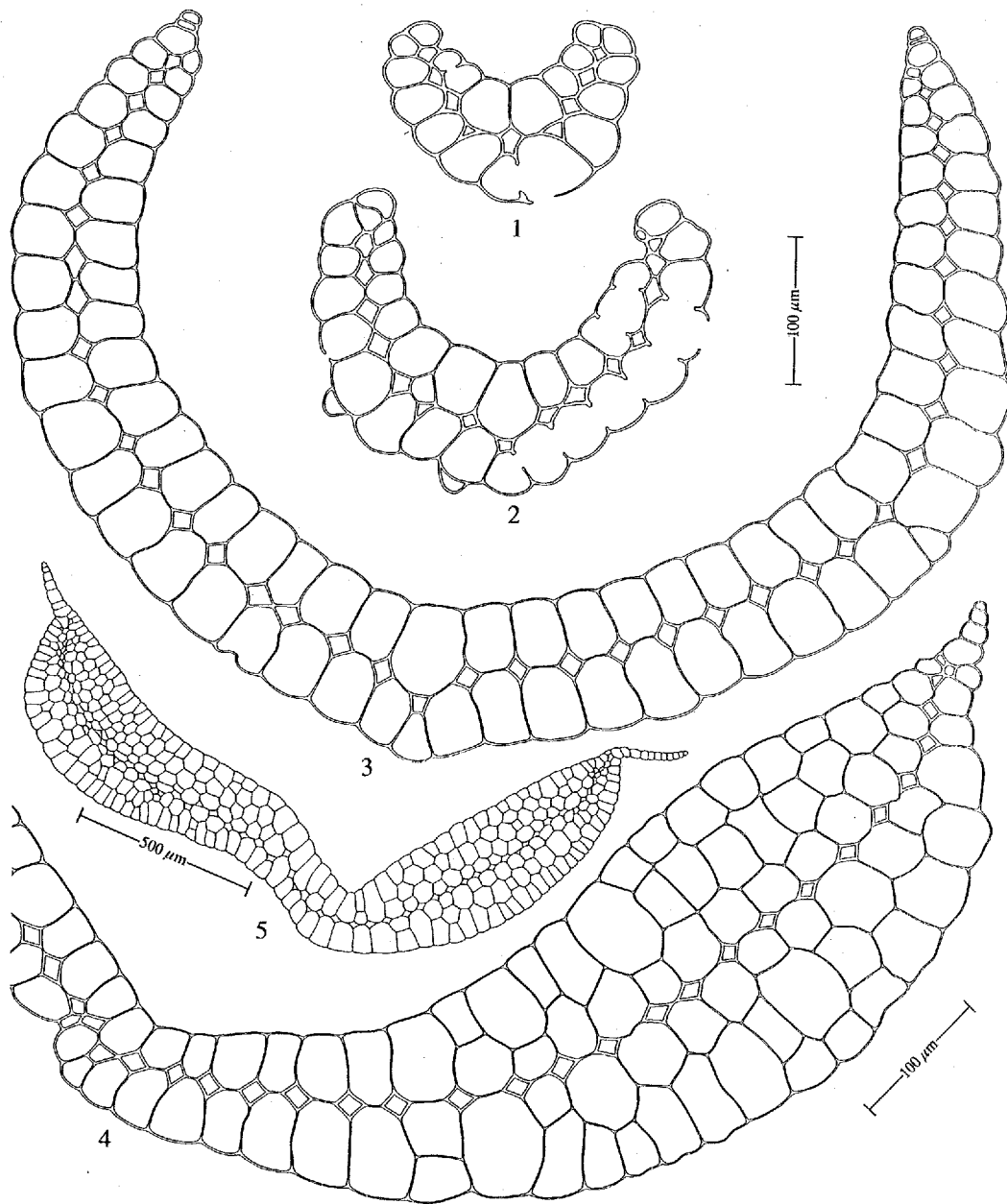


Figure XXXIX. *Leucobryum javense* (Brid. ex Schwägr.) Mitt. var. *javense*. 1-5. Cross-sections of leaves (1, 2, apical; 3, median; 4, 5, basal portions). Figs. 1-4 were drawn from holotype of *Sphagnum javense* (B); 5, Joncheere 1621 (L).



Figure XL. *Leucobryum javense* (Brid. ex Schwägr.) Mitt. var. *javense*. 1–4. Perichaetia (1, 4, with sporophyte). 5. Dwarf male plant. 6. Perigonia. 7. Antheridium. 8. Archegonium. 9. Paraphysis. All figures were drawn from Joncheere 1621 (L).

insulae Javae ad montem coeruleum legit (anno MDCCLXVIII. mense Octobri e Bridelio) Commersonus" – holotype (B).

Plants whitish tinged with yellow or purple when dry, forming loose tufts or cushions. Stems to 80 mm long with leaves; central strand not differentiated in cross-sections of stems but the cortical cells gradually smaller and thinner-walled inward. Leaves widely spreading, somewhat falcate secund, rarely erect spreading, sometimes flexuose above; 8-18 x 1.5-3.1 mm, lanceolate to narrowly lanceolate, gradually narrowed to subtubulous point from oblong base, acute to bluntly mucronate, papillose prorate from the apex to 3/10 of the leaf length on abaxial surface; laminae consisting of 3-6 rows of quadrate to rectangular cells near base, bordered by 2-3 rows of linear cells; in cross-sections near leaf base leucocysts in 3-4 cell layers on adaxial side and 3-4 cell layers on abaxial side at the thickest part; abaxial leucocysts ± decurrent on stems.

Dioicous. Dwarf male plants growing on stem leaves of female plants; independent normal male plants not observed. Perichaetia terminal on short lateral branches; inner perichaetial leaves around mature sporophytes very small (e. g. inner perichaetial leaf 6.4 x 1.6 mm when the stem leaf near the perichaetium 15.5 x 2.9 mm), 0.4 times longer than ordinary leaves; archegonia ca. 0.9 mm long. Perfect sporophytes not observed.

Representative specimens examined: Japan, Ryukyu Islands, Amami-ôshima, Mt. Yuwan, 680 m alt., 15 Dec. 1985, Yamaguchi 9054 (HIRO). Taiwan, Taichung, Tungshih, Mahanshan, 6 Dec. 1958, Wang 22 (NICH). China, Hainan, Kwantung, 6 Feb. 1962, Chen et al. 364 (L). Himalaya, central region, Hooker s. n., in herb. Mitten 1270 (NY). India, Mt. Khasia, Hooker & Thompson s. n., in herb. Mitten 1276 (NY). Sri Lanka, Rambodde, 1847, Gardner 49, in herb. Mitten 1278 (NY). Thailand, Udawn, sandstone massive Phu(Mt.) Krading, 16°50'N 101°45'E, 1200 m alt., 14 Jan. 1966, Touw 10897 (L). Cambodia, Province de Kampot, Poporkuil, ca. 1000 m alt., 4-6 Dec. 1964, Kira et al. 11 (HIRO). Vietnam, Tonkin, July 1927, Pételot s. n. (NICH 214153). Malay Peninsula, Pahang, Fraser's Hill, ca. 900 m alt., 25 Aug. 1974, Balgooy 2062B (L). Philippines, Mindanao, 5 Oct. 1965, Robbins 3989, mixed with L. javense var. cyathifolium (L). Borneo, Sarawak, Belengki, Bakelalan, 4500 ft. alt., 16 Aug. 1955, Brooke 10479 (L). Sulawesi, Mt. Wawonseru, SW of Soroako, 2°15'S 121°-121°45'E, 1050-1200 m alt., 27 June 1979, Hennipman 6034E (L). Sumatra, Brastagi-Tonkkeh, summit of Delangsikut, 1700 m alt., 19 June 1952, Wijk 1964 (L). Java, Prov. Preanger, Gedeh, Jan. 1894, Shiffner 10353 (L). Seram, Kecamatan Seram Utara, Manusela National Park, along a trail between



Kanikeh and Wae Angsela, 3°06-08'S 129°28-29'E, 1060 m alt.,  
2 Jan. 1985, Akiyama 8681 (KYO, HIRO).

Habitat: Usually on moist humus, occasionally on tree trunks and soil in shaded forests.

Distribution: Japan, Taiwan, China, Himalaya, India, Sri Lanka, Thailand, Cambodia, Vietnam, Malay Peninsula, Philippines, Borneo, Sulawesi, Sumatra, Java, Seram, New Guinea.

The present variety is characterized by (1) robust plants, (2) long and usually falcate leaves up to 18 mm long, (3) abaxially papillose proration of leaf apices down to 3/10 of the leaf length, (4) perichaetia which are terminal on short lateral branches, and (5) inner perichaetial leaves which are shorter than stem leaves.

L. javense var. javense has general appearances similar to L. scabrum Lac., but the leaves of L. scabrum are smaller (up to 8.2 mm long), while those of L. javense var. javense are larger (8.0-18.0 mm long). Moreover, in L. scabrum the apical part of leaves is abaxially undulate and spinosely prorate in upper 3/5 of the leaf length, while in L. javense var. javense papillose prorate in upper 3/10. L. scabrum usually grows on soil or rocks and forming relatively compact mats, whereas L. javense var. javense usually grows on humus and forming loose cushions or tufts.

L. javense is classified into four varieties based on the growing habits and leaf structure.

1a. Leucobryum javense var. cyathifolium (Dix.) T.  
Yamaguchi, stat. nov. (Fig. XLI-XLV, CXLI: 8)

Basionym: Leucobryum cyathifolium Dix., J. Linn. Soc. Bot. 45: 499 (1922). Type: New Guinea, Port Moresby District, Mt. Durigolo near Boku, 1916, Clark s. n. (in herb. Dixon, ref. no. 9) – holotype (BM).

Leucobryum brassii Bartr., Brittonia 9: 36 (1957), syn. nov. Type: New Guinea, Milne Bay District, Maneau Range, north slopes of Mt. Dayman, 2230 m. alt., on ground and lower tree trunks in mossy forest, 23 May 1953, Brass 22466 – holotype (FH).

Plants whitish when dry, forming loose tufts. Stems to 80 mm long with leaves; central strand not differentiated in cross-sections of stems but the walls of cortical cells thinner inward. Leaves erect spreading, somewhat falcate secund or squarrose; 9.1-13.0 x 2.0-3.5 mm, lanceolate, gradually narrowed to broadly channeled point from oblong base, rounded and apiculate at apex (Fig. XLII: 2), papillosely prorate from the apex to 1/10 of the leaf length on abaxial surface; laminae and borders consisting of 5-7 rows of narrowly rectangular cells near base, the differentiation between laminal cells and border cells

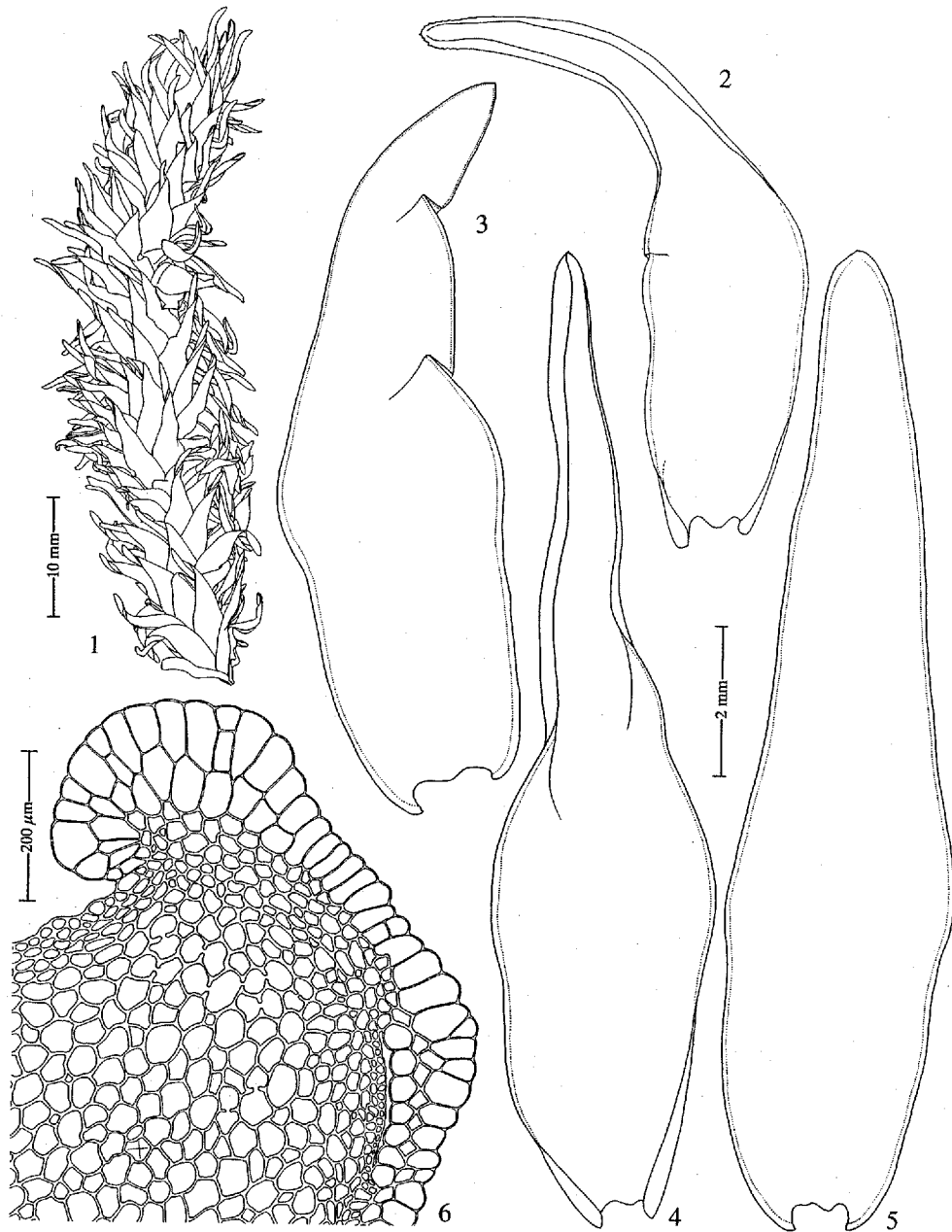


Figure XLI. *Leucobryum javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 1. Plant. 2–5. Leaves (3, 5, expanded). 6. Cross-section of stem. Figs. 1, 4, 5 were drawn from holotype of *L. brassii* (FH); 2, 3, 6, from holotype of *L. cyathifolium* (BM).

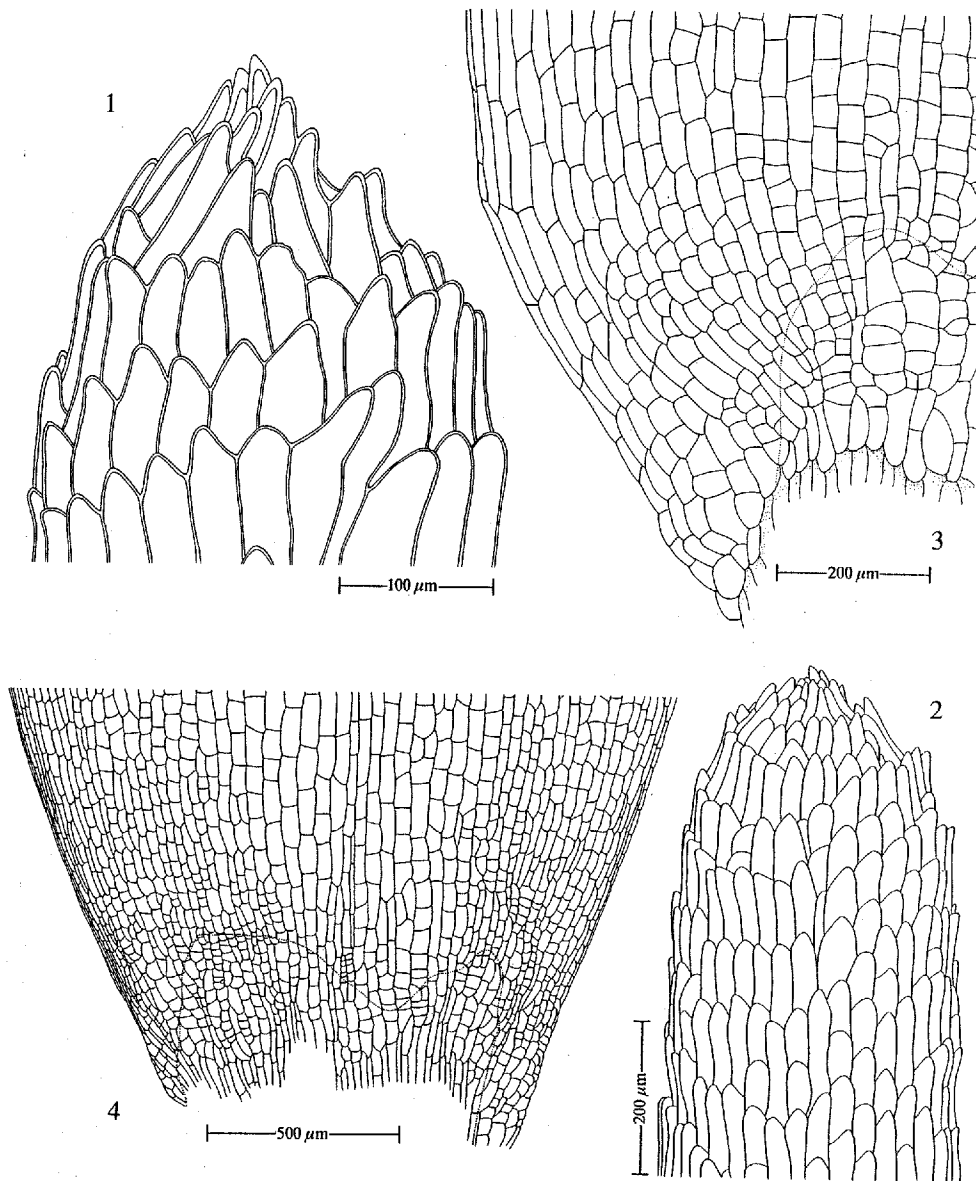


Figure XLII. *Leucobryum javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 1, 2. Leaf apices. 3, 4. Leaf base (abaxial view). All figures were drawn from holotype of *L. cyathifolium* (BM).

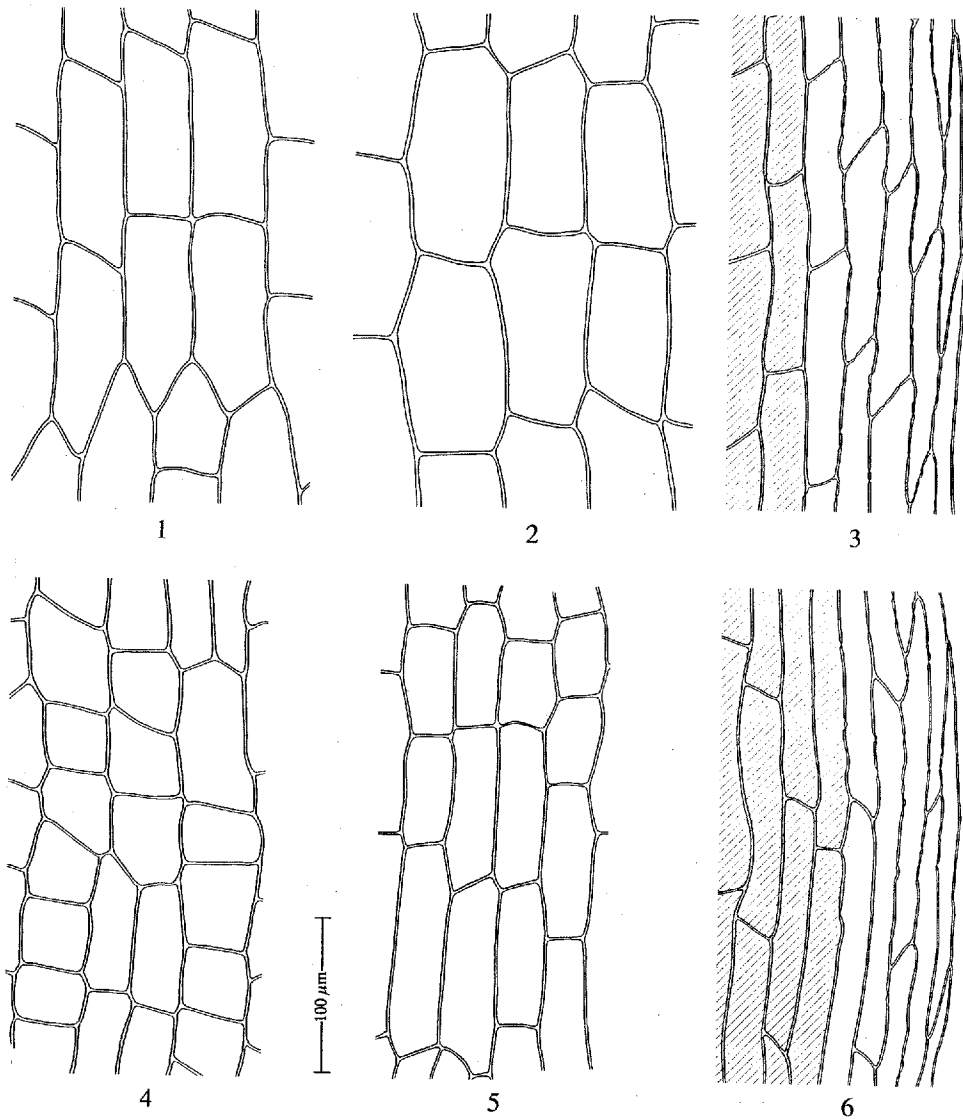


Figure XLIII. *Leucobryum javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 1-3. Median cells of leaf (1, 3, abaxial view; 2, adaxial view). 4-6. Basal cells of leaf (4, 6, abaxial view; 5, adaxial view). All figures were drawn from holotype of *L. cyathifolium* (BM).

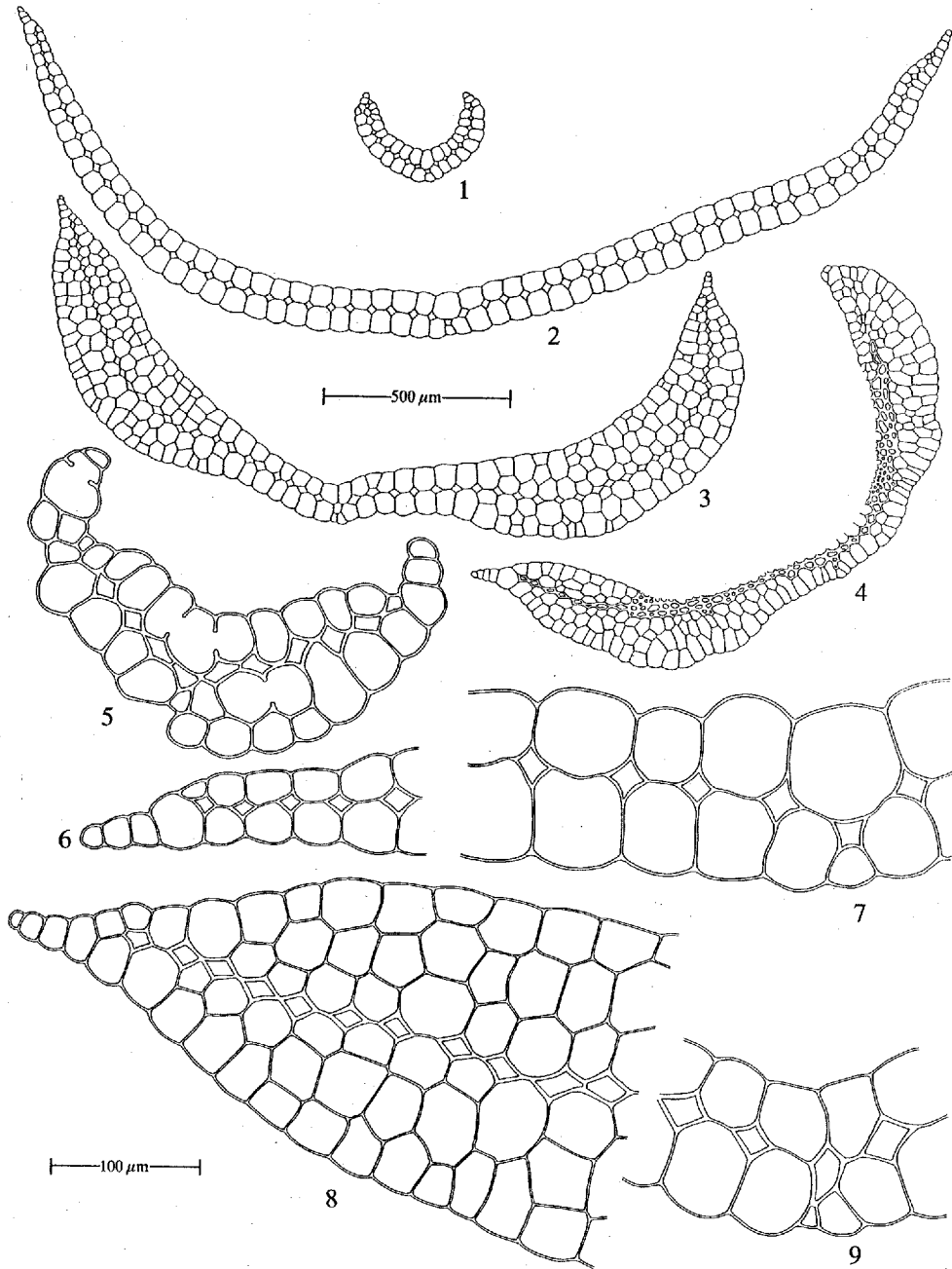


Figure XLIV. *Leucobryum javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 1-9. Cross-sections of leaves (1, 5, apical; 2, 6, 7, median; 3, 4, 8, 9, basal portions). All figures were drawn from holotype of *L. cyathifolium* (BM).

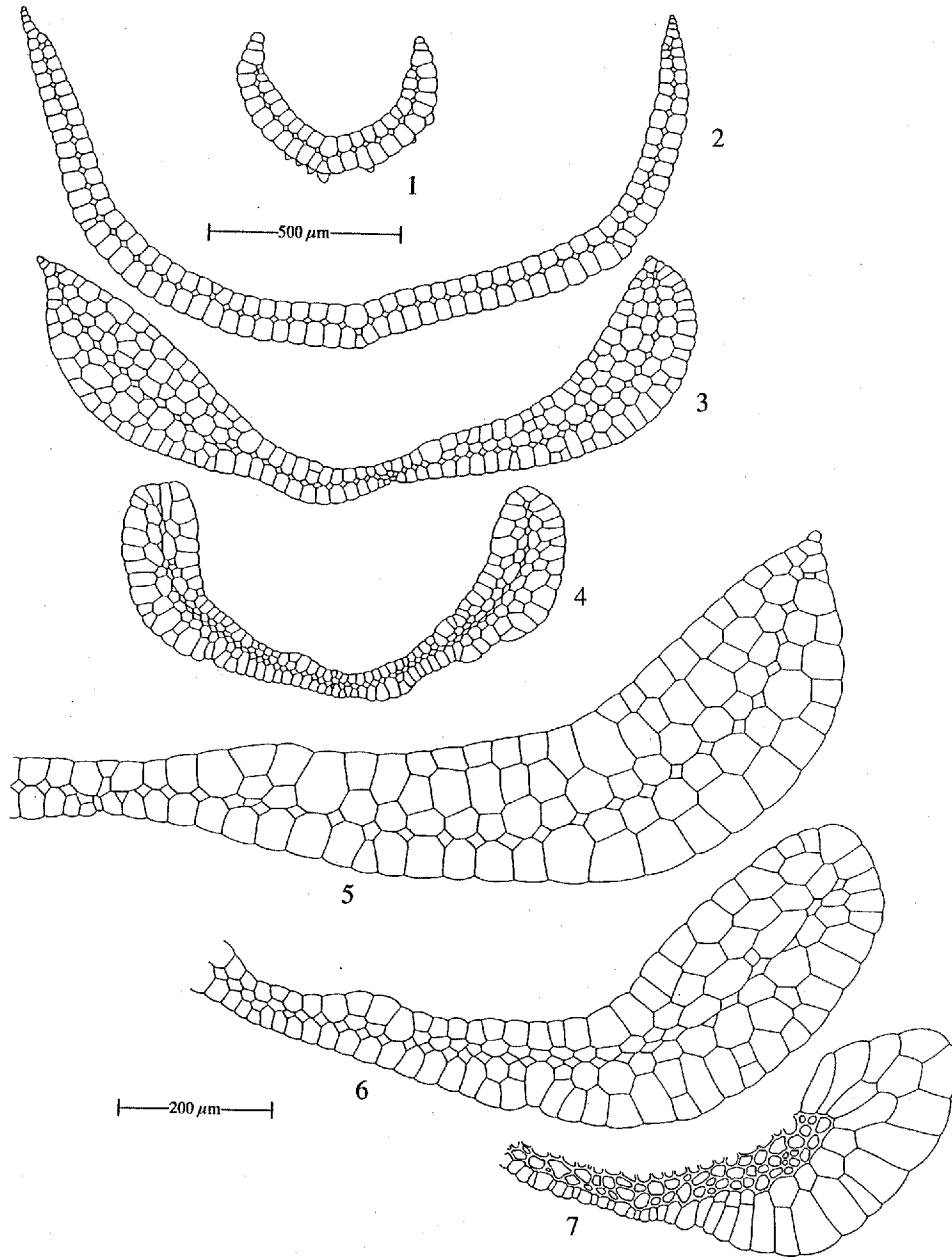


Figure XLV. *Leucobryum javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 1–7. Cross-sections of leaf (1, apical; 2, median; 3–7, basal portions). All figures were drawn from holotype of *L. brassii* (FH).

indistinct; alar parts bulged, the edges rounded (Fig. XLV: 6, 7) in cross-sections, without 1 cell layered wings; in cross-sections near leaf base leucocysts in 3-4 cell layers on adaxial side and 3-4 cell layers on abaxial side at the thickest part; abaxial leucocysts distinctly decurrent on stems, in cross-sections at insertional parts to stem usually 3-4 cell layers of leucocysts at the thickest part (Fig. XLIV: 4).

Dioicous. Male plants not observed. Perichaetia terminal on short lateral branches, small and bud-like; archegonia ca. 0.7 mm long. Sporophytes not observed.

Representative specimens examined: Philippines, Mindanao, 5 Oct. 1965, Robbins 3989, mixed with L. javense var. javense (L). Borneo, Sarawak, 4th Division, Gunong Mulu National Park, G. Mulu, 4°05'N 114°55'E, 1900 m alt., 30 May 1978, Touw 21109 (L). New Guinea, Morobe, Mt. Kaindi, 8000 ft. alt., 1 Sept. 1965, Hewson 479 (L); Vogelkop Peninsula, Arfak Mts., Mt. Saru-mot near Iray, Angi Gigi Lake, 2100 m alt., 26 Jan. 1962, Sleumer & Vink 4468 (L); Western Highlands, Minj valley, Kubor Ranges, 8000 ft. alt., 1 Aug. 1957, Robbins 581 (L); Milne Bay District, Mt. Gamatawa, 6000 ft. alt., 18 July 1973, Cruttwell 84 (L).

Habitat: On soil or tree trunks.

Distribution: Philippines, Borneo, New Guinea.



The present variety is differentiated from var. javense by (1) somewhat squarrose leaves, (2) rounded and apiculate leaf apices, (3) bulged alar parts of leaves with rounded edges in cross-sections, and (4) distinct decurrency of abaxial leucocysts of leaves.

1b. Leucobryum javense var. novae-guineae (Bartr.) T.  
Yamaguchi, stat. nov. (Fig. XLVI-XLIX, CXLI: 7)

Basionym: Leucobryum novae-guineae Bartr., Svensk. Bot. Tidskr. 47(3): 397 (1953). Type: New Guinea, Mt. Hagen distr., Western Highlands, Wahgi Valley (south or the Bismarck Mts.), Nondugl, 1600 m alt., IX.-XI. 1951, Nils and Creta Gyldenstolpe 39 - holotype (FH).

Leucobryum antareense Zant., Nova Guinea, Botany 16: 276. (1964), syn. nov. Type: New Guinea, Star Mts., Mt. Antares, bivouac 39a, 1500 m alt., hanging down from branch of tree at edge of rain forest, 27 June 1959, Zanten 716 - holotype (L).

Plants darkish or brownish when dry, forming loose tufts or pendulous. Stems elongate, to 150 mm long with leaves; central strand not differentiated in cross-sections of stems but the walls of cortical cells thinner inward. Leaves appressed to erect spreading, somewhat arranged in 5-rows; 6.6-10.0 x 1.2-1.8 mm, lanceolate, gradually narrowed to broadly and deeply channeled point from oblong base,

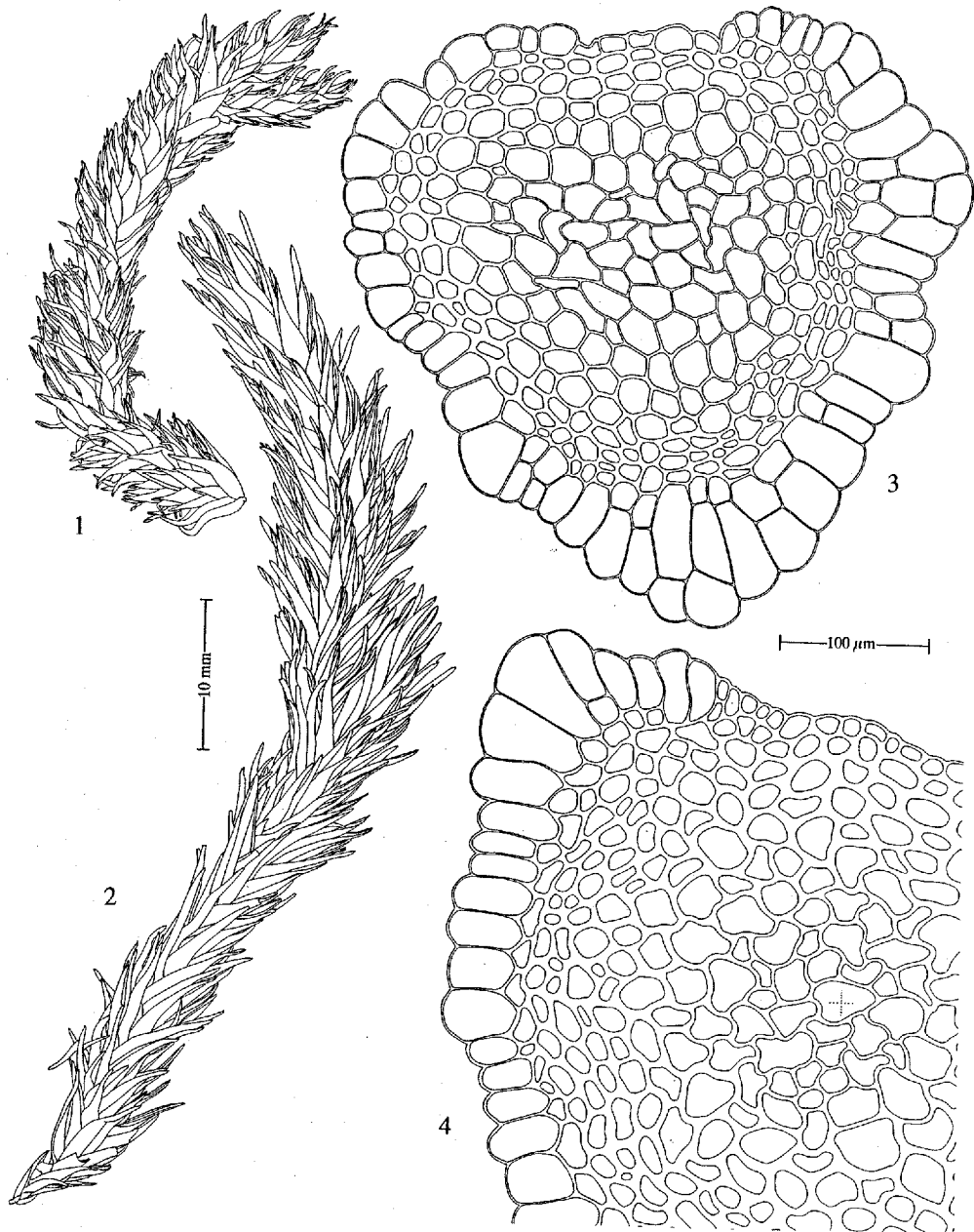


Figure XLVI. *Leucobryum javense* var. *novae-guineae* (Bartr.) T. Yamaguchi. 1, 2. Plants. 3, 4. Cross-sections of stems. Figs. 1, 3 were drawn from holotype of *L. novae-guineae* (FH); 2, 4, from holotype of *L. antarense* (L).

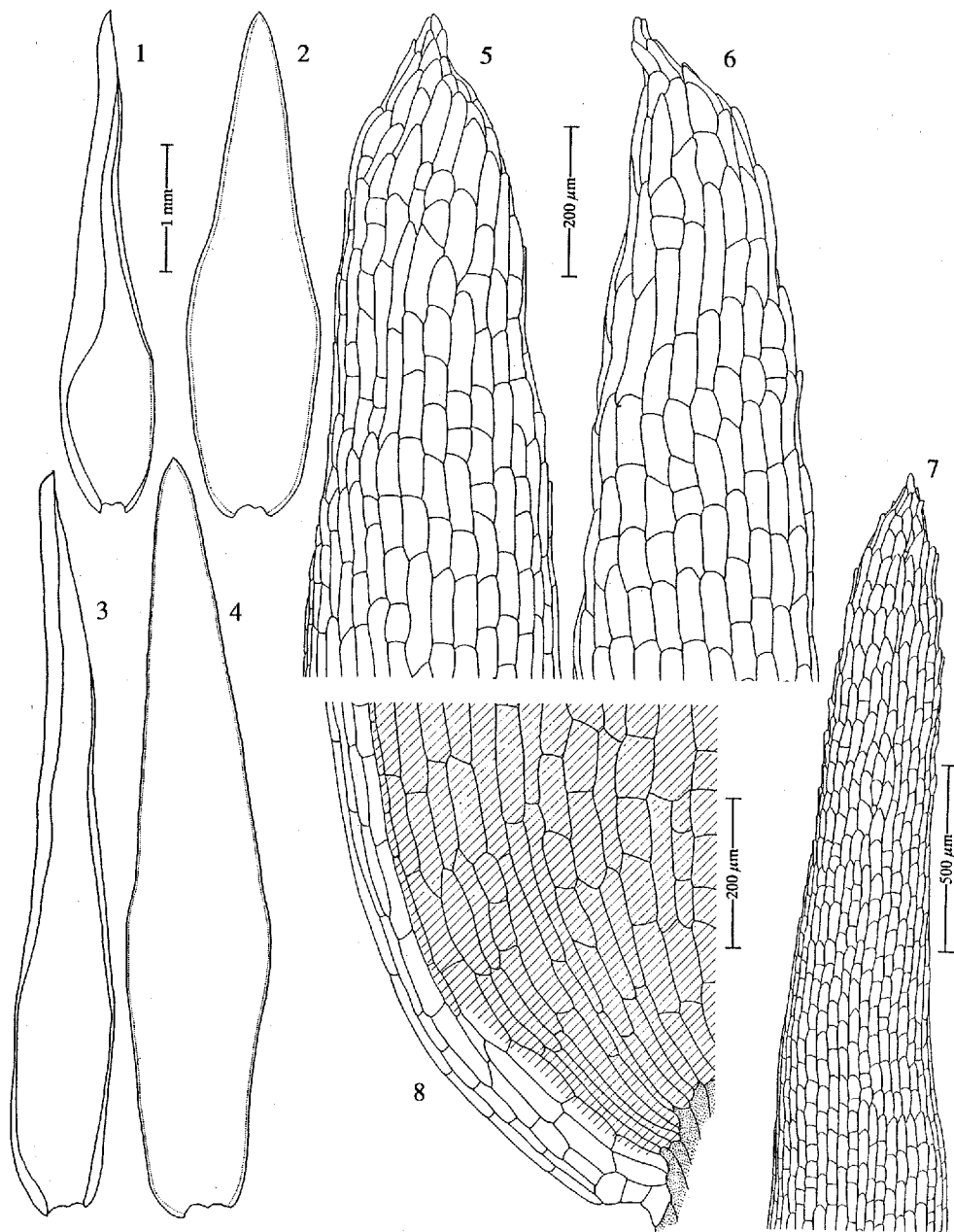


Figure XLVII. *Leucobryum javense* var. *novae-guineae* (Bartr.) T. Yamaguchi. 1–4. Leaves (2, 4, expanded). 5–7. Leaf apices. 8. Leaf base (adaxial view). Figs. 1, 2, 7 were drawn from holotype of *L. novae-guineae* (FH); 3–6, 8, from holotype of *L. antarense* (L).

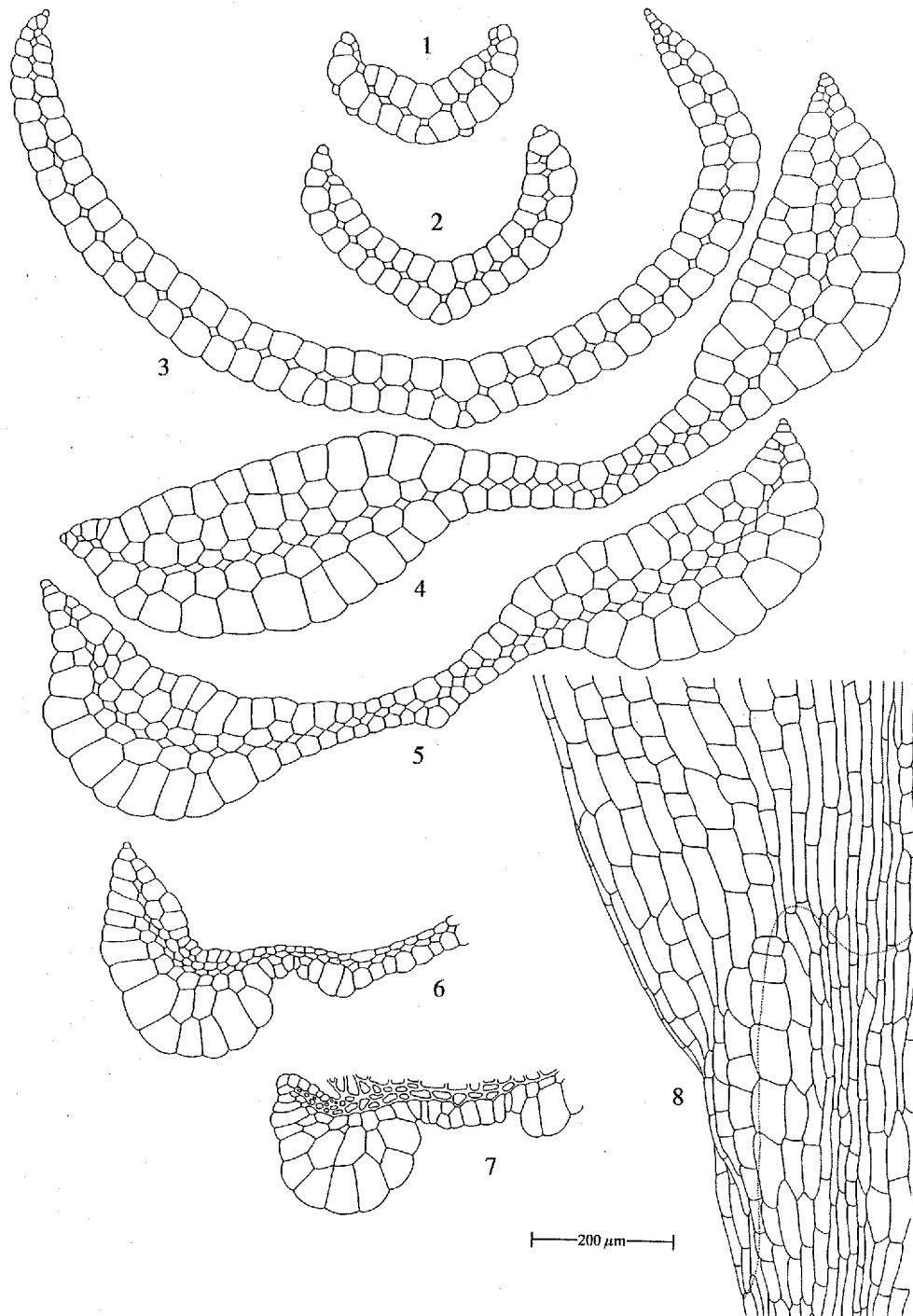


Figure XLVIII. *Leucobryum javense* var. *novae-guineae* (Bartr.) T. Yamaguchi. 1-7. Cross-sections of leaf (1, 2, apical; 3, median; 4-7, basal portions). 8. Leaf base (abaxial view). All figures were drawn from holotype of *L. antarense* (L).

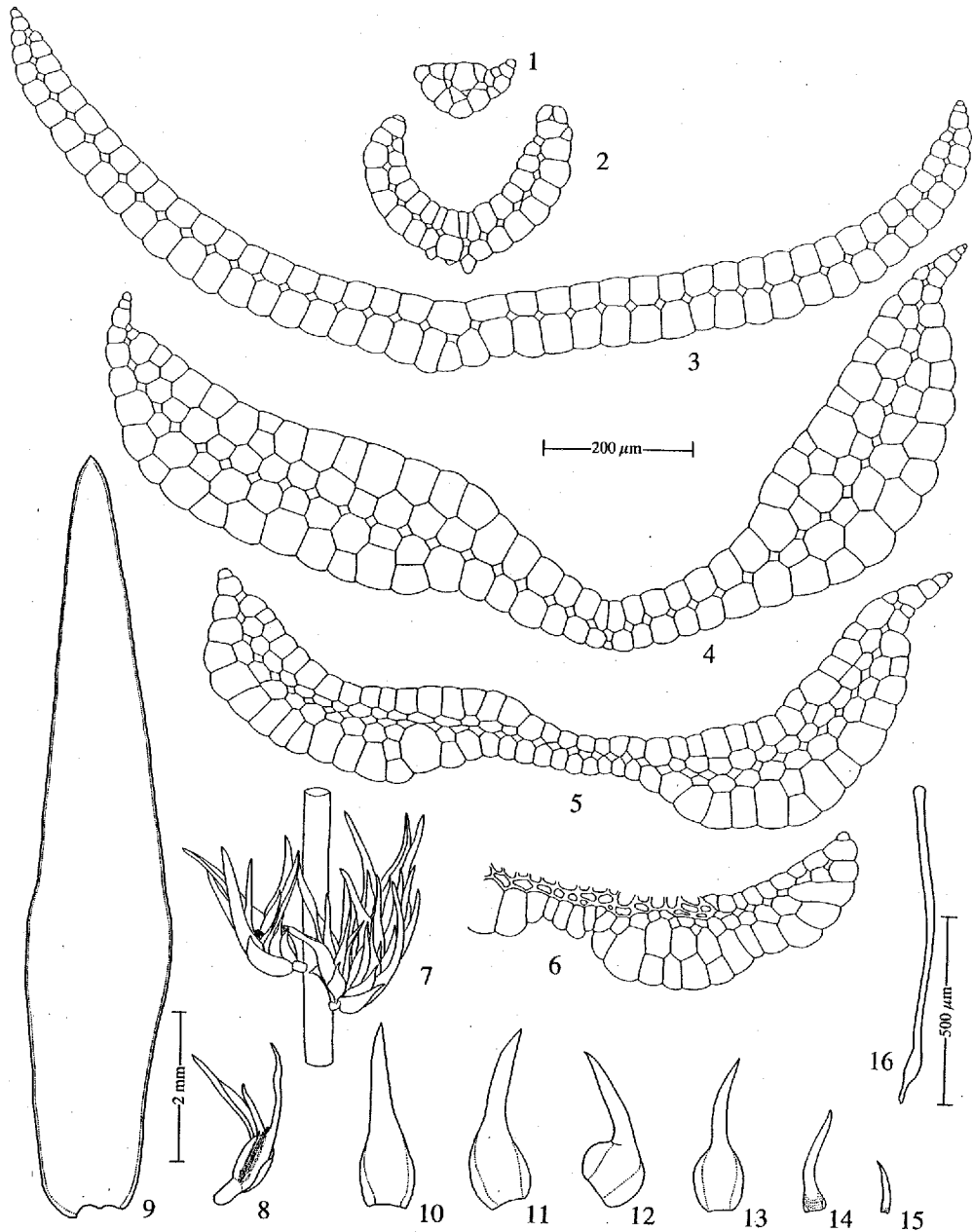


Figure XLIX. *Leucobryum javense* var. *novae-guineae* (Bartr.) T. Yamaguchi. 1-6. Cross-sections of leaf (1, 2, apical; 3, median; 4-6, basal portions). 7, 8. Perichaetia. 9. Stem leaves (expanded) near perichaetium. 10-15. Perigonal leaves [expanded; numbers show the order of perigonal leaves from the innermost leaf (number 15)]. 16. Archegonium. Figs. 1-6 were drawn from holotype of *L. novae-guineae* (FH); 7-16, from holotype of *L. antarensis* (L).

acute to bluntly mucronate, papilloso-prorate from the apex to 3/10 of the leaf length on abaxial surface; laminae and borders consisting of 2-7 rows of narrowly rectangular cells near base, the differentiation between laminal cells and border cells indistinct; alar parts bulged, the edge of alar part with narrow (1-2 cell rows) wing in cross-sections (Fig. XLVIII: 6, 7); in cross-sections near leaf base leucocysts in 2-3 cell layers on adaxial side and 3 cell layers on abaxial side at the thickest part; abaxial leucocysts distinctly decurrent on stems, in cross-sections at insertional parts to stem usually 3 cell layers of leucocysts at the thickest part (Fig. XLVI: 3, XLVIII: 6, 7, XLIX: 6).

Dioicous. Male plants not observed. Perichaetia terminal on short lateral branches, small and bud-like; archegonia 0.9-1.2 mm long. Sporophytes not observed.

Representative specimens examined: Borneo, Sarawak, 4th Division, Gunung Mulu National Park, G. Mulu, summit area, 4°05'N 114°55'E, 2375 m alt., 29 May 1978, Touw 20979 (L).  
Seram, Kecamatan Seram Utara, Sawai, Gunung Musisi, Manusela National Park, 3°03'S 129°14'E, 1300 m alt., 25 Jan. 1985, Akiyama 9790 (KYO, HIRO). New Guinea, Star Mts., Mt. Antares, 1500 m alt., 27 June 1959, Zanten 348 – paratype of L. antarensis (L, HIRO); Star Mts., Sibil-valley, Basis Camp, 1300 m alt., 26 Aug. 1959, Zanten 817 – paratype of L.

antarensis (L); West Sepik Distr., Star Mts., 5°00'S  
141°05'E, 3050 m alt., 5 Apr. 1975, Touw 15749 (L).

Habitat: On tree trunks or soil at tree base.

Distribution: Borneo, Seram, New Guinea.

The present variety is differentiated from var. javense by (1) appressed to erect spreading leaves, (2) bulged alar parts of leaves with narrow wings, (3) distinct decurrency of abaxial leucocysts of leaves.

1c. Leucobryum javense var. uncinatum (Fl.) T. Yamaguchi,  
stat. nov. (Fig. L, LI, CXLI: 6)

Basionym: Leucobryum uncinatum Fl., Musc. Fl.

Buitenzorg 1: 149 (1904). Type: Borneo, Nieuwenhuis s. n.  
— holotype (FH).

Plants dark or brownish when dry, forming loose tufts. Stems to 80 mm long with leaves; central strand not differentiated in cross-sections of stems but the walls of cortical cells thinner inward. Leaves erect to widely spreading; 8.4-9.7 x 1.8-1.9 mm, lanceolate, gradually narrowed to broadly channeled point from oblong base, acute and distinctly uncinata at apex (Fig. L: 6-9), papilloso-prorate from the apex to 2/5 of the leaf length on abaxial surface; laminae and borders consisting of 3-4 rows of narrowly rectangular cells near base, the differentiation between laminal cells and border cells indistinct; alar

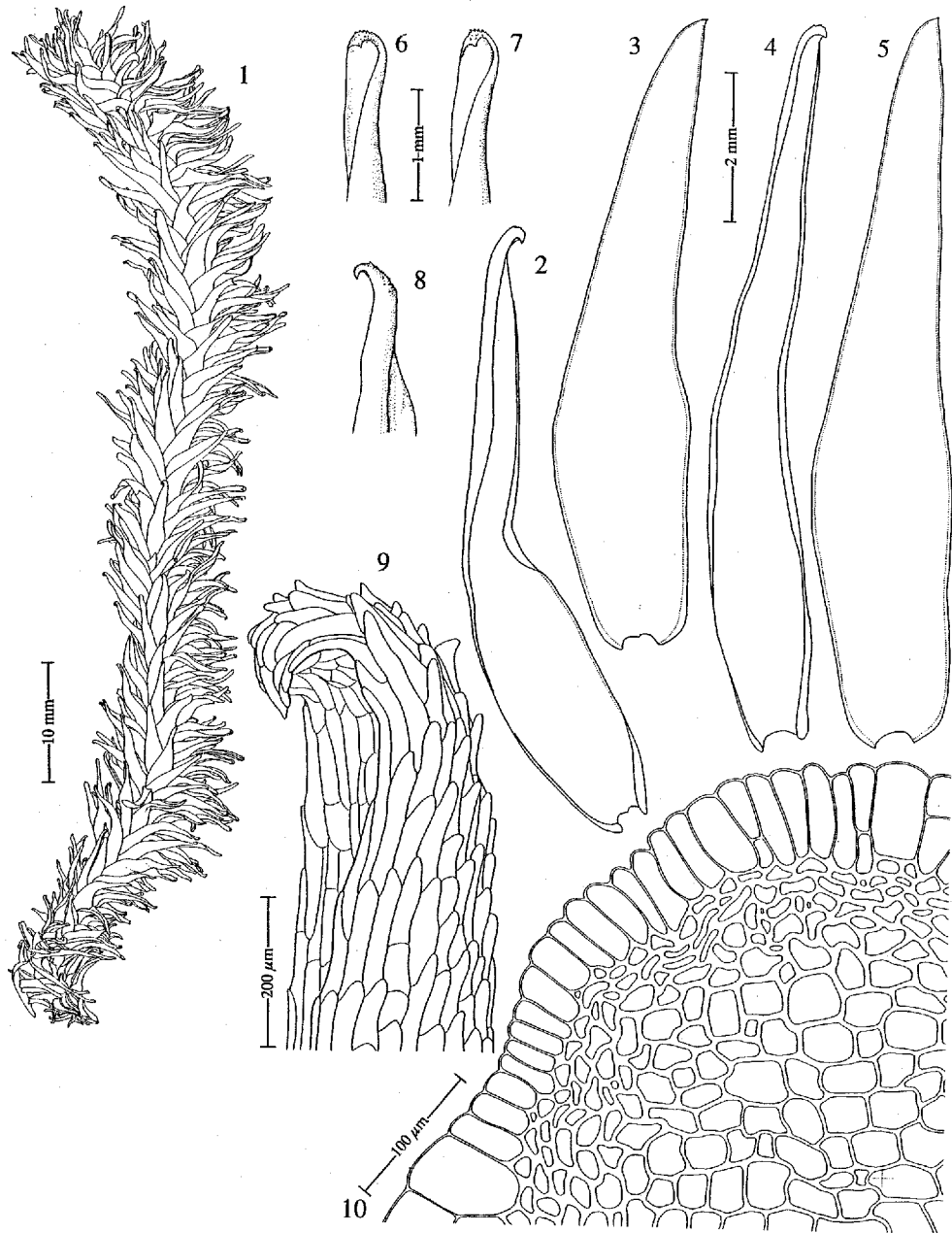


Figure L. *Leucobryum javense* var. *uncinatum* (Fl.) T. Yamaguchi. 1. Plant. 2-5. Leaves (3, 5, expanded). 6-9. Leaf apices. 10. Cross-section of stem. All figures were drawn from holotype of *L. uncinatum* (FH).



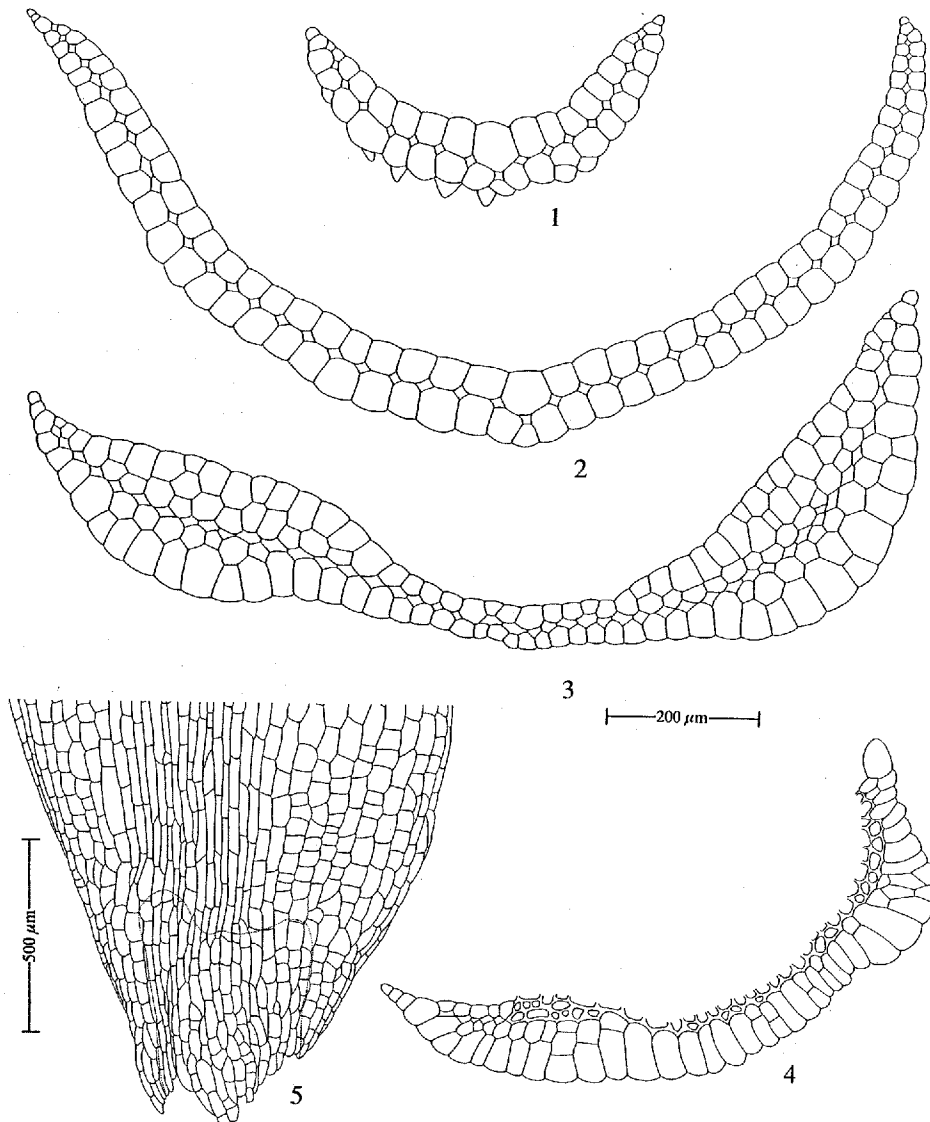


Figure L1. *Leucobryum javense* var. *uncinatum* (Fl.) T. Yamaguchi. 1–4. Cross-sections of leaf (1, apical; 2, median; 3, 4, basal portions). 5. Leaf base (abaxial view). All figures were drawn from holotype of *L. uncinatum* (FH).

parts somewhat bulged; in cross-sections near leaf base leucocysts in 2-3 cell layers on adaxial side and 3 cell layers on abaxial side at the thickest part; abaxial leucocysts distinctly decurrent on stems, in cross-sections at insertional parts to stem 2-3 cell layers of leucocysts at the thickest part (Fig. LI: 4).

Dioicous. Male plants not observed. Perichaetia terminal on short lateral branches, small and bud-like; matured archegonia not observed. Sporophytes not observed.

Representative specimens examined: Borneo, Sarawak, 4th Division, Gunong Mulu National Park, G. Mulu, summit area, 4°05'N 114°55'E, 2375 m alt., 29 May 1978, Touw 20978 (L).

Habitat: On humus.

Distribution: Borneo.

L. javense var. uncinatum is closely related to var. novae-guineae, but is differentiated from var. novae-guineae and other taxa of Leucobryum by the distinctly uncinata leaf apices.

2. Leucobryum scabrum Lac. (Fig. XIX, XXX, XXXIII, LII-LV, CXLI: 3)

Ann. Mus. Bot. Lugd. Bat. 2: 292 (1866). Type: Japan, Siebold s. n. - holotype (L).

Plants grayish or whitish tinged with brown when dry, forming compact tufts or mats. Stems to 60 mm long with

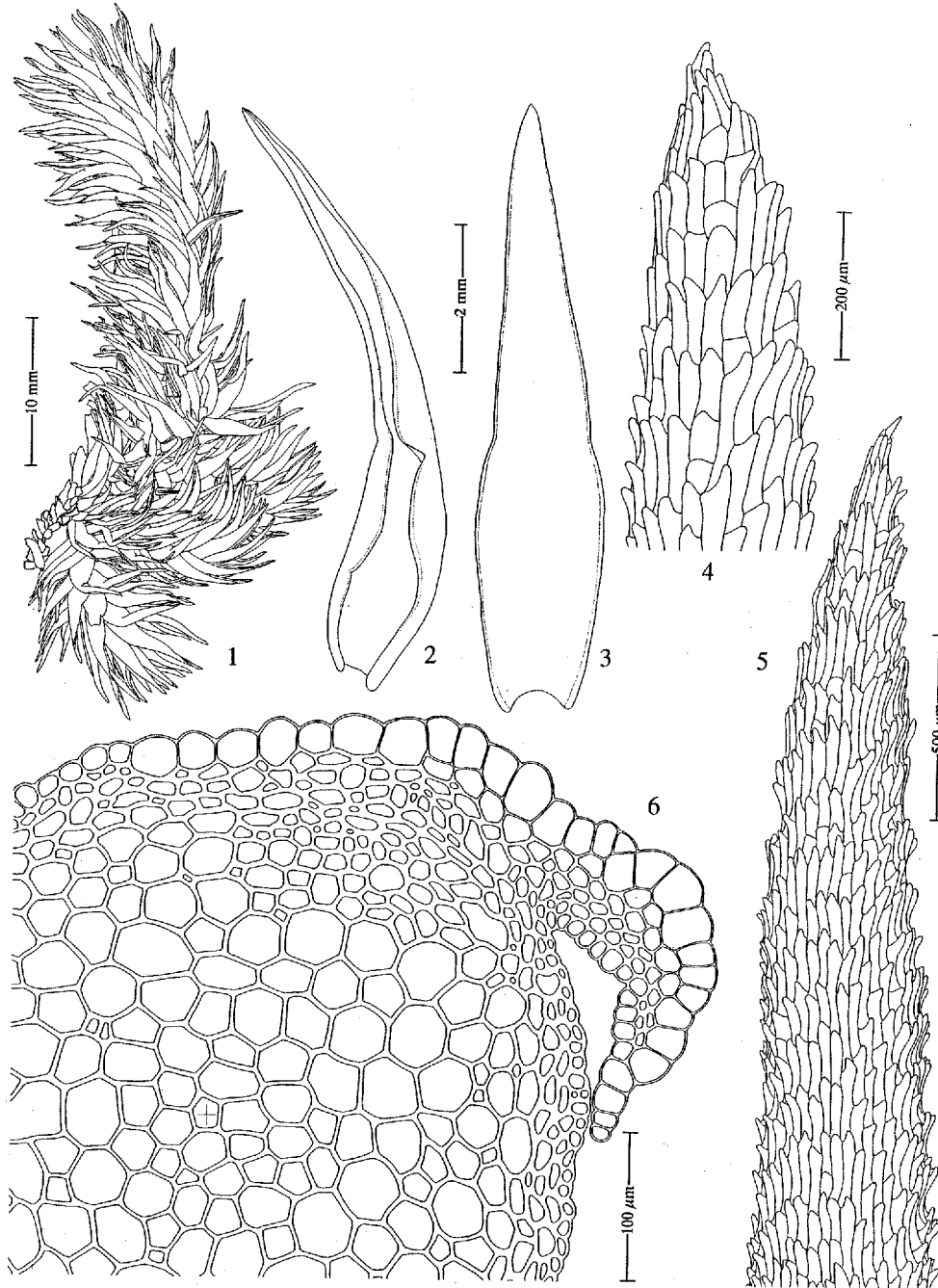


Figure LII. Leucobryum scabrum Lac. 1. Plant. 2, 3. Leaves (3, expanded). 4, 5. Leaf apices. 6. Cross-section of stem. Figs. 1-4 were drawn from holotype of L. scabrum (L); 5, 6, from Yamaguchi 7188 (HIRO).

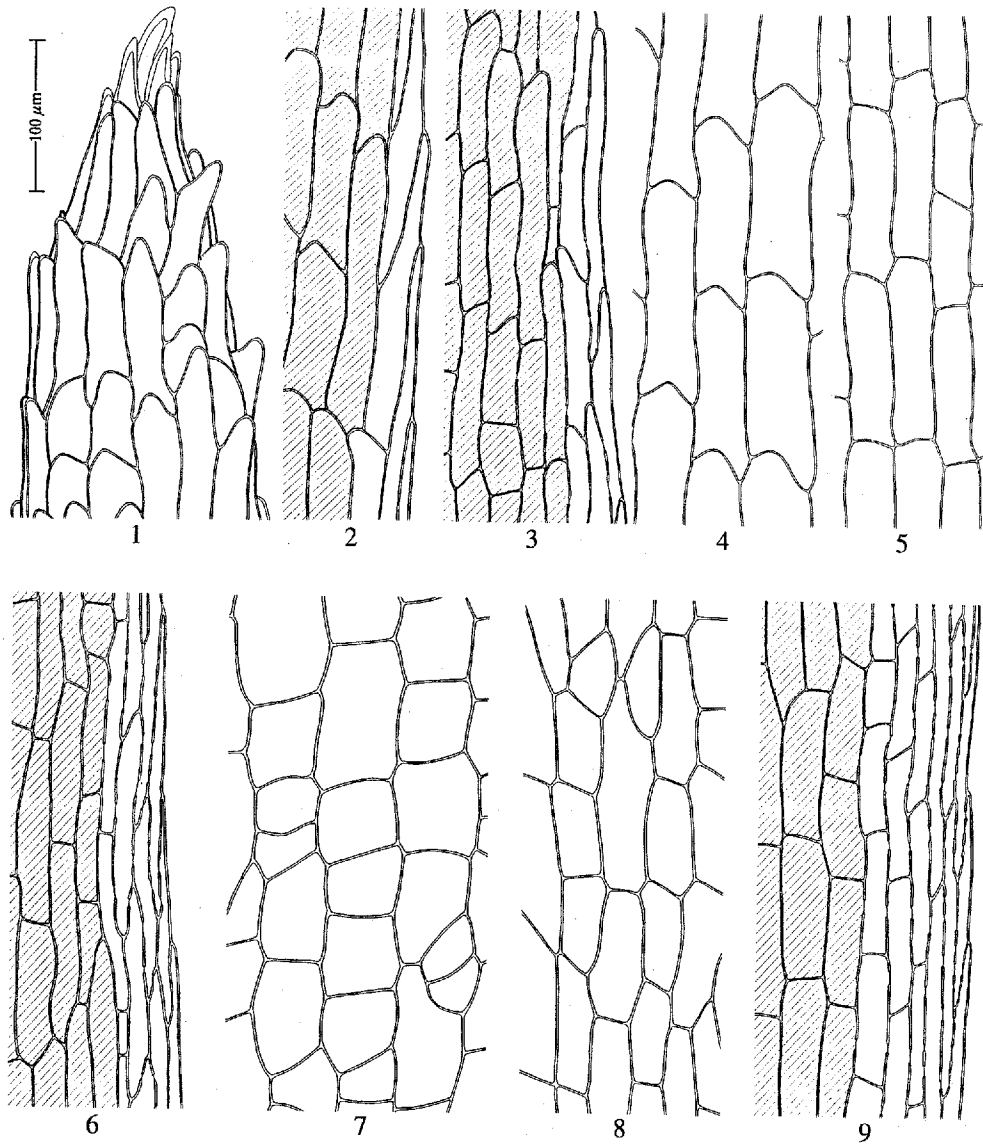


Figure LIII. *Leucobryum scabrum* Lac. 1-3. Cells near leaf apex (1, 2, abaxial view; 3, adaxial view). 4-6. Median cells of leaf (4, abaxial view; 5, 6, adaxial view). 7-9. Basal cells of leaf (7, 9, abaxial view; 8, adaxial view). All figures were drawn from holotype of *L. scabrum* (L).

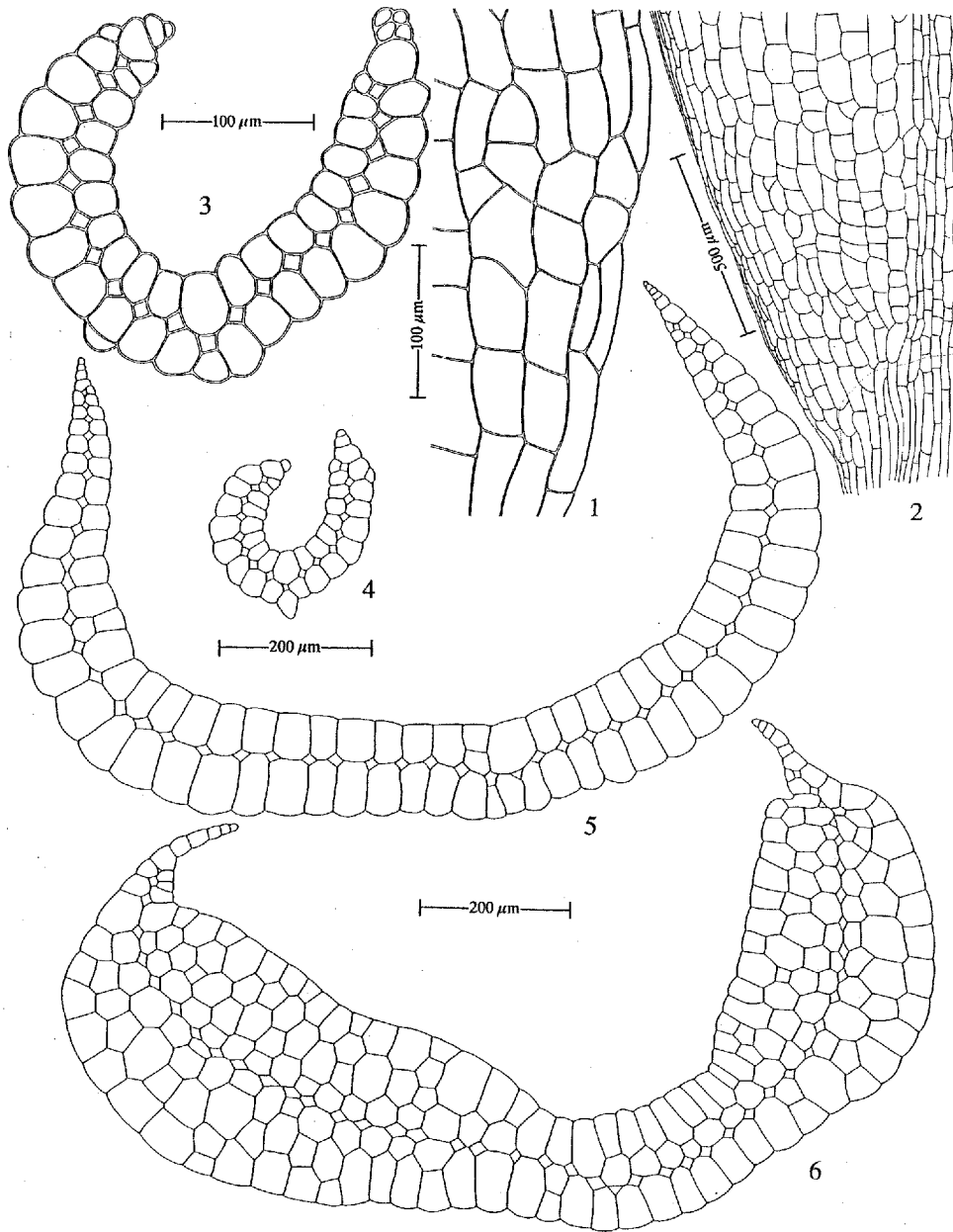


Figure LIV. Leucobryum scabrum Lac. 1, 2. Leaf bases (abaxial view). 3–6. Cross-sections of leaf (3, 4, apical; 5, median; 6, basal portions). All figures were drawn from holotype of L. scabrum (L).

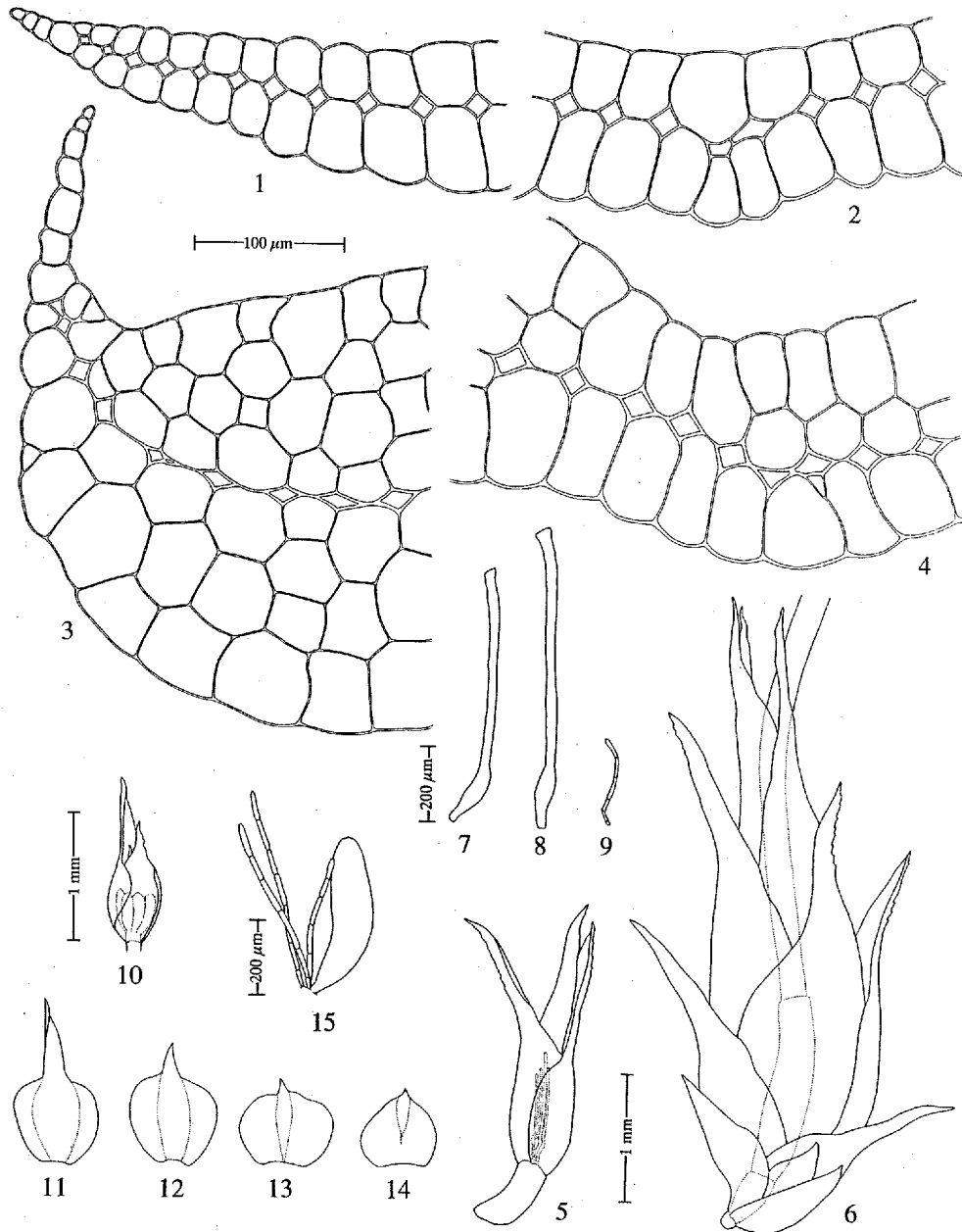


Figure LV. *Leucobryum scabrum* Lac. 1-4. Cross-sections of leaf (1, 2, median; 3, 4, basal portions). 5, 6. Perichaetia (6, with sporophyte). 7, 8. Archegonia. 9. Paraphysis. 10. Perigonium. 11-14. Perigonial leaves [expanded; numbers show the order of perigonial leaves from the innermost leaf (number 14)]. 15. Antheridium. Figs. 1-4 were drawn from holotype of *L. scabrum* (L.); 5-15, from Iwatsuki & Minamidani s. n., Musci Japonici Exsiccati 28: 1378 (NICH).

leaves; central strand not differentiated in cross-sections of stems. Leaves erect spreading, somewhat falcate secund; 7.9-8.2 x 1.7-1.9 mm, lanceolate to narrowly lanceolate, gradually narrowed to subtubulous point from oblong base, acute, undulate and spinosely prorate from the apex to 3/5 of the leaf length on abaxial surface; laminae and borders consisting of 5-7 rows of narrowly rectangular cells near base, the differentiation between laminal cells and border cells indistinct; in cross-sections near leaf base leucocysts in 3-4 cell layers on adaxial side and 3-4 cell layers on abaxial side at the thickest part, the thickest parts distributed near edge sides and abruptly thinned to the wing parts in cross-sections; abaxial leucocysts  $\pm$  decurrent on stems.

Dioicous. Dwarf male plants growing on stem leaves of female plants; independent normal male plants not observed. Perichaetia terminal on short lateral branches; inner perichaetial leaves around mature sporophytes very small (e. g. inner perichaetial leaf 4.2 x 1.4 mm when the stem leaf near the perichaetium 8.2 x 1.9 mm), 0.3-0.6 times longer than ordinary leaves; archegonia ca. 0.8 mm long. Setae 25-32 mm long. Capsules inclined, ovoid to ellipsoid; urns 1.6-1.8 mm long, 1.0-1.1 mm wide. Apices of peristome teeth divided to 2/3 of the length, ca. 0.9 mm long, ca. 0.15 mm

wide at base, the prongs often subdivided. Spores 10-12  $\mu\text{m}$  in diameter.

Representative specimens examined: Japan, Kyushu, Miyazaki-ken, Koyu-gun, Tsuno-cho, Mt. Osuzu, Keyaki Valley, trail to Sagiri Falls, 360-580 m alt., 13-14 May 1976, Iwatsuki & Minamidani, Musci Japonici Exsiccati 28: 1378 (NICH 155711); Shikoku, Ehime-ken, Uwajima-shi, Nametoko Gorge, Mt. Sanbonkui, 500 m alt., 2 Aug. 1984, Yamaguchi 7188 (HIRO). Taiwan, Nantou-hsien, Luku-hsiang, Sunlink-sea, 1700 m alt., 31 May 1984, Yamaguchi et al. 6762 (HIRO).

Habitat: On soil and rocks, sometimes on rock cliffs splashed with water.

Distribution: Japan, Taiwan.

The present species is characterized by (1) large plants, (2) usually falcate leaves up to 8.2 mm long, (3) abaxially undulate and spinosely prorate in upper 3/5 of the leaf length, (4) thickest parts of leaf bases which are distributed near edge and abruptly thinned to the wing parts in cross-sections, (5) perichaetia which are terminal on short lateral branches, and (6) inner perichaetial leaves shorter than stem leaves.

The present species shows similar appearance to small sized *L. javense* var. *javense* as mentioned in the taxonomic note of the latter taxon. In Japan (Ryukyu Isls., Amami Isl.) both taxa grow in the same place, but it is easily



distinguished by naked eyes because L. scabrum forms rather compact mats on soil and rocks, while L. javense var. javense forms loose tufts on humus.

3. Leucobryum aduncum Dozy & Molk. var. aduncum (Fig. XX, LVI-LX, CXLII: 2)

Pl. Jungh. 3: 319 (1854). Type: Java, Junghuhn s. n. (Herb. Lugd. Bat. 20. Ind. Or. no. 910.132-1671) – lectotype (L).

Leucobryum pentastichum Dozy & Molk., Pl. Jungh. 3: 319 (1854) = Leucobryum candidum (Brid. ex P. Beauv.) Wils. var. pentastichum (Dozy & Molk.) Dix., New Zealand Inst. Bull. 3(3): 97 (1923), syn. nov. Type: Java, Junghuhn s. n. (Herb. Lugd. Bat., 20. Ind. Or. no. 910.132-790) – holotype (L).

Plants grayish or whitish tinged with brown when dry, forming tufts. Stems to 50 mm long with leaves; central strand not differentiated in cross-sections of stems. Leaves falcate secund, somewhat arranged in 5 rows; 3.4-4.1 x 0.8-1.2 mm, lanceolate, gradually narrowed to subtubulous point from ovate to oblong base, acute, undulate and spinosely prorate from the apex to 3/5 of the leaf length on abaxial surface; laminae and borders consisting of 3-6 rows of narrowly rectangular to linear cells near base, the quadrate laminal cells restricted to alar parts; in cross-sections near leaf base leucocysts in 2-3 cell layers on

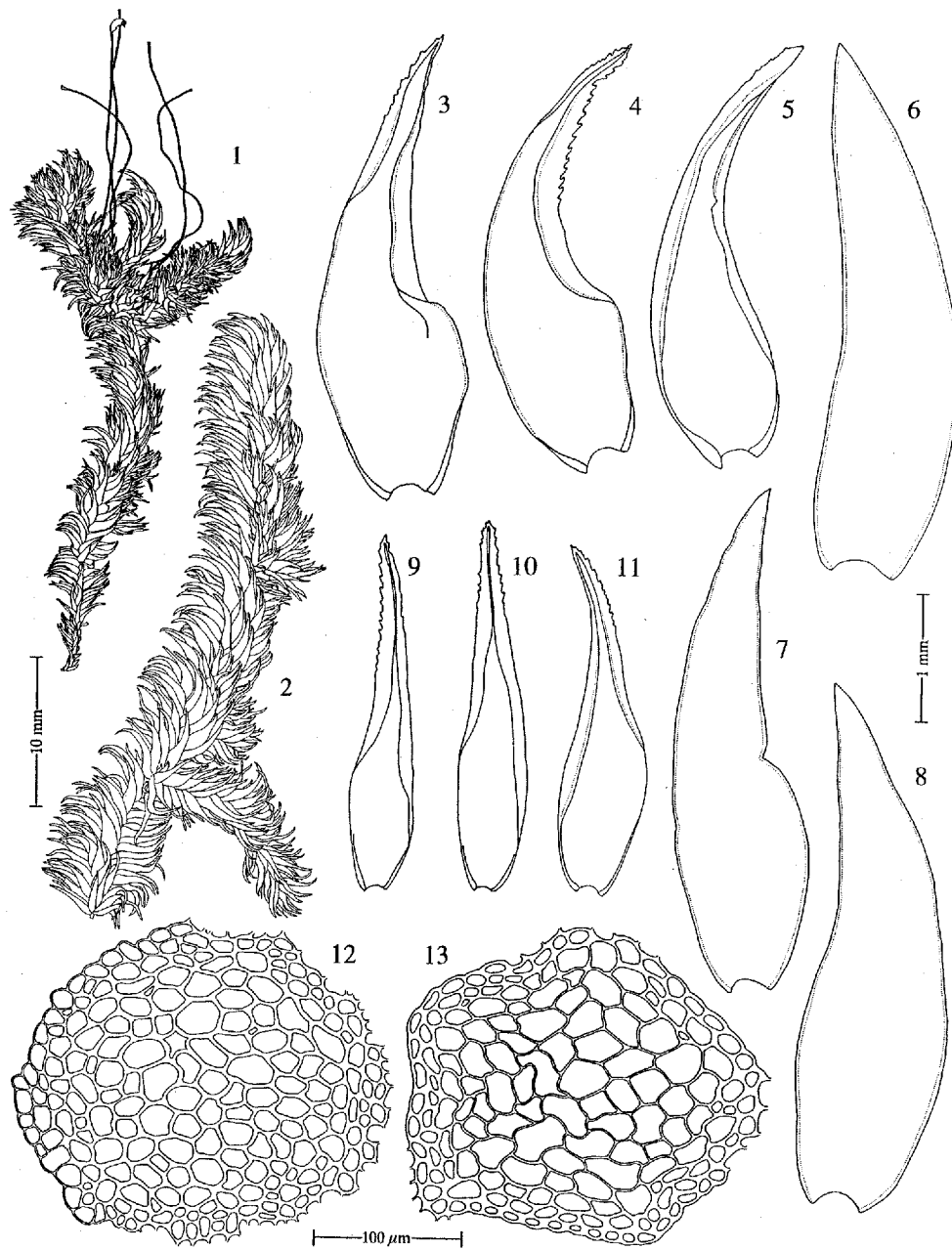


Figure LVI. Leucobryum aduncum Dozy & Molk. var. aduncum. 1, 2. Plants. 3-11. Leaves (6-8, expanded). 12, 13. Cross-sections of stems. Figs. 1, 3, 4, 7-11, 13 were drawn from lectotype of L. aduncum (L); 2, 5, 6, 12, from holotype of L. pentastichum (L).

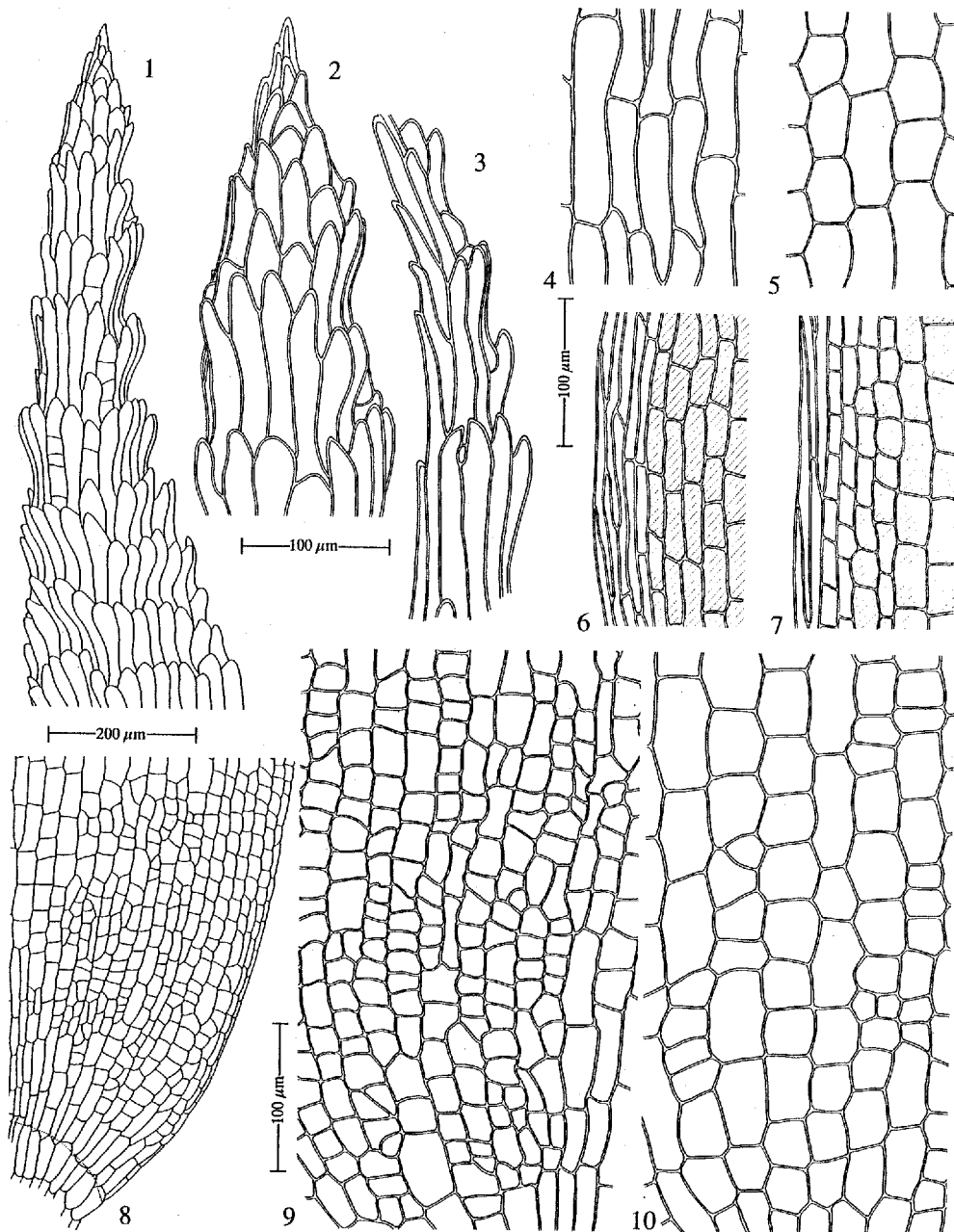


Figure LVII. *Leucobryum aduncum* Dozy & Molk. var. *aduncum*. 1-3. Leaf apices (3, lateral view). 4-6. Median cells of leaf (4, abaxial view; 5, 6, adaxial view). 7-10. Basal cells of leaf (7-9, abaxial view; 10, adaxial view). All figures were drawn from lectotype of *L. aduncum* (L).

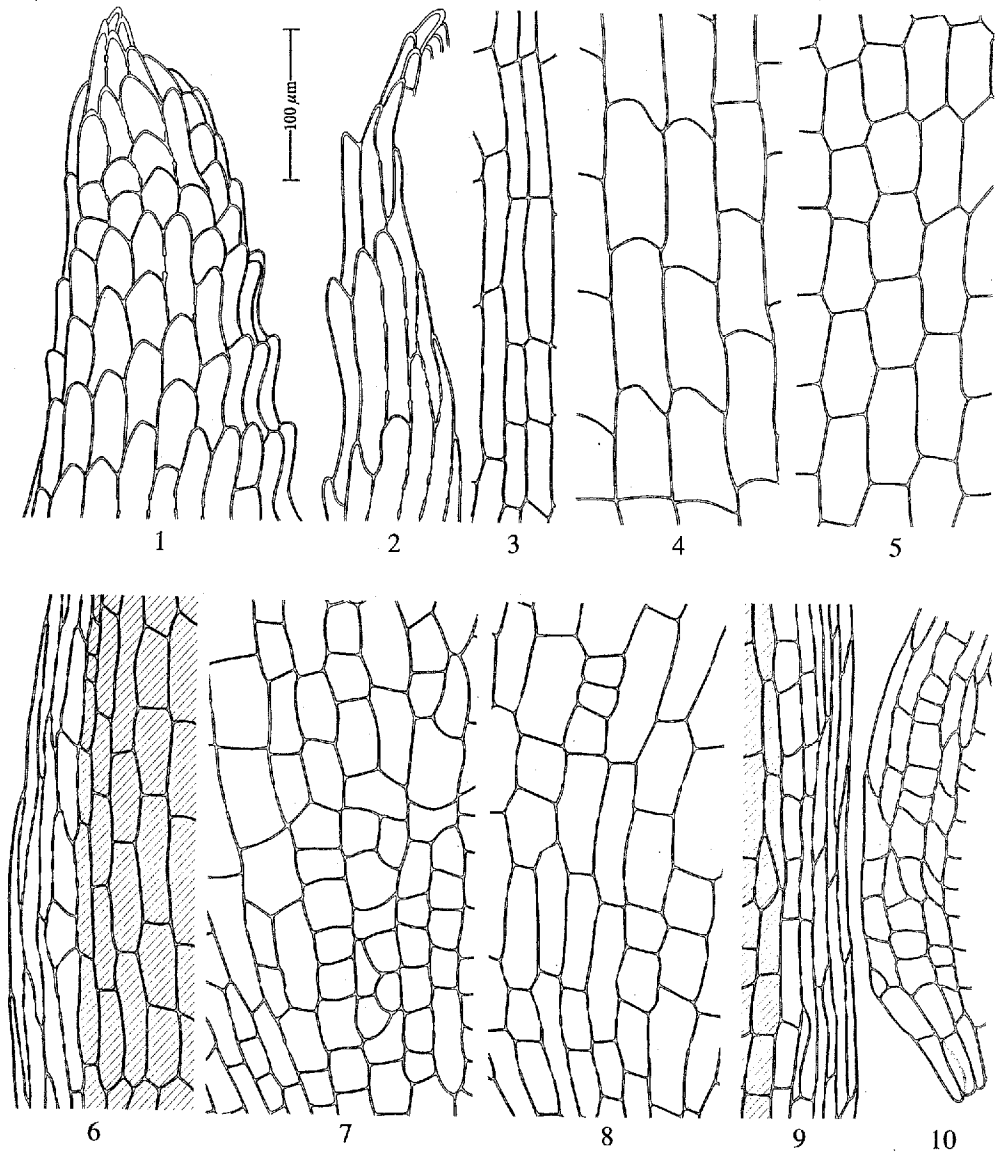


Figure LVIII. Leucobryum aduncum Dozy & Molk. var. aduncum. 1-3. Cells near leaf apex (1, abaxial view; 2, 3, adaxial view). 4-6. Median cells of leaf (4, abaxial view; 5, 6, adaxial view). 7-10. Basal cells of leaf (7, 10, abaxial view; 8, 9, adaxial view). All figures were drawn from holotype of L. pentastichum (L).

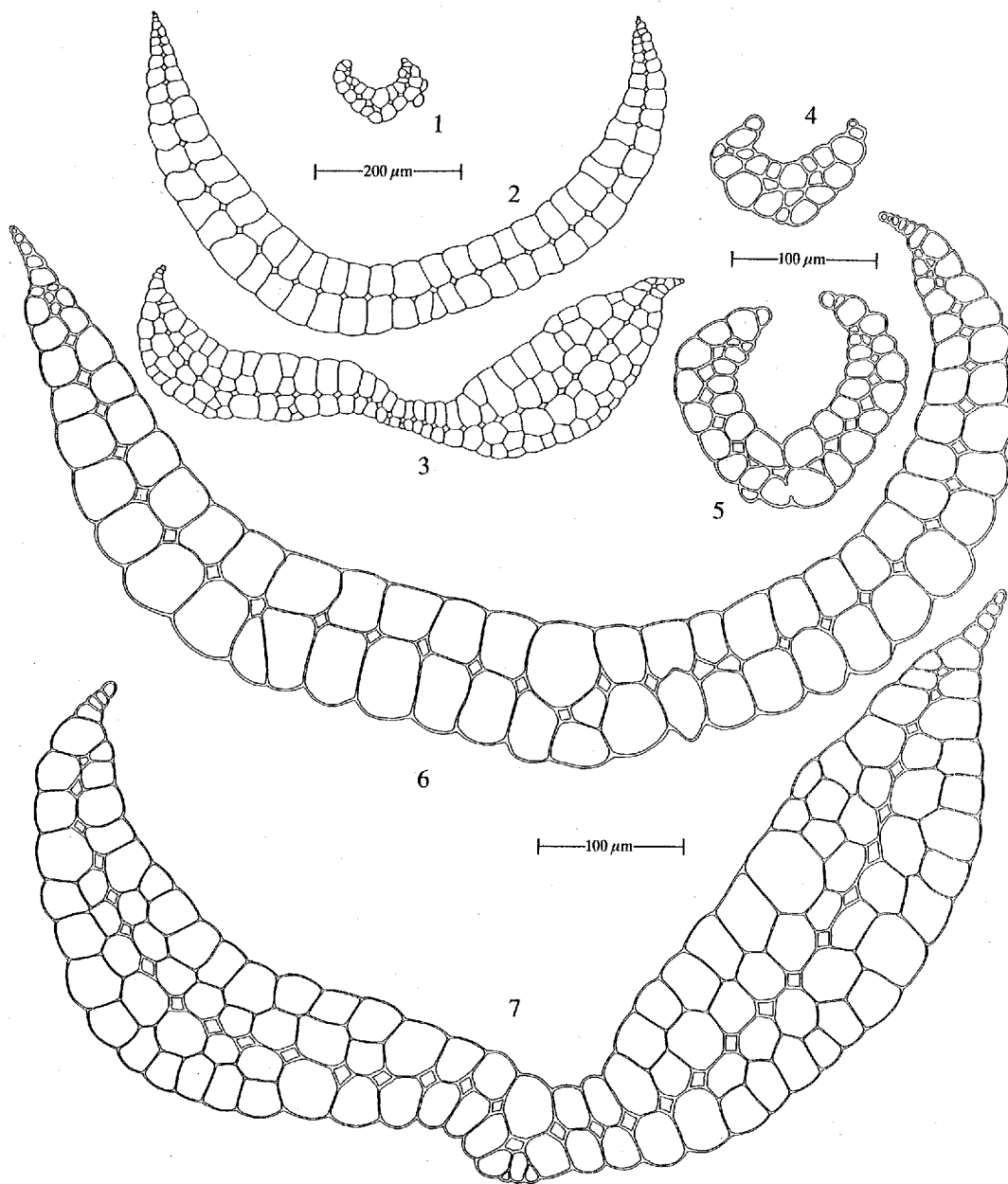


Figure LIX. Leucobryum aduncum Dozy & Molk. var. aduncum. 1-7. Cross-sections of leaves (1, 4, 5, apical; 2, 6, median; 3, 4, basal portions). Figs. 1-3 were drawn from lectotype of L. aduncum (L); 4-7, from holotype of L. pentastichum (L).

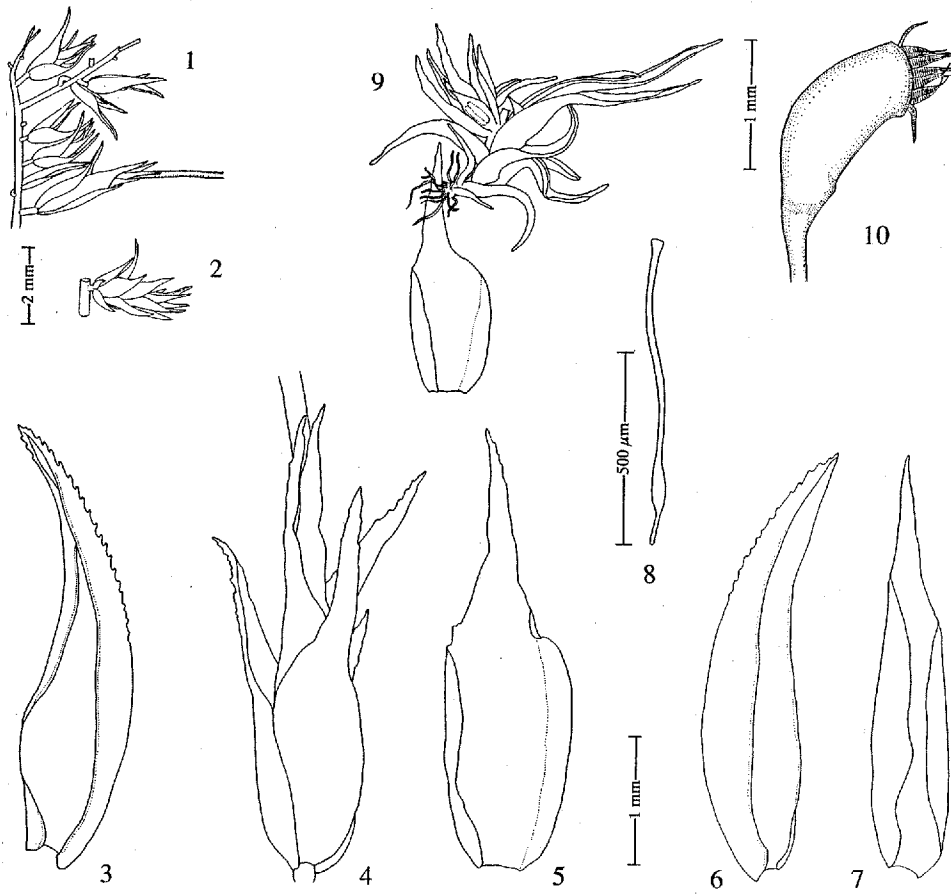


Figure LX. *Leucobryum aduncum* Dozy & Molk. var. *aduncum*. 1, 2, 4. Perichaetia. 3. Stem leaf near perichaetium 4. 5. Inner perichaetial leaf from perichaetium 4. 6. Stem leaf near perichaetial leaf 7. Inner perichaetial leaf. 8. Archegonium. 9. Dwarf male plant growing on perichaetial leaf. 10. Capsule. Figs. 1, 3, 4, 5, 8–10 were drawn from lectotype of *L. aduncum* (L); 2, from holotype of *L. pentastichum* (L); 6, 7, from paratype of *L. aduncum* (L).

adaxial side and 2-3 cell layers on abaxial side at the thickest part; abaxial leucocysts of leaves hardly decurrent on stems; abaxial leucocysts of leaf bases vertically subdivided and forming groups of small quadrate cells (LVII: 9); abaxial leucocysts at insertional parts to stem clearly enlarged and in 1 cell row (Fig. LVII: 8).

Dioicous. Dwarf male plants usually growing on tomentum enclosed by perichaetial leaves; independent normal male plants not observed. Perichaetia terminal on short lateral branches; inner perichaetial leaves around mature sporophytes as long as or somewhat shorter than ordinary leaves; archegonia 0.5-0.8 mm long. Setae 16-18 mm long. Capsules inclined, ovoid to ellipsoid; urns ca. 1.3 mm long, ca. 0.6 mm wide

Representative specimens examined: Thailand, Nakorn Ratchasima Province, Sikiew District, Khao Phrik, 14°55'N 101°35'E, 630 m alt., 9 May 1976, Maxwell B36 (L). Cambodia, Province de Koh Kong, Chékô, 10 Mar. 1965, Kira et al. 137 (HIRO). Vietnam, 14 Feb. 1971, Khiem 198 (L). Malay Peninsula, Selangor, Kanching Forest Reserve, 80 m alt., 16 Jan. 1954, Steenis 18513 (L). Philippines, Palawan, Victoria Mountains, Mar.-Apr. 1951, Edaño 14260 (L). Borneo, Interior Res., Sipitang, Mengalong Forest Reserve, 21 June 1960, Meijer B12423 (L). Sulawesi, Batu Besi, between Tabarano and Larona River, 2°15'-3°S 121°-

121°45'E, 300 m alt., 19 July 1979, Balgooy 4081A (L).  
Sumatra, Harau-canyon, Pajakumbuh, ca. 600 m alt., 31 July  
1955, Meijer 6022 (L). Java, Holle and Teysmann s. n.  
(Herb. Lugd. Bat. 20. Ind. Or. no. 910.132-1683) – paratype  
of L. aduncum (L). Lesser Sunda Islands, W. Flores-  
Manggarai, 5 Mar. 1981, Schmutz 4856 (L). Seram, Kacamatan  
Taniwel, Batu Putih (limestone cliff) and Batu Soli  
(limestone cliff) near Buria, 2°55-57'S 128°27-28'E, 360 m  
alt., 4 Feb. 1985, Akiyama 10067 (KYO, HIRO).

Habitat: On logs, tree trunks, humus and rocks.

Distribution: Thailand, Cambodia, Vietnam, Malaya,  
Philippines, Borneo, Sulawesi, Sumatra, Java, Lesser Sunda  
Islands, Seram, New Guinea.

L. aduncum and its varieties are characterized by (1)  
small to medium sized plants, (2) abaxially undulate and  
spinose prorate leaf apices, and (3) perichaetia usually  
terminal on short lateral branches. Among the taxa included  
in L. aduncum group, var. aduncum is characterized by (1)  
falcate secund leaves arranged somewhat in 5 rows, and (2)  
inner perichaetial leaves which are as long as or somewhat  
shorter than the ordinary leaves around the perichaetium.

L. pentastichum and L. teysmannianum have been  
considered closely related to Australian L. candidum (Brid.  
ex P. Beauv.) Wils. (Dixon 1923, Dixon 1932b, Johnson 1964,  
Enroth 1989, Eddy 1990), based on the common characters such



as the leaves in 5 rows and the scabrous leaf apices. Dixon (1923) combined L. pentastichum with L. candidum as L. candidum (Brid. ex P. Beauv.) Wils. var. pentastichum (Dozy & Molk.) Dix. Johnson (1964) synonymized L. teysmannianum under L. candidum var. pentastichum. Eddy (1990) included both L. candidum var. pentastichum and L. teysmannianum in L. candidum. Furthermore, Enroth (1989) treated above three species, L. candidum, L. pentastichum and L. teysmannianum, as synonyms of L. javense.

The pentastichous leaf arrangement is found in some species of Leucobryum, such as L. aduncum var. aduncum and L. boninense. Therefore, the pentastichous leaf arrangement is not a specific characters observed only in L. candidum. According to Yamaguchi and Iwatsuki (1987), L. candidum is characterized by (1) relatively large plants (stems to 7 cm long with leaves), (2) leaves sometimes arranged spirally or in 5 ranks on stems, (3) leaves with spinosely prorate abaxial cells in the upper half, and (4) small inner perichaetial leaves which are 0.6-0.7 (-0.9) times longer than ordinary leaves. Yamaguchi and Iwatsuki (1987) also mentioned that the leaves (3.0-) 4.0-6.0 x 1.0-1.3 mm. L. pentastichum and L. teysmannianum are medium sized and somewhat soft plants, while L. candidum is relatively large plants. I concluded that L. pentastichum and L. teysmannianum should be compared with L. aduncum based on

the habits and the sexual organs. I do not agree with treatment by Enroth (1989) who synonymized L. teysmannianum, L. pentastichum and L. candidum under L. javense.

3a. Leucobryum aduncum var. teysmannianum (Dozy & Molk.) T. Yamaguchi, stat. nov. (Fig. LXI, LXIII, CXLII: 4)

Basionym: Leucobryum teysmannianum Dozy & Molk., Bryol. Jav. 1: 17, t. 15 (1855). Type: Java, Teysmann s. n. (Herb. Lugd. Bat. no. Ind. Or. no. 910.139-2186) – holotype (L).

Plants grayish or whitish tinged with brown when dry, forming tufts. Stems to 55 mm long with leaves; central strand not differentiated in cross-sections of stems. Leaves erect spreading, distinctly arranged in 5 rows; 3.7-4.3 x 1.0-1.1 mm, lanceolate, gradually narrowed to subtubulous point from oblong base, acute, undulate and spinosely prorate down to mid leaf on abaxial surface; laminae, borders and alar parts similar to those of var. aduncum; in cross-sections near leaf base leucocysts usually in 2 cell layers on adaxial side and 2-3 cell layers on abaxial side at the thickest part; abaxial leucocysts of leaves hardly decurrent on stems; groups of small quadrate cells and enlarged cells at insertional parts indistinct.

Dioicous. Male not observed. Perichaetia terminal on short lateral branches, small and bud-like when

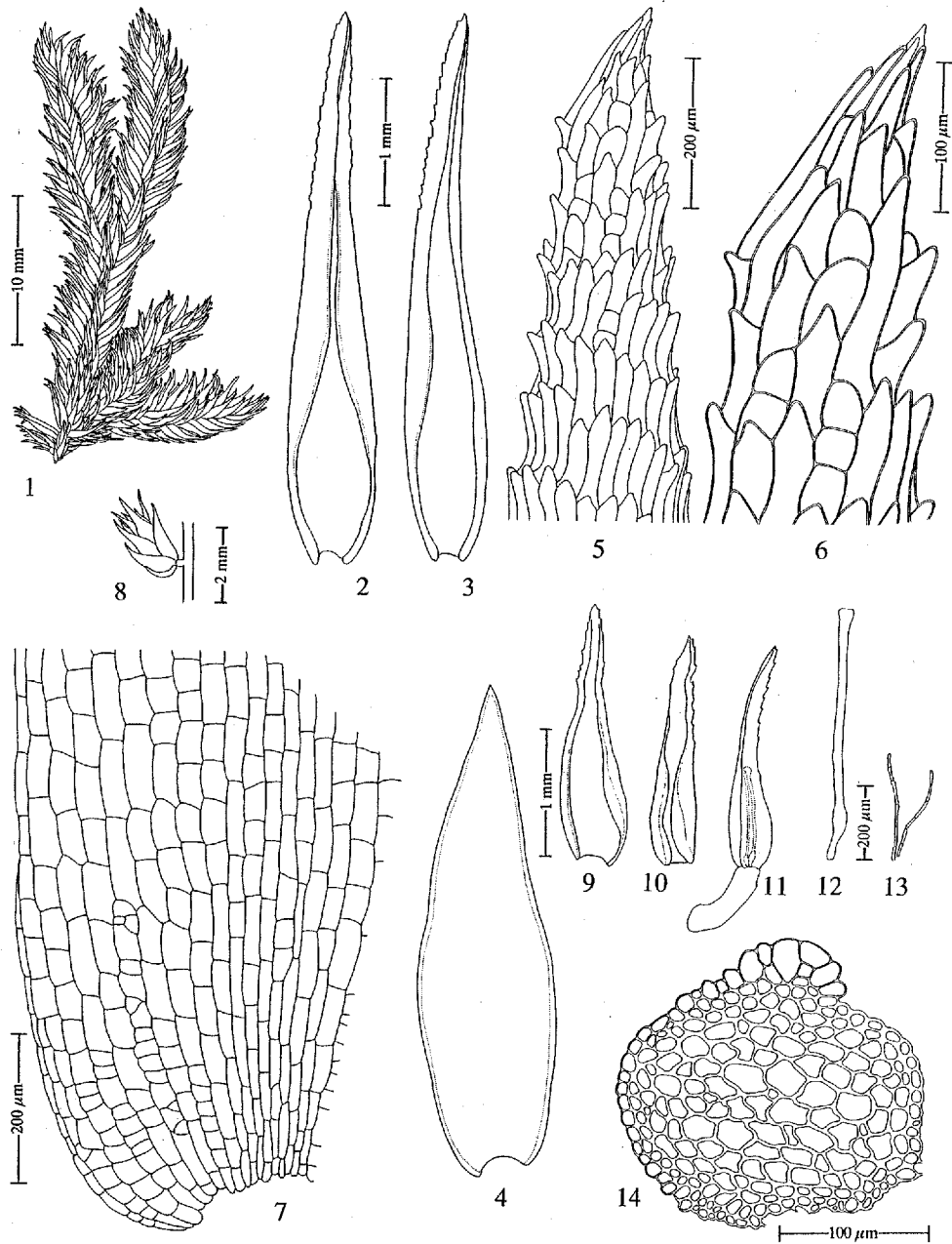


Figure LXI. *Leucobryum aduncum* var. *teysmannianum* (Dozy & Molk.) T. Yamaguchi. 1. Plant. 2-4. Leaves (4, expanded). 5, 6. Leaf apices. 7. Leaf base (abaxial view). 8, 11. Perichaetia. 9, 10. Inner perichaetial leaves. 12. Archegonium. 13. Paraphyses. 14. Cross-section of stem. All figures were drawn from holotype of *L. teysmannianum* (L.).

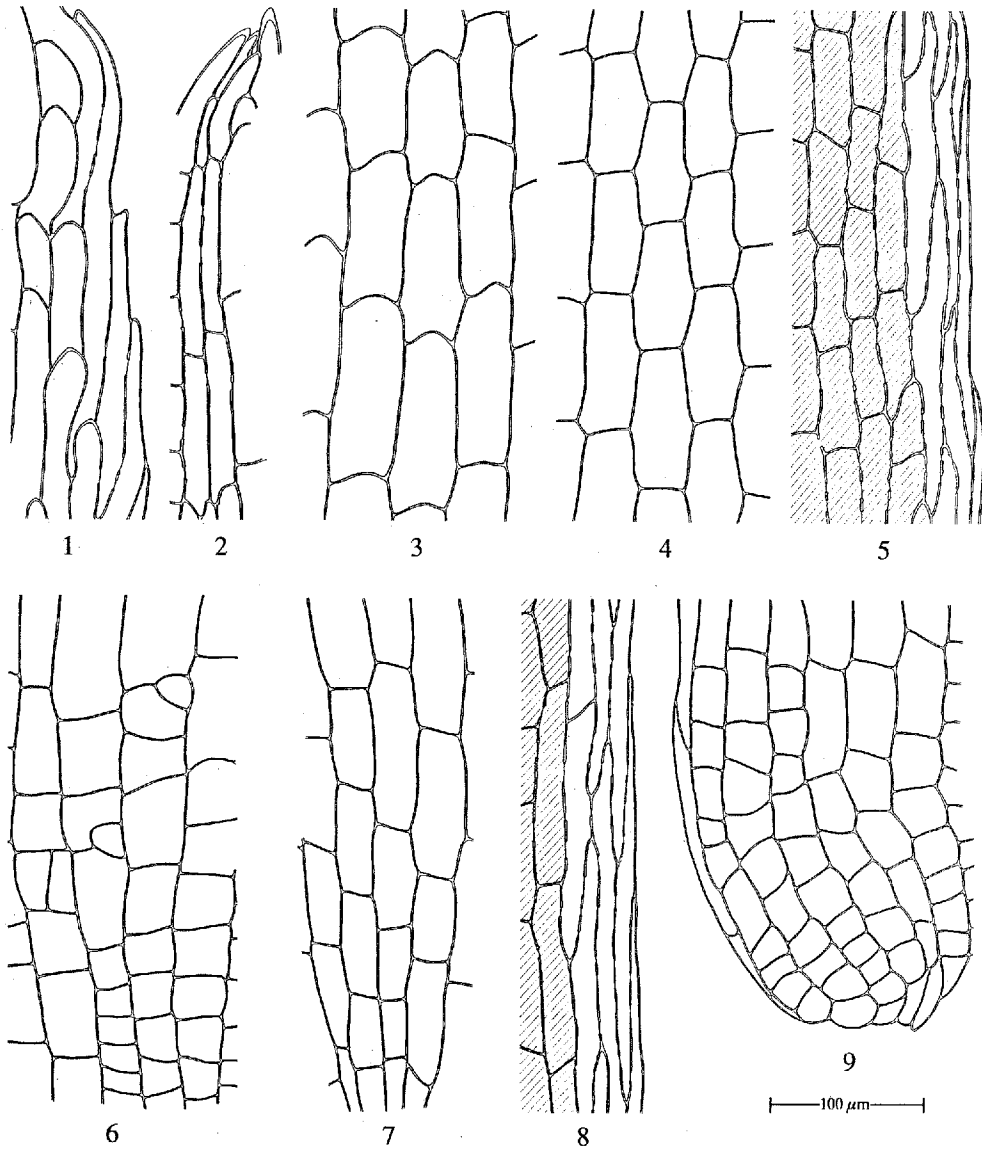


Figure LXII. *Leucobryum aduncum* var. *teysmannianum* (Dozy & Molk.) T. Yamaguchi. 1, 2. Cells near leaf apex (1, abaxial view; 2, adaxial view). 3–5. Median cells of leaf (3, 5, abaxial view; 4, adaxial view). 6–9. Basal cells of leaf (6, 8, 9, abaxial view; 7, adaxial view). All figures were drawn from holotype of *L. teysmannianum* (L).

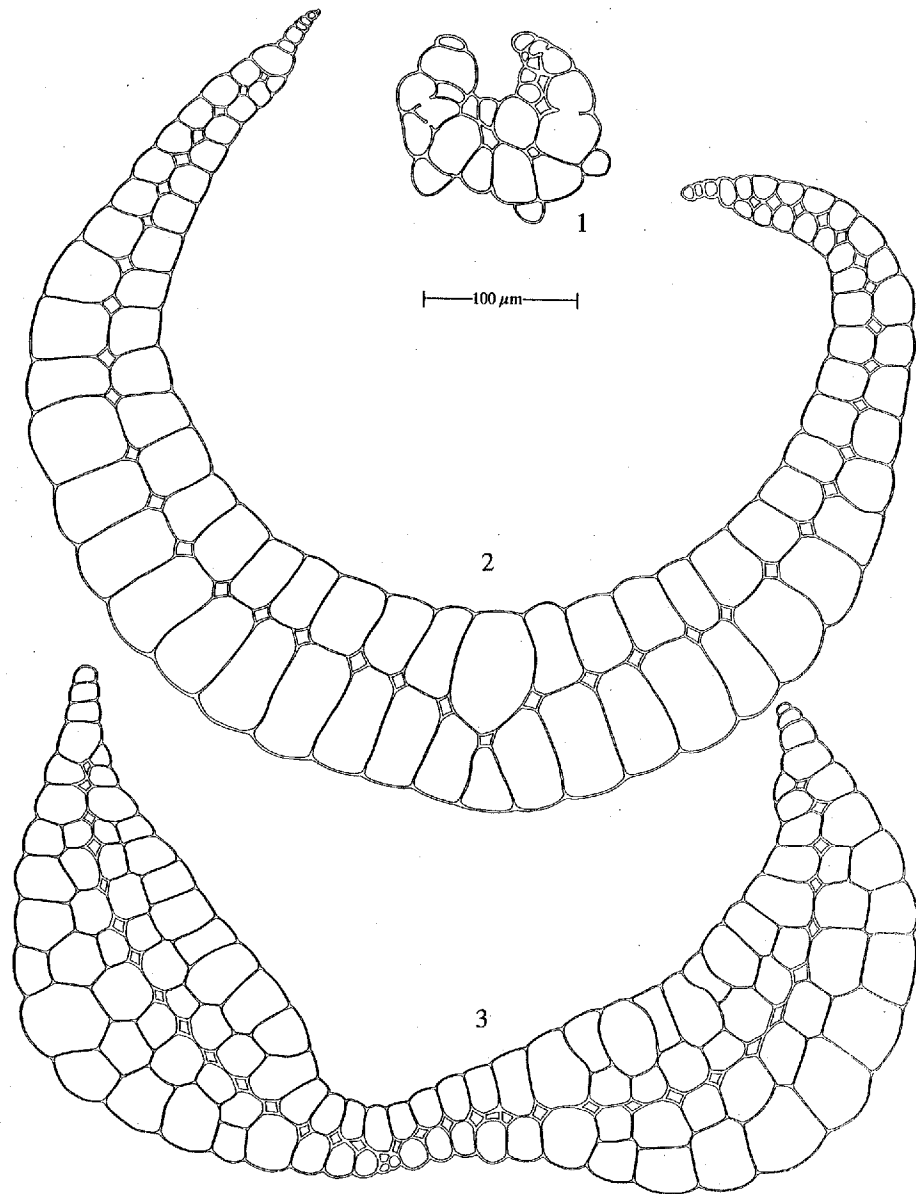


Figure LXIII. Leucobryum aduncum var. teysmannianum (Dozy & Molk.) T. Yamaguchi. 1-3. Cross-sections of leaf (1, apical; 2, median; 3, basal portions). All figures were drawn from holotype of L. teysmannianum (L).

unfertilized; archegonia ca. 0.7 mm long. Sporophytes not observed.

Representative specimens examined: Thailand, Phuket Island, near Thalang, 8°N 98°20'E, 300-350 m alt., 25 Jan. 1966, Touw 11225 (L). Sumatra, Harau-canyon, Pajakumbuh, 600 m alt., 31 July 1955, Meijer 6014 (L). Mentawai Islands, N. Pagai, Sikakap, 7 July 1953, Borssum Waalkes 2701 (L). Java, Prov. Preanger, Pangerango, Tjibodas, 1500 m alt., 18 Apr. 1894, Schiffner 10373 (L). New Guinea, Morobe District, Oomsis, 25 Apr. 1959, Brass s. n. (L).

Habitat: On tree trunks, rocks and soil.

Distribution: Thailand, Sumatra, Java, New Guinea.

L. aduncum var. teysmannianum is characterized by (1) distinct pentastichous leaf arrangement, (2) straight leaves which are 3.7-4.3 mm long and gradually narrowed from oblong base, and (3) indistinct differentiation of abaxial leucocysts at leaf bases. L. aduncum var. aduncum is closely related to var. teysmannianum, but differs in having falcate leaves and differentiated abaxial leucocysts at leaf bases. L. aduncum var. scalare is also related to this taxon, but differs in having closely imbricated and spirally arranged small (2.0-3.5 mm long) leaves.

3b. Leucobryum aduncum var. scalare (C. Müll. ex Fl.) A.

Eddy (Fig. XXI, XXV: A, LXIV-LXX, CXL: 4)

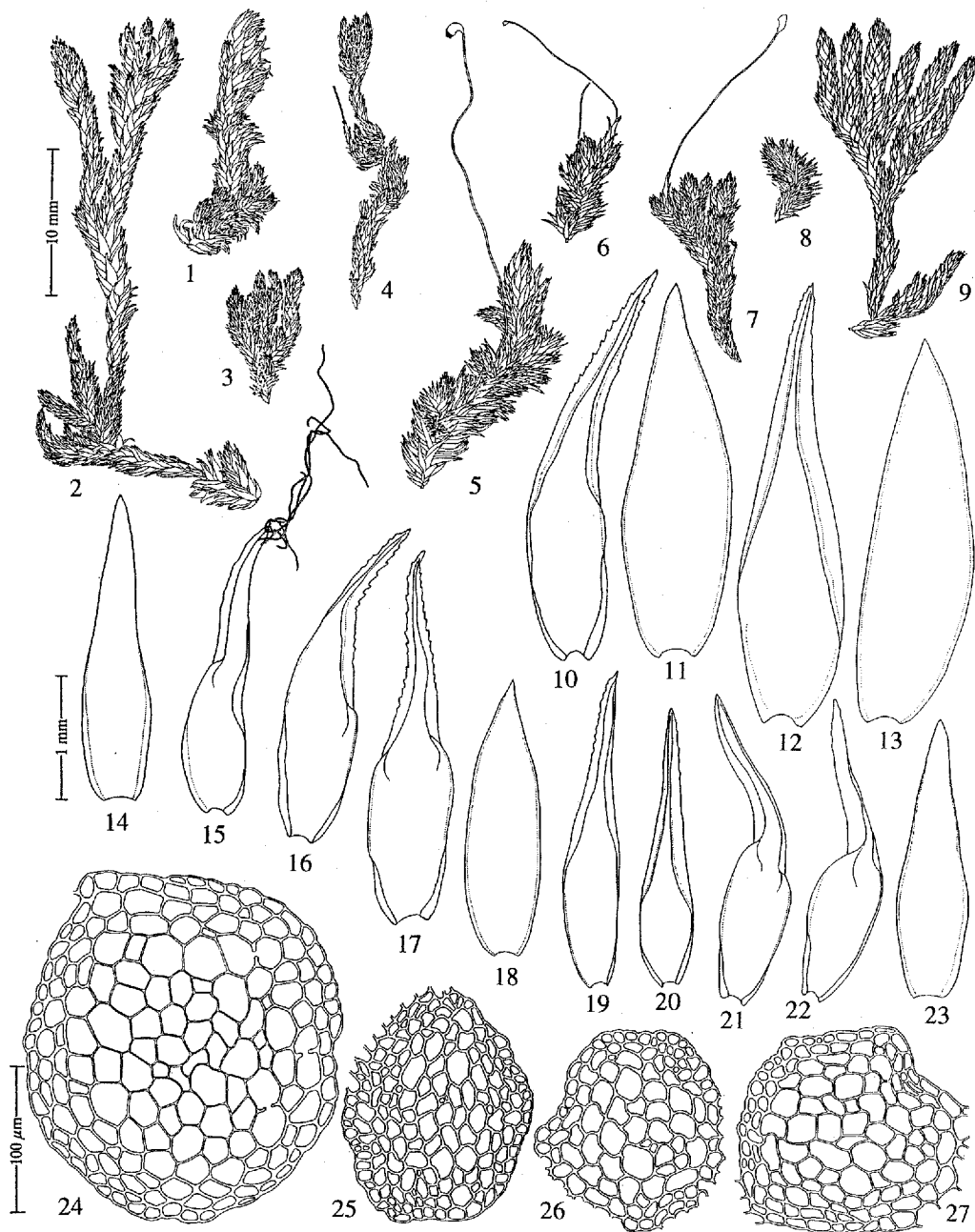


Figure LXIV. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 1-9. Plants. 10-23. Leaves (11, 13, 14, 18, 23, expanded). 24-27. Cross-sections of stems. Figs. 1, 27 were drawn from lectotype of *L. scalare* (FH); 2, from holotype of *L. scalare* var. *tjibodense* (FH); 3, 4, from lectotype of *L. scalare* var. *marschmeyerii* (FH); 5, 10, 11, 20, from isotype of *L. poilanei* (NICH); 6, 9, from Micholitz 264 determined as *L. subscalare* by Brotherus (H); 7, 18, from Touw 10733 (L); 8, from holotype of *L. krempfii* (PC); 12, 13, 24, form isotype of *L. aduncum* var. *arnottii* (GE); 14, 15, 26, from holotype of *L. krempfii* (PC); 16, 17, from isotype of *L. scalare* var. *tjibodense* (HIRO); 19, from isotype of *L. flavulum* (FI); 21-23, 25, from holotype of *L. microleucophanoides*.

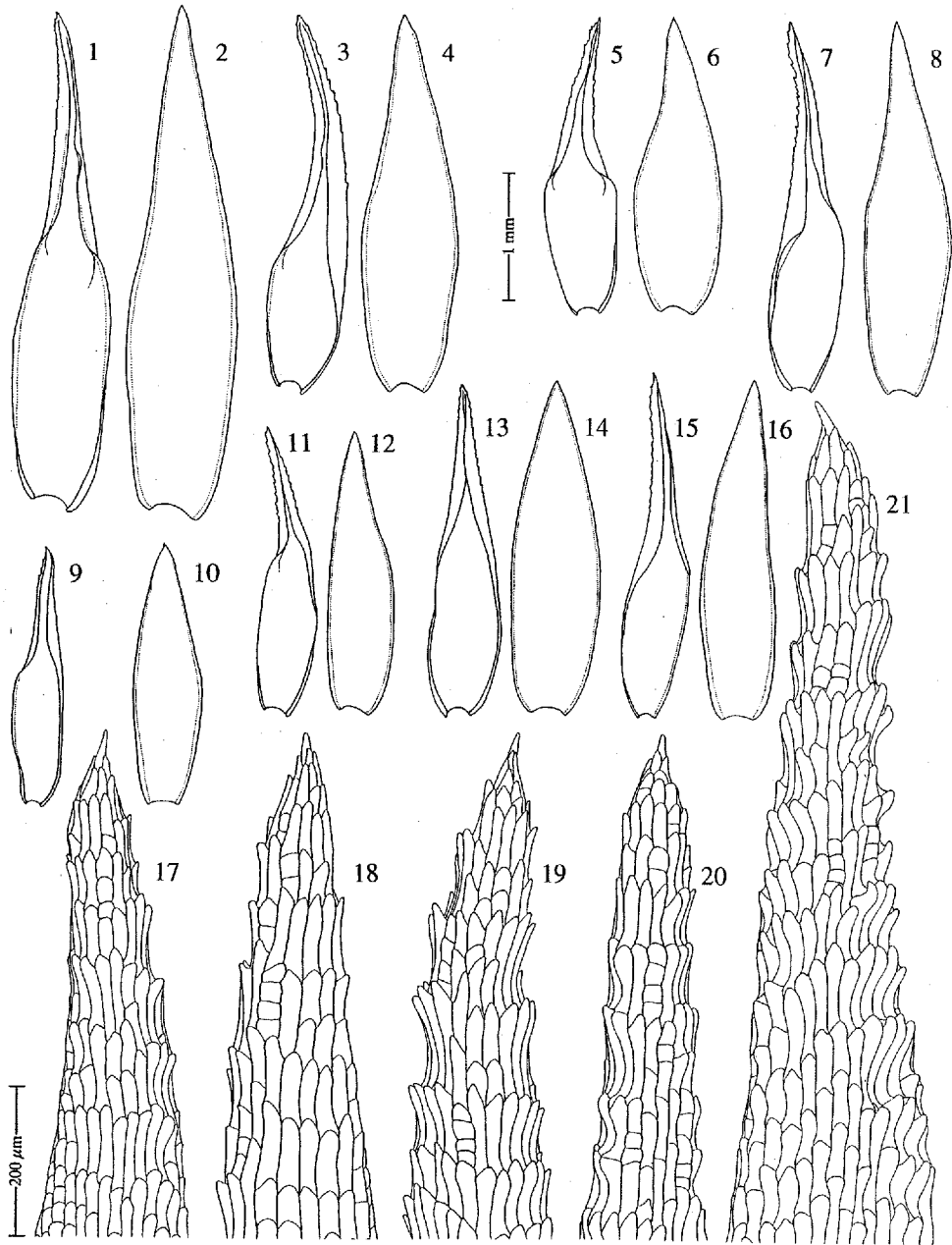


Figure LXV. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 1–16. Leaves (2, 4, 6, 8, 10, 12, 14, 16, expanded). 17–21. Leaf apices. Figs. 1–4, 21 were drawn from lectotype of *L. scalare* (FH); 5–8, from isotype of *L. scalare* var. *tjibodense* (HIRO); 9, 10, 17, from holotype of *L. perichaetiale* (BM); 11, 12, from isolectotype of *L. scalare* var. *marschmeyeri* (HIRO); 13, 14, from Micholitz 264 determined as *L. subscalare* by Brotherus (H); 15, 16, 20, from isotype of *L. flavulum* (Fl); 18, from isotype of *L. aduncum* var. *arnottii* (GE); 19, from isotype of *L. poilanei* (NICH).



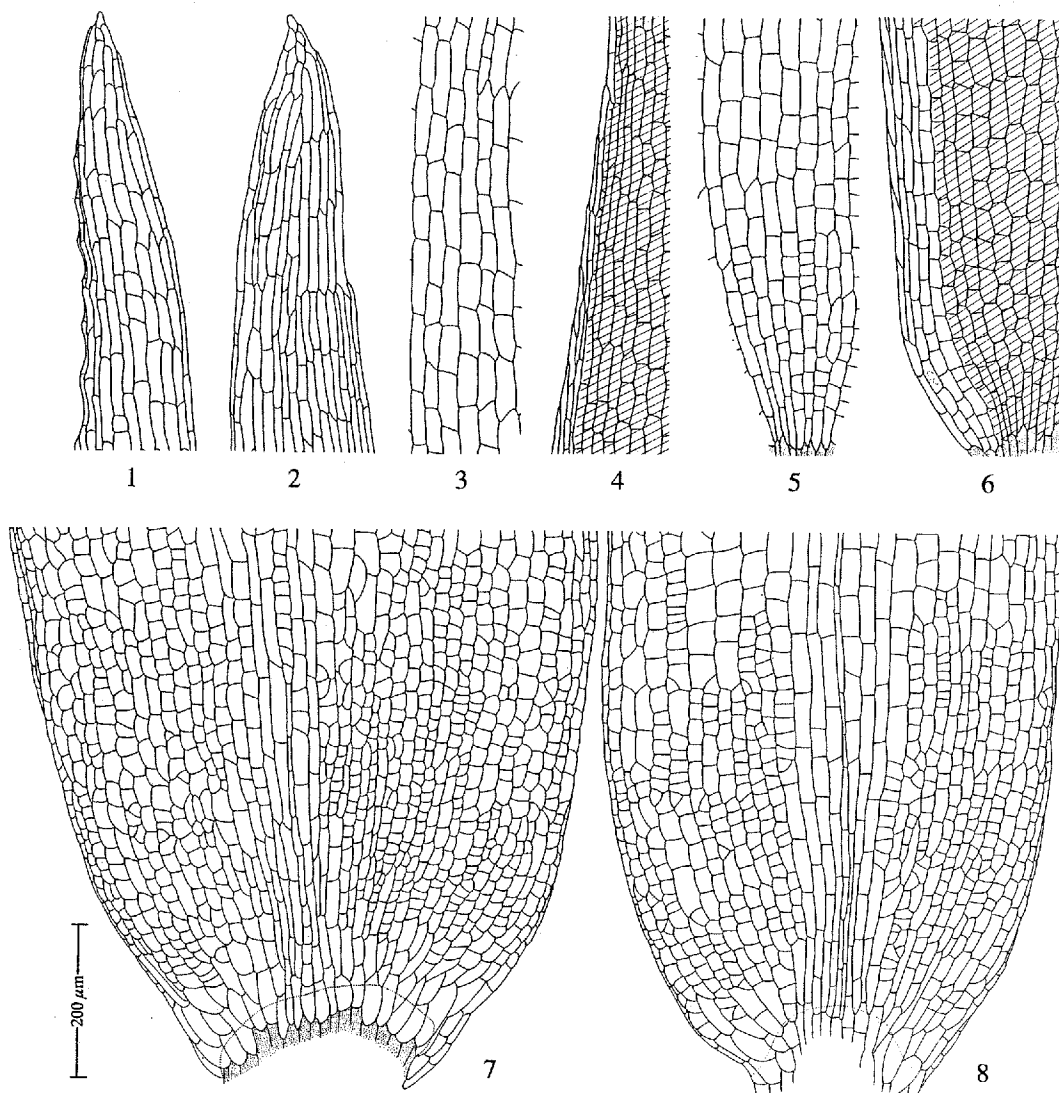


Figure LXVI. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 1, 2. Cells near leaf apex (1, abaxial view; 2, adaxial view). 3, 4. Median cells of leaf (3, abaxial view; 4, adaxial view). 5, 6. Basal cells of leaf (5, abaxial view; 6, adaxial view). 7, 8. Leaf bases (abaxial view). Figs. 1-6 were drawn from holotype of *L. krempfii* (PC); 7, from lectotype of *L. scalare* (FH); 8, from isotype of *L. poilanei* (NICH).

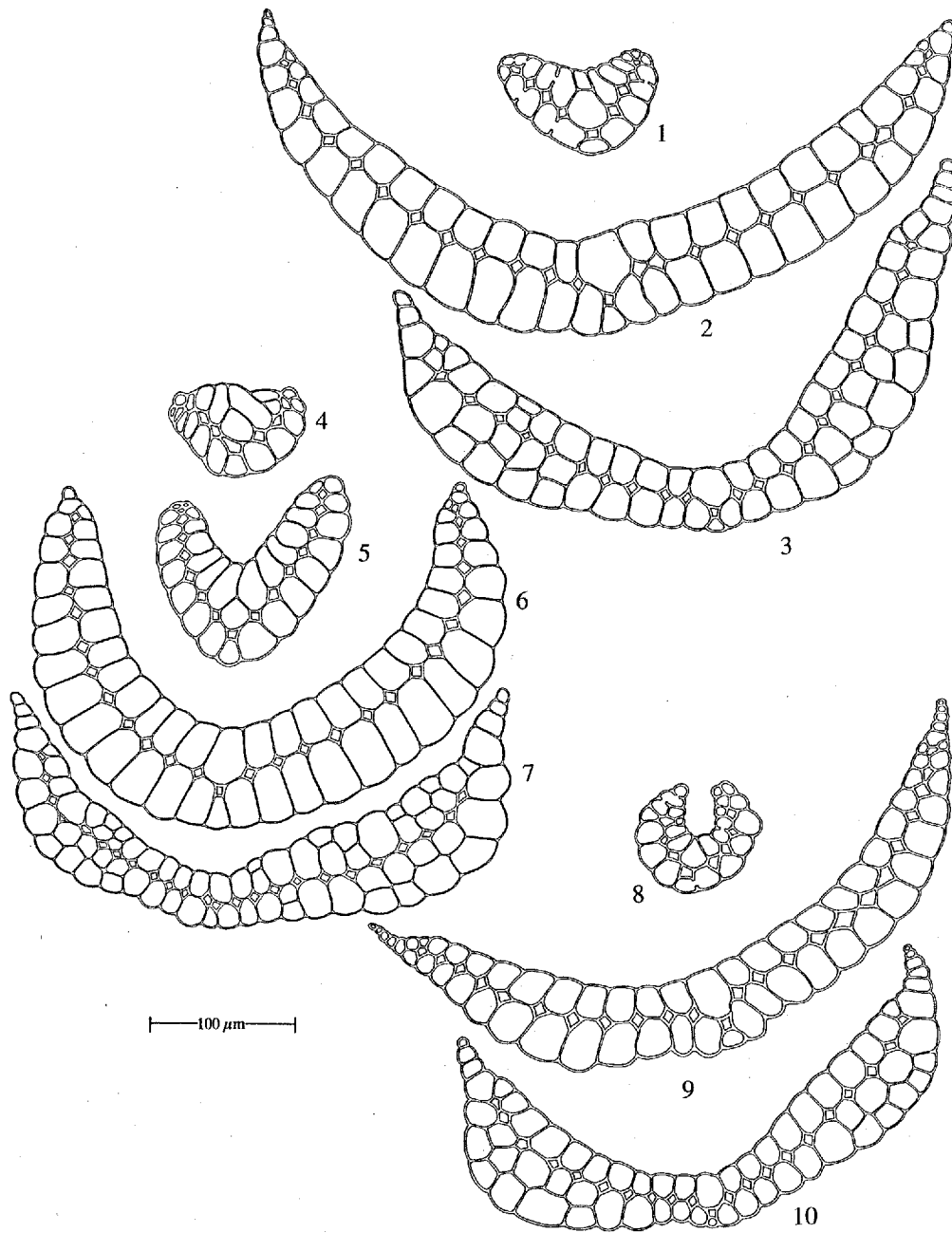


Figure LXVII. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 1–10. Cross-sections of leaves (1, 4, 5, 8, apical; 2, 6, 9, median; 3, 7, 10, basal portions). Figs. 1–3 were drawn from holotype of *L. microleucophanoides* (BM); 4–7, from holotype of *L. krempfii* (PC); 8–10, from holotype of *L. perichaetiale* (BM).

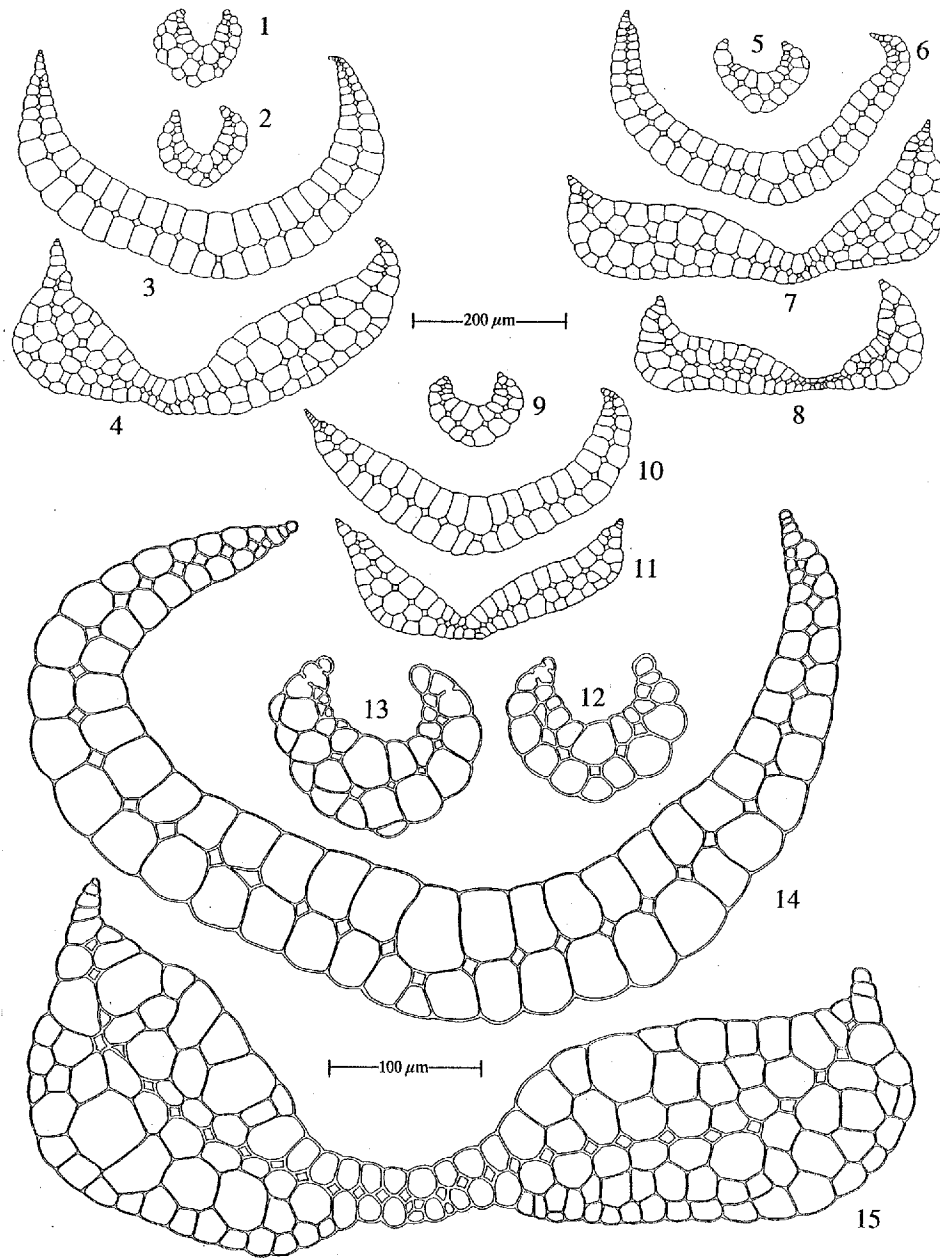


Figure LXVIII. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 1–15. Cross-sections of leaves (1, 2, 5, 9, 12, 13, apical; 3, 6, 10, 14, median; 4, 7, 8, 11, 15, basal portions). Figs. 1–4 were drawn from isotype of *L. poilanei* (NICH); 5–8, from lectotype of *L. scalare* (FH); 9–11, from isotype of *L. flavulum* (FI); 12–15, from isotype of *L. aduncum* var. *arnottii* (GE).

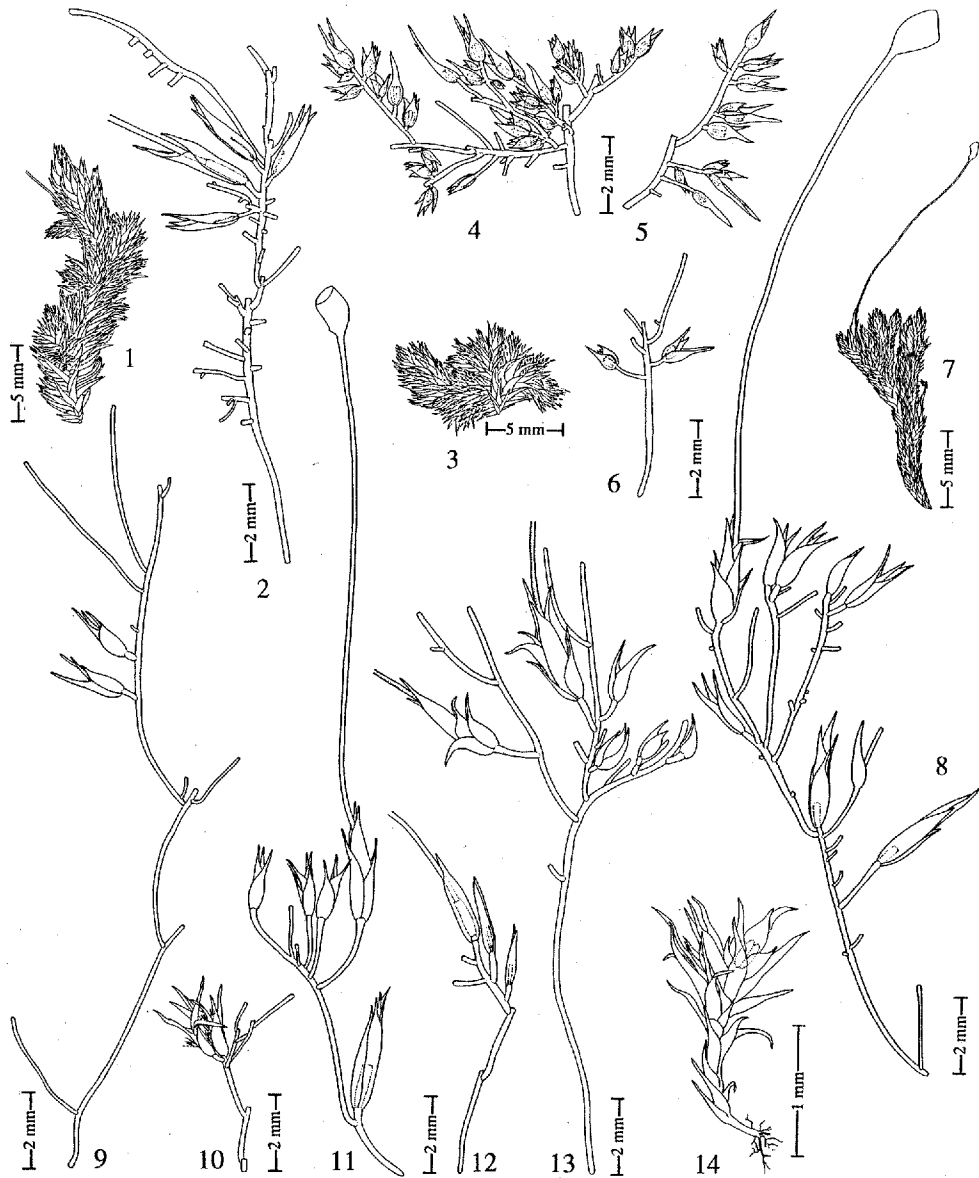


Figure LXIX. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 1, 7. Female plants. 2, 8–13. Branching of female plants showing position of perichaetia (2, 8, from female plants 1 and 7 respectively). 3. Male plant. 4–6. Branching of male plants (4, from male plant 3). 14. Dwarf male plant. Figs. 1–5 were drawn from isotype of *L. poilanei* (NICH); 6, from lectotype of *L. scalare* (FH); 7, 8, 11, from Touw 10733 (L); 9, from isotype of *L. scalare* var. *tjibodense* (HIRO); 10, from holotype of *L. krempfii* (PC); 12, 14, from holotype of *L. perichaetiale* (BM); 13, from isolectotype of *L. scalare* var. *marschmeyeri* (HIRO).

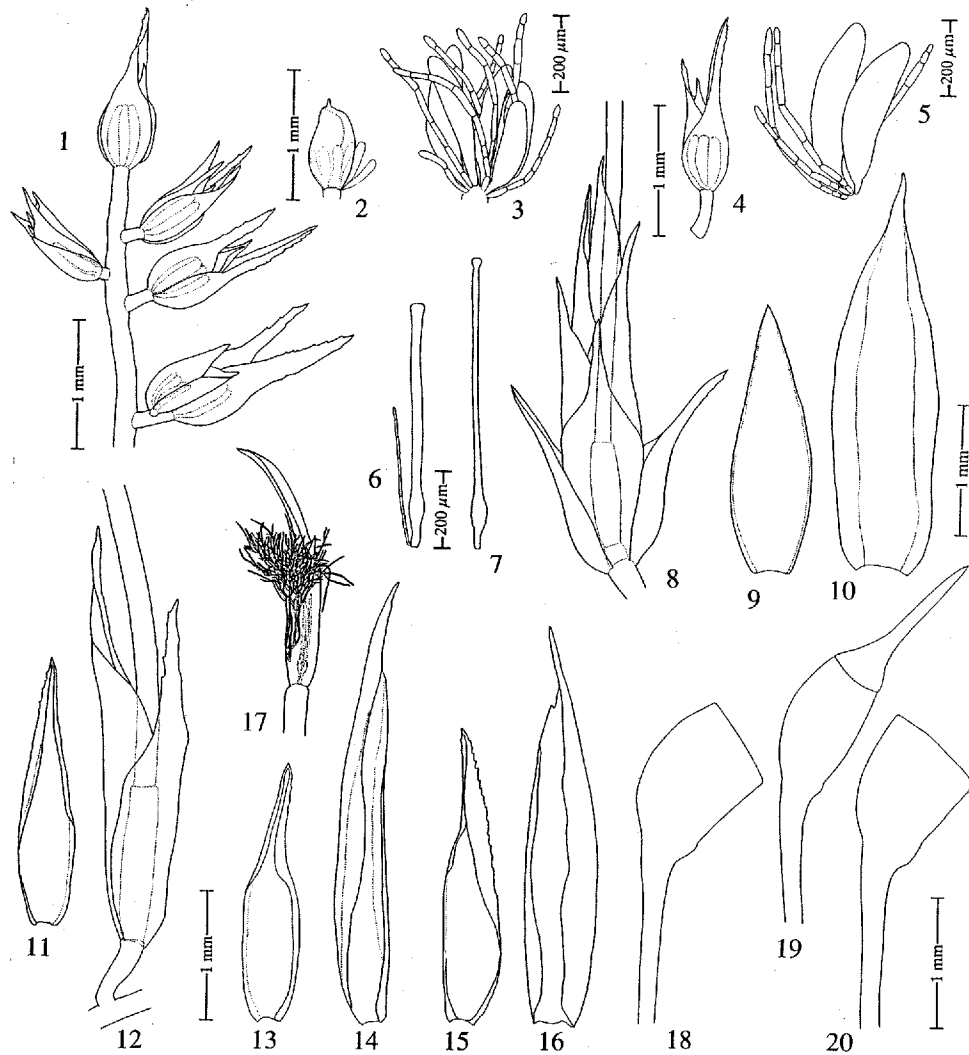


Figure LXX. *Leucobryum aduncum* var. *scalare* (C. Müll. ex Fl.) A. Eddy. 1, 2, 4. Perigonia. 3, 5. Antheridia. 6, 7. Archegonia. 8, 12. Perichaetia with sporophytes. 9, 11. Stem leaves near perichaetia 8 and 12 respectively (9, expanded). 10. Inner perichaetial leaf from perichaetium 8. 13, 15. Stem leaves near perichaetial leaves 14 and 16 respectively. 14, 16. Inner perichaetial leaves. 17. Inner perichaetial leaves with tomentum. 18–20. Capsules. Figs. 1–3, 6, 11, 12 were drawn from isotype of *L. poilanei* (NICH); 4, 5, from lectotype of *L. scalare* (FH); 7–10, 18–20, Touw 10733 (L); 13, 14, from holotype of *L. perichaetiale* (BM); 15, 16, from isolectotype of *L. scalare* var. *marschmeyeri* (HIRO); 17, from holotype of *L. krempfii* (PC).

Malesian Mosses 2: 11, f. 170 (1990).

Basionym: Leucobryum scalare C. Müll. ex Fl., Musci Fl.  
Buitenzorg 1: 143 (1904). Type: Philippines, Luzon,  
Benguet, 5000 ft. alt., Micholitz 173 (Leucobryum scalare C.  
Müll. n. sp. in sched.) – lectotype (FH).

Leucobryum scalare var. marschmeyeri Fl., Musci Fl.  
Buitenzorg 1: 144 (1904). Type: Timor, bei Koepang, an  
morscher Rinde, Oct. 1899, Marschmeyer s. n. (Musci Frond.  
Archipelagi Indici ser. VIII, no. 352) – lectotype (FH),  
isolectotype (HIRO).

Leucobryum scalare var. tjibodense Fl., Musci Fl.  
Buitenzorg 1: 145 (1904). Type: Java, Berggarten von  
Tjibodas, 1450 m alt., an Baumrinde, June 1900, Fleischer s.  
n. (Musci Archipelagi Indici ser. IV, no. 151) – holotype  
(FH), isotype (HIRO).

Leucobryum flavulum Card. in Ren. & Card., Bull. Soc.  
R. Bot. Belg. 41(1): 28 (1905), syn. nov. Type: Sri Lanka,  
Hinidoon Kanda hills, Oct. 1901, Wright s. n. (in herb. E.  
Levier) – holotype (PC), isotype (FI).

Leucobryum subscalare Broth. ex Vard., Rev. de Bot. 29:  
292 (1917), syn. nov. Type: Vietnam, Annam, Plaine de Chu-  
Mai a Thua-Liu, pied des arbrisseaux (nos. 416-417) –  
syntypes (not seen).

Leucobryum krempfii Thér., Recueil Publ. Soc. Havraise,  
Etud. Div. 1919: 35, pl. 1, f. 3 (1919), syn. nov. Type:

Vietnam, Annam, Vallee du Fong Man, 1200 m alt., June 1912, Krempf 1624pp – holotype (PC).

Leucobryum poilanei Thér., Rev. Bryol. n. sér. 2: 18, f. 2 (1929), syn. nov. Type: Cambodia, Pron Thma So, près village Ko-Virk pro, 800-100 m alt, 5 May 1928, Poilane 15222 – isotype (NICH).

Leucobryum perichaetiale Dix., J. Siam Soc., Nat. Hist. Suppl. 9(1): 11 (1932), syn. nov. Type: Thailand, Pāyap, Doi Sutêp, ca. 1500 m alt., 6 Sept. 1914, Kerr s. n. (in herb. Dixon, ref. no. 8) – holotype (BM).

Leucobryum aduncum var. arnottii Thér., Bull. Soc. Bot. Genève sér. 2, 26: 82 (1936), syn. nov. Type: Indes-orientales, 1838, Arnott 38 – holotype (PC), isotype (GE).

Leucobryum microleucophanoides Dix. ex Johnson, Gard. Bull. Straits Settlem, ser. 3, 20: 333, f. 12 (1964), syn. nov. Type: Malaya, Kedah, Inchang Estate, on decaying trunk, 24 Apr. 1940, Spare s. n. (in herb. Dixon, ref. no. 2941) – holotype (BM).

Plants grayish or whitish tinged with brown when dry, forming compact cushions. Stems to 35 mm long with leaves; central strand not differentiated in cross-sections of stems. Leaves closely imbricate, forming conical point at shoot apex; 2.0-3.5 x 0.5-1.0 mm, lanceolate, gradually or abruptly narrowed to subtubulous point from oblong to ovate base, acute, undulate and spinosely prorate down to mid leaf

on abaxial surface; laminae, borders and alar parts similar to those of var. aduncum; in cross-sections near leaf base leucocysts in 1-3 cell layers on adaxial side and 2-3 cell layers on abaxial side at the thickest part; abaxial leucocysts of leaves hardly decurrent on stems; abaxial leucocysts of leaf bases vertically subdivided and forming conspicuous groups of small quadrate cells (LXVI: 7, 8); abaxial leucocysts at insertional parts to stem clearly enlarged and in 1 cell row (Fig. LXVI: 7, 8).

Dioicous. Male plants dimorphous; dwarf male plants tiny, growing on tomentum enclosed by perichaetial leaves; normal male plants as large as female plants, perigonia small, terminal on short or long lateral branches. Perichaetia terminal on short or long lateral branches, sometimes terminal on main stems, the mature perichaetia with sporophytes prominent, protruded from shoots; inner perichaetial leaves around mature sporophytes 1.4-1.8 times longer than ordinary leaves near the perichaetia. Setae 13-24 mm long. Capsules inclined to horizontal, subglobose to ovoid; urns 1.0-1.1 mm long, 0.6-0.8mm wide.

Representative specimens examined: China, Hainan, Kwangtung, 13 Feb. 1962, Chen et al. 861B (L). India, Madras State, Madura District, Palni Hills, Kodaikanal and surrounding region, Foreau 1923 (L). Sri Lanka, Ratnapura District, Sri Pada (Adams Peak), descent to Carney, 23 Feb.



1978, Ruinard 23/176 (L). Myanmar, Southern Shan States, 4500 ft. alt., Jan. 1899, Micholitz s. n., labeled as Leucobryum subscalare Broth. n. sp., sub. no. 264 (H). Thailand, Lôi, Kao Krading, ca. 1200 m alt., Mar. 1924, Kerr s. n. (in herb Dixon, ref. no. 84) – paratype of L. perichaetiale (BM); Lôi, Po Tong, ca. 1000 m alt., Mar. 1924, Kerr s. n. (in herb. Dixon, ref. no. 102) – paratype of L. perichaetiale (BM). Cambodia, Province de Koh Kong, Chékô, 5 Mar. 1965, Kira et al. 189 (HIRO). Vietnam, 15 June 1963, Pócs 2507/1 (L). Malay Peninsula, Singapore, Bukit-Timah, 100 m alt., Fleischer s. n. – paratype of L. scalare (FH); Perak, Hermitage Hill, 1500 ft. alt., 19 Dec. 1939, Spare s. n. (in herb. Dixon ref. no. 2760) – paratype of L. microleucophanoides (BM); Perak, Hermitage Hill, 3000 ft. alt., 19 Dec. 1939, Spare s. n. (in herb. Dixon 2776) – paratype of L. microleucophanoides (BM); Kedah, Gunong Bongsu Forest Reserve, 21 July 1941, Spare s. n. (in herb. Dixon, ref. no. 3048) – paratype of L. microleucophanoides (BM); Kedah, Gunong Bongsu Forest Reserve, 21 July 1940, Spare s. n. (in herb. Dixon, ref. no. 3070) – paratype of L. microleucophanoides (BM); Perak, Lembok Kluang, 17 Nov. 1940, Spare s. n. (in herb. Dixon, ref. no. 3642) – paratype of L. microleucophanoides (BM). Philippines, Negros, Negros Occidental Province, Mt. Canlaon National Park near Bacolod City, ca. 4000 ft. alt., 3 Apr. 1981, Tan & Alvarez 81-306

(NICH). Borneo, Sandakan Res., Leila Forest Reserve, 31 Jan. 1960, Meijer B10058 (L). Sumatra, Taluk, Kilirandjau, 24 Nov. 1955, Meijer B9652 (L). Java, Sindanglaya, 1000 m alt., an Felsen, June 1901, Fleischer s. n. - paratype of L. scalare (FH); Papandajan bei Garoet, 1300 m alt., Fleischer s. n. - paratype of L. scalare (FH); Ardjoeno bei Lalidjiwa, 2000 m alt., Fleischer s. n. - paratype of L. scalare var. marschmeyeri (FH). Sumbawa, Sambori, 4000 ft. (1200 m) alt., Warburg s. n. - paratype of L. scalare (FH). Bali, Penulisan temple complex, 1700 m alt., 10 July 1975, Veldkamp 7139 (L). Seram, Kecamatan Kairatu, en route from Kamarian to the upper elevation of Gunung(Mt.) Totaniwel, 3°23-26'S 128°25-28'E, ca. 700 m alt., 22 Aug. 1986, Akiyama 15881 (KYO, HIRO). New Guinea, Central Mountains, Swart Valley, Kadubaka, 1600-2000 m alt., 7 Oct. 1957, Bergman M39 (L).

Habitat: On logs, tree trunks and rocks.

Distribution: China, India, Sri Lanka, Myanmar, Thailand, Cambodia, Vietnam, Malay Peninsula, Philippines, Borneo, Sumatra, Java, Seram, New Guinea, New Caledonia.

The present variety is characterized by (1) closely imbricated small leaves, (2) conical appearance at shoot apices, and (3) distinctly differentiated abaxial leucocysts of leaf bases which form group of small quadrate cells.

I could not locate type specimen of L. subscalare, but I could examine a specimen from Myanmar (coll. Micholitz s. n.) determined as L. subscalare by Brotherus, and found L. subscalare was identical with the present variety.

The present variety is closely related L. aduncum var. aduncum and L. aduncum var. teysmannianum as mentioned in each taxonomic note of latter two taxa.

4. Leucobryum chlorophyllosum C. Müll. (Fig. LXXI-LXIII, CXL: 5)

Syn. 2: 535 (1851). Type: Sumbawa, Zollinger s. n. (Herb. Lugd. Bat. 20. Ind. Or. no. 910.137-1201) – isotype (L).

Leucobryum stenophyllum Besch., Ann. Sc. Nat. Bot. sér. 5, 18: 204 (1873), syn. nov. Type: New Caledonia, Prony, Sept. 1869, Balansa 2531 – holotype (PC).

Leucobryum byssaceum C. Müll. ex Johnson, Gard. Bull. Straits Settle. ser. 3, 20: 334, f. 8: c, f. 9: h (1964), syn. nov. Type: New Guinea, distr. Moresby, Mt. Mo-roka, 1300 m alt., July-Aug. 1893, Loria s. n. (det. Müller, sub. no. 703, in herb. Levier) – holotype (BM).

Plants greenish white when dry, forming loose to compact cushions. Stems to 20 mm long with leaves; central strand not differentiated in cross-sections of stems. Leaves erect to widely spreading; 2.9-4.0 x 0.4-0.6 mm, linear to narrowly lanceolate, gradually narrowed to subtubulous point

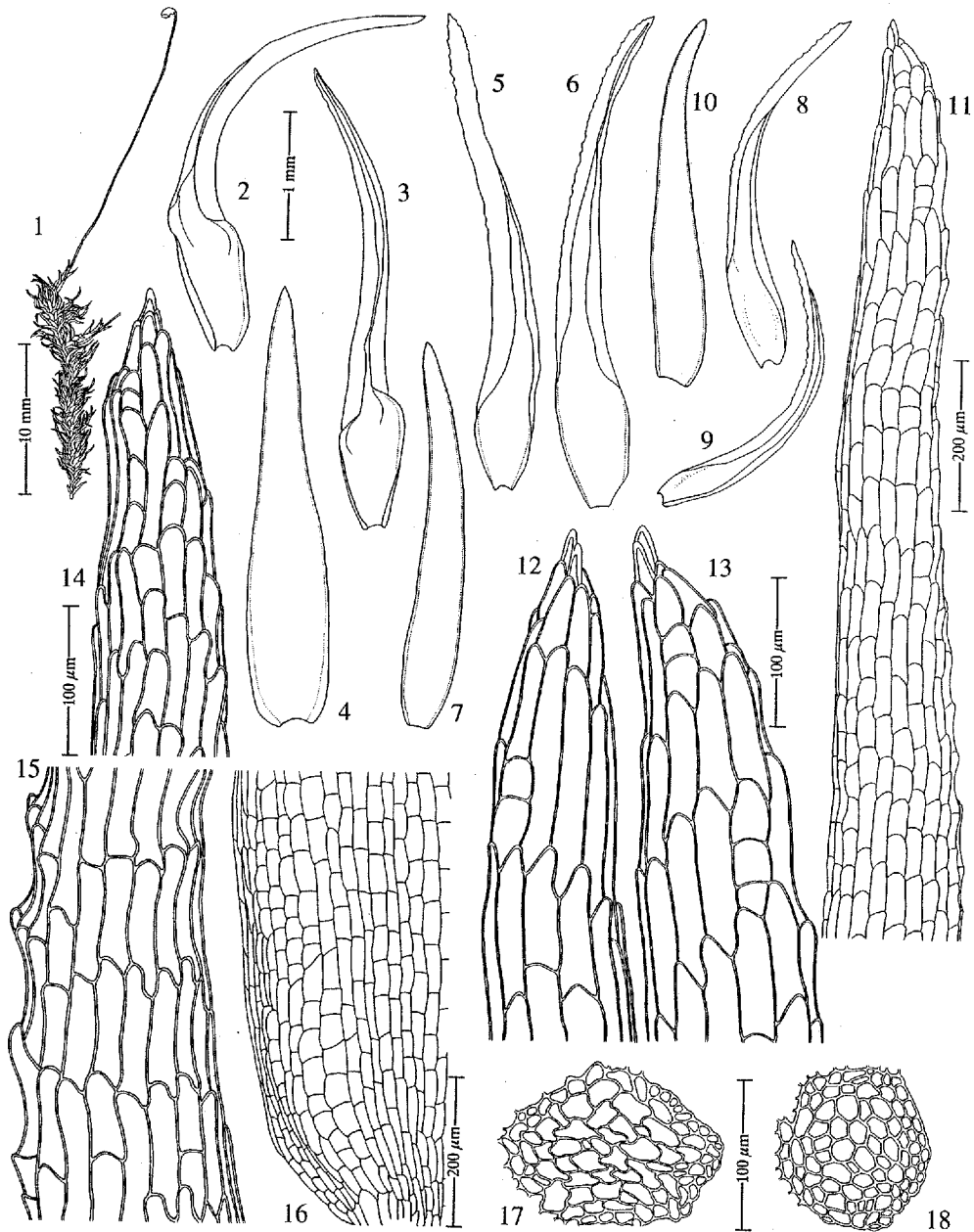


Figure LXXI. *Leucobryum chlorophyllum* C. Müll. 1. Plant. 2-10. Leaves (4, 7, 10, expanded). 11-14. Leaf apices. 15. Apical part of leaf (lateral view). 16. Leaf base (abaxial view). 17, 18. Cross-sections of stems. Figs. 1-4, 11-13, 17 were drawn from isotype of *L. chlorophyllum* (L); 5-7, from holotype of *L. stenophyllum* (PC); 8-10, 14-16, 18, from holotype of *L. byssaceum* (BM).

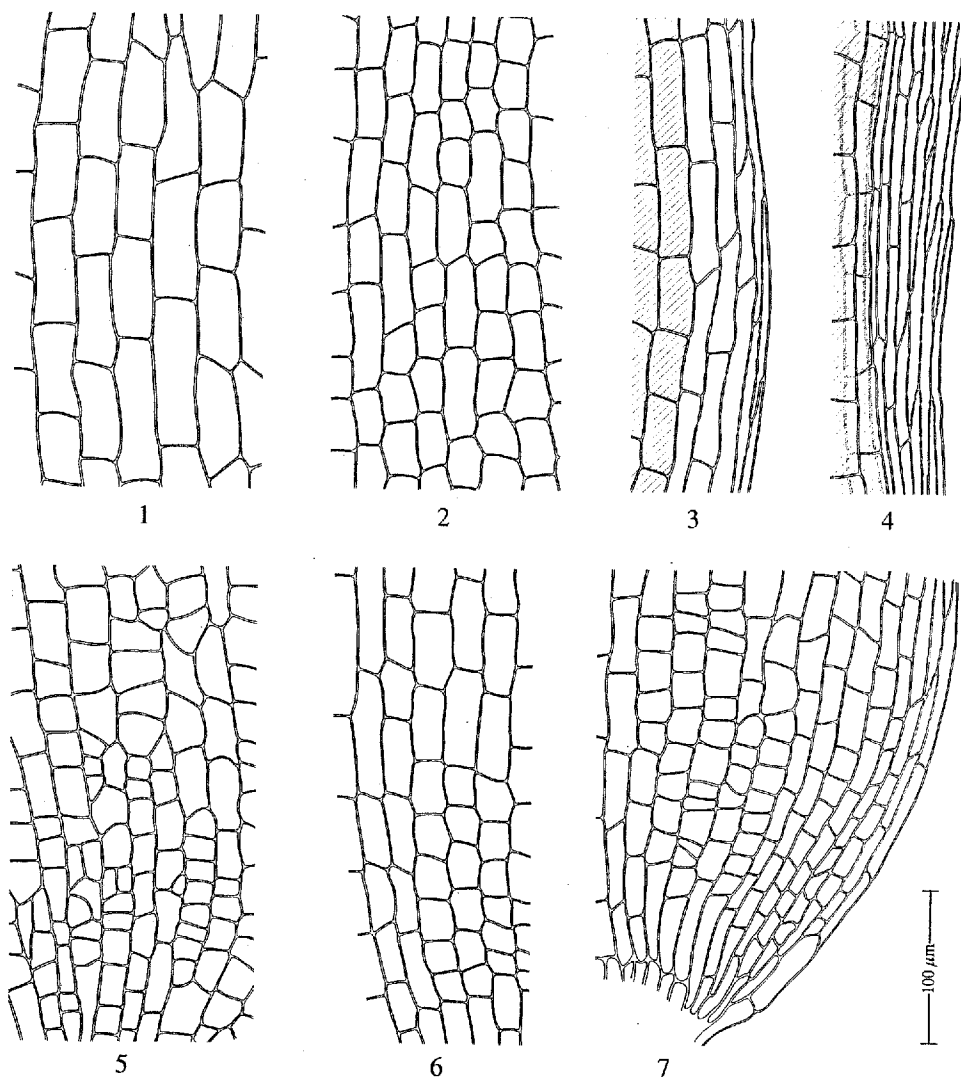


Figure LXXII. *Leucobryum chlorophyllum* C. Müll. 1-3. Median cells of leaf (1, 3, abaxial view; 2, adaxial view). 4-7. Basal cells of leaf (4, 5, 7, abaxial view; 6, adaxial view). All figures were drawn from isotype of *L. chlorophyllum* (L).

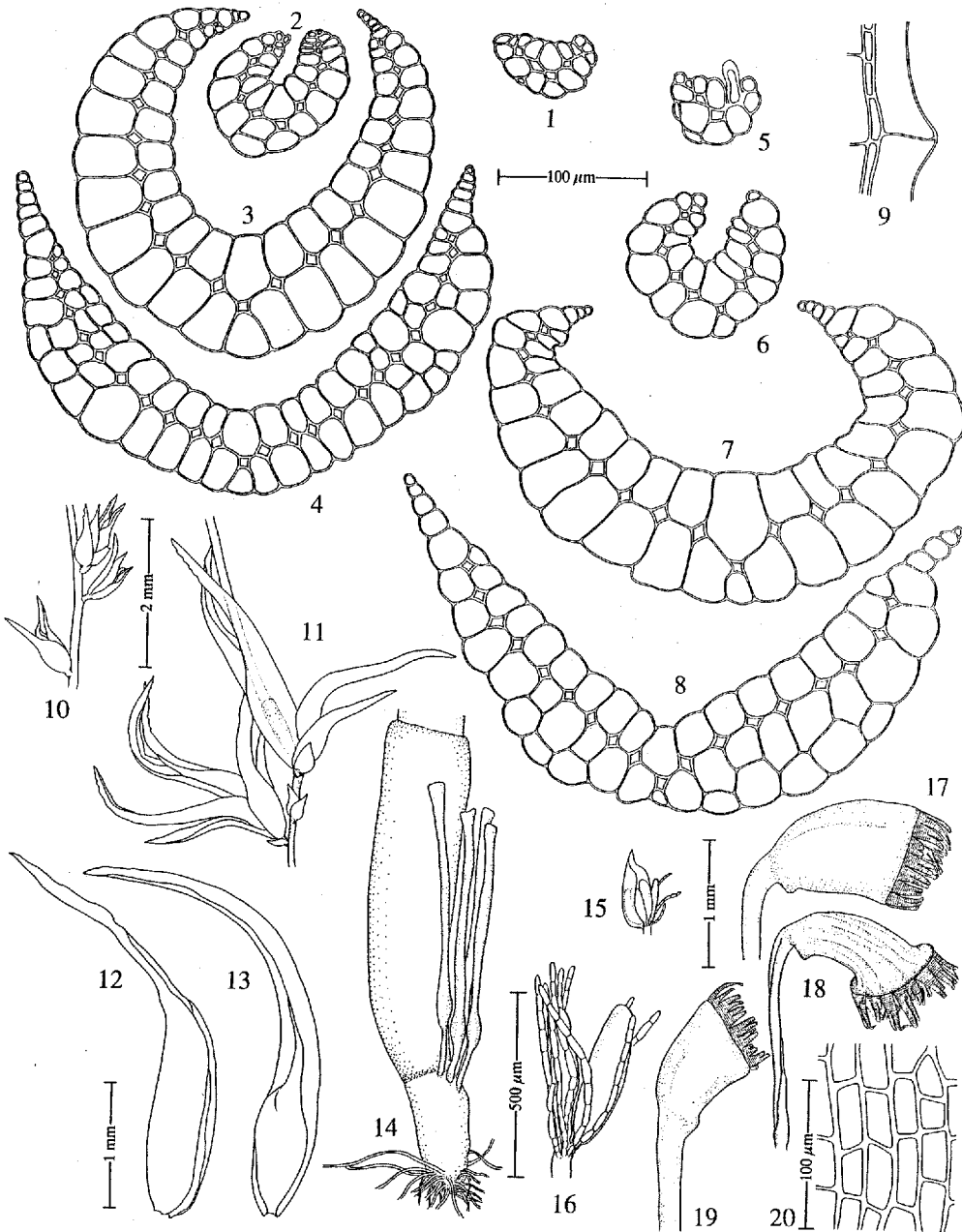


Figure LXXIII. *Leucobryum chlorophyllum* C. Müll. 1-8. Cross-sections of leaves (1, 2, 5, 6, apical; 3, 7, median; 4, 8, basal portions). 9. Longitudinal section of leaf near apex. 10. Perigonia. 11. Perichaetia. 12, 13. Inner perichaetial leaves. 14. Vaginula and archegonia. 15. Inner perigonial leaf. 16. Antheridium. 17-19. Capsules. 20. Exothecial cells. Figs. 1-4 were drawn from holotype of *L. byssaceum* (BM); 5-8, 10-20, from isotype of *L. chlorophyllum* (L); 9, from holotype of *L. stenophyllum* (PC); 11, from holotype of *L. scaberulum* var. *divaricatum* (BM).

from oblong base, acute, weakly scabrous down to mid leaf on abaxial surface due to undulation or minute proration of leucocysts (Fig. LXXI: 11-15); laminae and borders consisting of 6-8 rows of narrowly rectangular cells near base, the differentiation between laminal cells and border cells indistinct; in cross-sections near leaf base leucocysts in 1-2 cell layers on adaxial side and 2 (-3) cell layers on abaxial side at the thickest part; abaxial leucocysts of leaves hardly decurrent on stems.

Dioicous. Male plants dimorphous; dwarf male plants tiny, usually growing on tomentum enclosed by perichaetial leaves; normal male plants as large as female plants, perigonia small, bud-like, terminal on short or long lateral branches. Perichaetia terminal on short or long lateral branches, sometimes terminal on main stems; inner perichaetial leaves around mature sporophytes almost as long as ordinary leaves near the perichaetium. Setae 14-20 mm long. Capsules inclined to horizontal, ovoid; urns 0.8-1.0 mm long, 0.6-0.8 mm wide; opercula long rostrate, ca. 1.4 mm long. Annulus of 1 (-2) rows of cells. Apices of peristome teeth divided to the middle, ca. 0.5 mm long, ca. 0.09 mm wide at base. Spores 14-18  $\mu\text{m}$  in diameter.

Representative specimens examined: Vietnam, Prov. Hoa-Binh, Montes Nui Bieu, 400 m alt., 5 Jan. 1966, Pócs 31471/ac (NICH). Philippines, Luzon, Sierra Madre

Mountains, NNW of Dingalan, Auroa Memorial Park, 15°29'N 121°23'E, 600-700 m alt., 23 Mar. 1968, Jacobs B785 (L). Borneo, Sandakan Res., Upper Kinabatangan River, E of Lanas, 9 Dec. 1960, Meijer B10923 (L). Java, Leuwiliang above tea estate, Tji Anten, 1000 m alt., 21 Sept. 1952, Meijer B1136 (L). Lesser Sunda Islands, Flores, Prov. Manggarai, Paku, Poco Pakikaka area, near confluent of Wae Ngencung, 350-380 m alt., 28 June 1988, Schmutz 6750 (L). Seram, Kacamatan Seram Utara, Sawai, Manusela National Park, along a trail between Wae Niniyoa and Wae Puo, 3°00-03'S 129°14'E, 200-1000 m alt., 22 Jan. 1985, Akiyama 9567 (KYO, HIRO). New Guinea, Morobe District, Oomsis, 200 m alt., 25 Apr. 1959, Brass 29268a (L).

Habitat: On logs and tree trunks, or on soil at tree base.

Distribution: Vietnam, Philippines, Borneo, Java, Lesser Sunda Islands, Seram, New Guinea, New Caledonia.

The present species is characterized by (1) narrow leaves (5.7-7.8 times longer than wide), (2) weakly scabrous leaves on abaxial surface due to undulation or minute proration of leucocysts, and (3) usually 3-4 cell layered leucocysts near leaf bases in cross-sections.

Fleischer (1904) described the present species as monoicous (Einhäusig). I carefully examined the holotype specimen of the present species and found female plants and



independent normal male plants among the shoots. I am sure that the present species is dioicous.

5. Leucobryum boninense Sull. & Lesq. (Fig. LXIV-LXXXI, CXLI: 4)

Proc. Am. Ac. Arts Sc. 4: 277 (1859). Type: Japan, Bonin Islands, Hillside, in dense tufts on rotten stumps, 1 Nov. 1854, Wright s. n. (in herb. Sullivant, ref. no. 5) – holotype (FH).

Leucobryum salmonii Card. in Ren. & Card., Bull. Soc. R. Bot. Belg. 41(1): 27 (1905), syn. nov. Type: China, Kwangtung, Lo Fan Shan, 900 ft. alt., Aug. 1883, Salmon s. n. (Hort. Bot. Hongkong, no. 81) – holotype (PC).

Leucobryum scaberulum Card. in Ren. & Card., Bull. Soc. R. Bot. Belg. 41(1): 26 (1905), syn. nov. Type: China, Hongkong, 31 Oct. 1889, Ford s. n. (Herb. Hongkong Botanic Garden no. 222) – isotype (BM).

Leucobryum armatum Broth., Symb. Sin. 4: 28 (1929), syn. nov. Type: China, Kweitschou, Nandjing-schan, ca. 750 m alt., on soil, 25 July 1917, Handel-Mazzetti 10985 – holotype (H).

Leucobryum scaberulum var. divaricatum Dix., Hong Kong Natural. Suppl. 2: 7 (1933), syn. nov. Type: China, Hongkong, Victoria Peak, below 1000 ft. alt., between

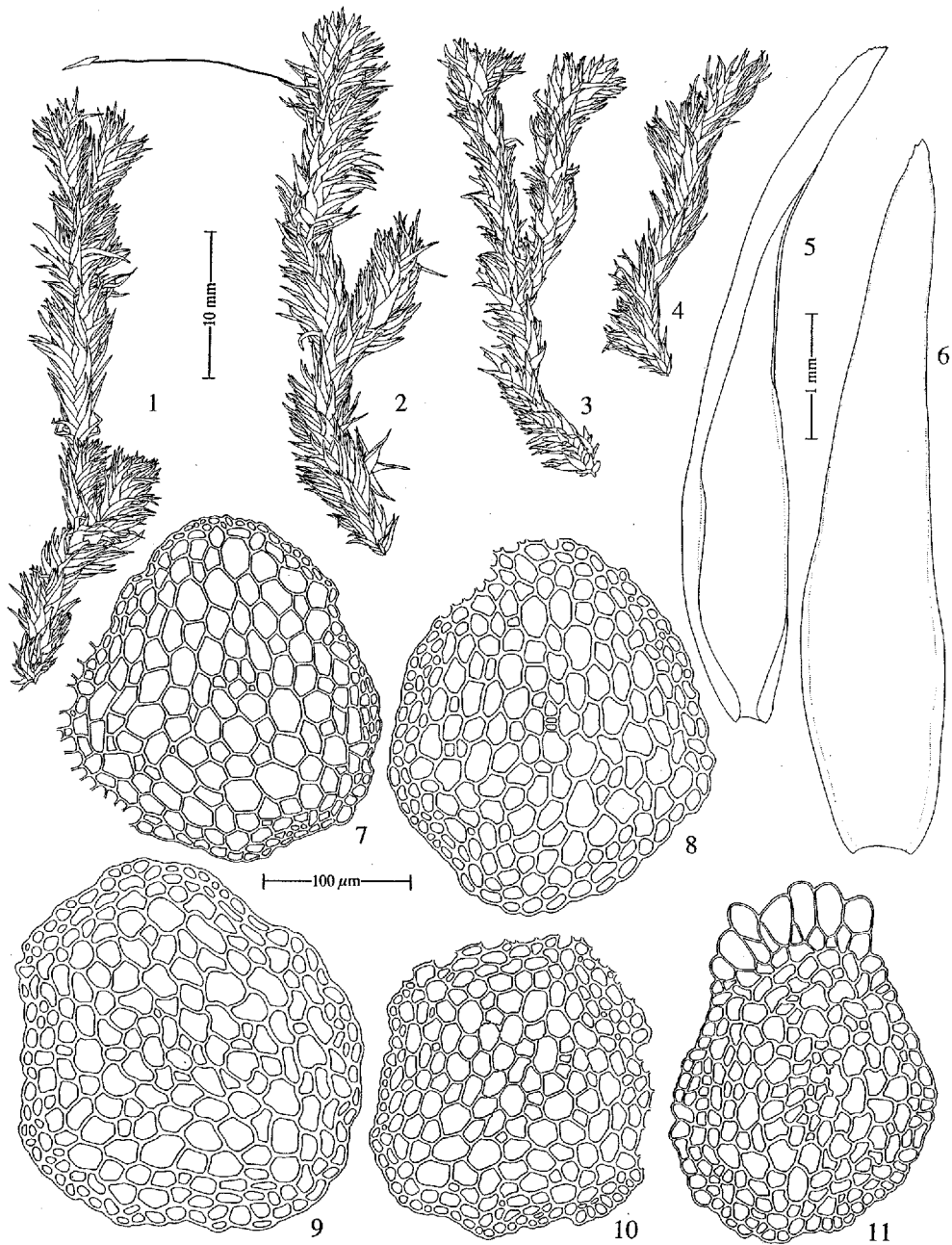


Figure LXXIV. *Leucobryum boninense* Sull. & Lesq. 1-4. Plants (1, male plant). 5, 6. Leaves (6, expanded). 7-11. Cross-sections of stems. Figs. 1, 2, 5, 6, 10 were drawn from holotype of *L. boninense* (FH); 3, 8, from holotype of *L. armatum* (H); 4, 9, from isotype of *L. scaberulum* (BM); 7, from Lai 16511 (HIRO); 11, from holotype of *L. scaberulum* var. *divaricatum* (BM).

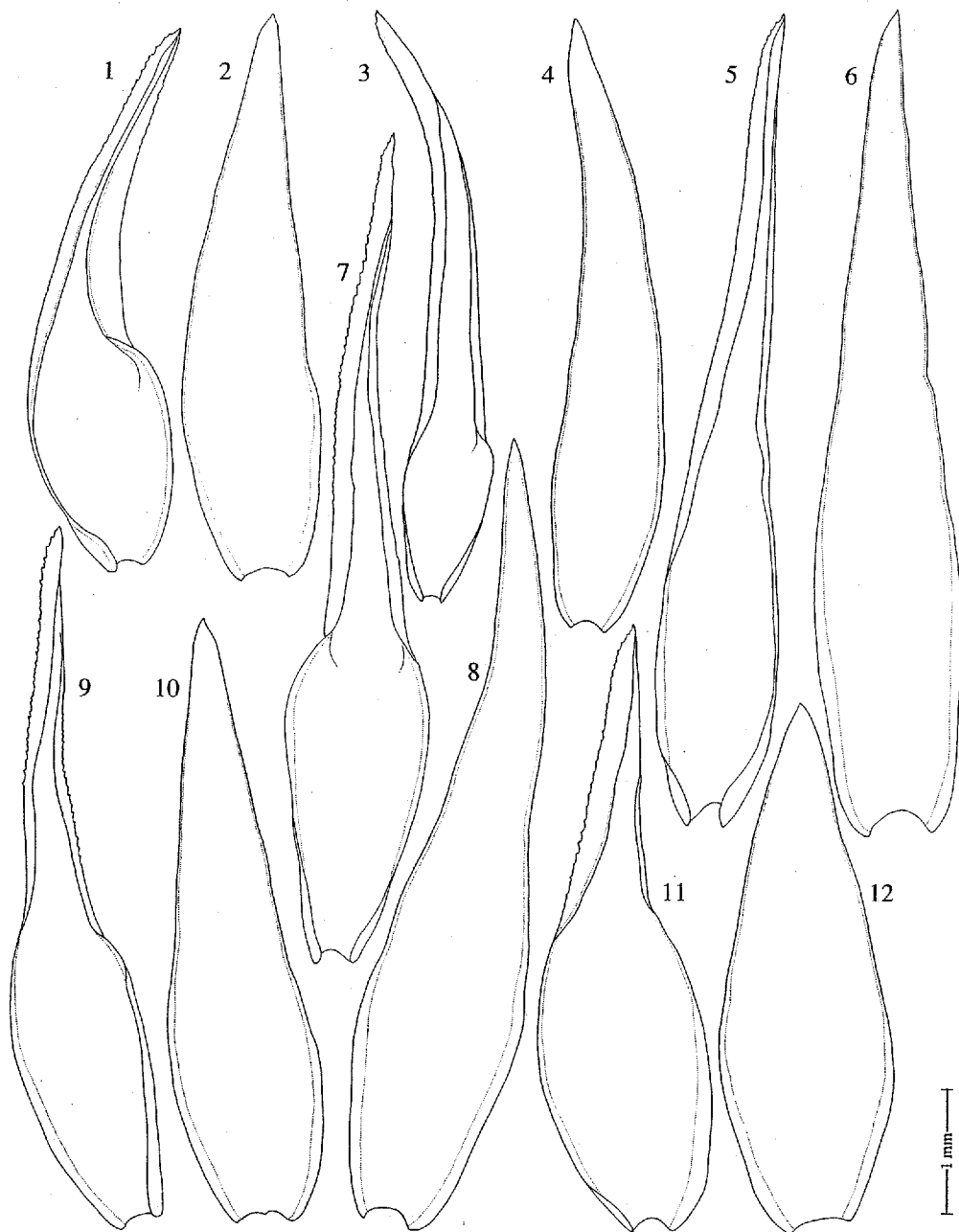


Figure LXXV. Leucobryum boninense Sull. & Lesq. 1-12. Leaves (2, 4, 6, 8, 10, 12, expanded). Figs. 1, 2 were drawn from holotype of L. boninense (FH); 3, 4, Furuki and Imura s. n. (Yamaguchi 8828, HIRO); 5, 6, from holotype of L. salmonii (PC); 7, 8, from holotype of L. scaberulum var. divaricatum (BM); 9, 10, from isotype of L. scaberulum (BM); 11, 12, from holotype of L. armatum (H).

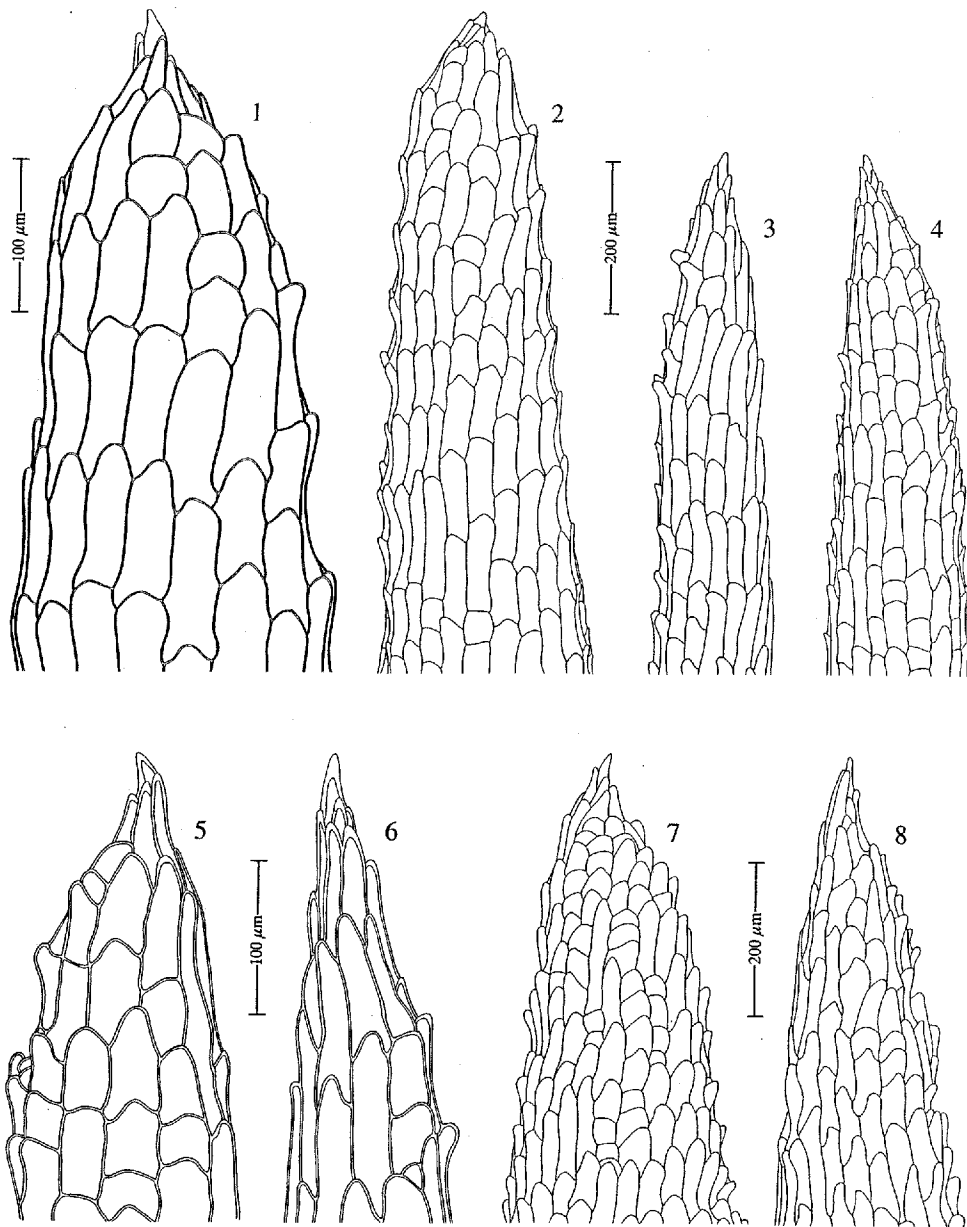


Figure LXXVI. *Leucobryum boninense* Sull. & Lesq. 1-8. Leaf apices. Figs. 1, 2 were drawn from holotype of *L. boninense* (FH); 3, from isotype of *L. scaberulum* (BM); 4, from holotype of *L. salmonii* (PC); 5, Lai 16511. (HIRO); 6, from holotype of *L. scaberulum* var. *divaricatum* (BM); 7, 8, from holotype of *L. armatum* (H).

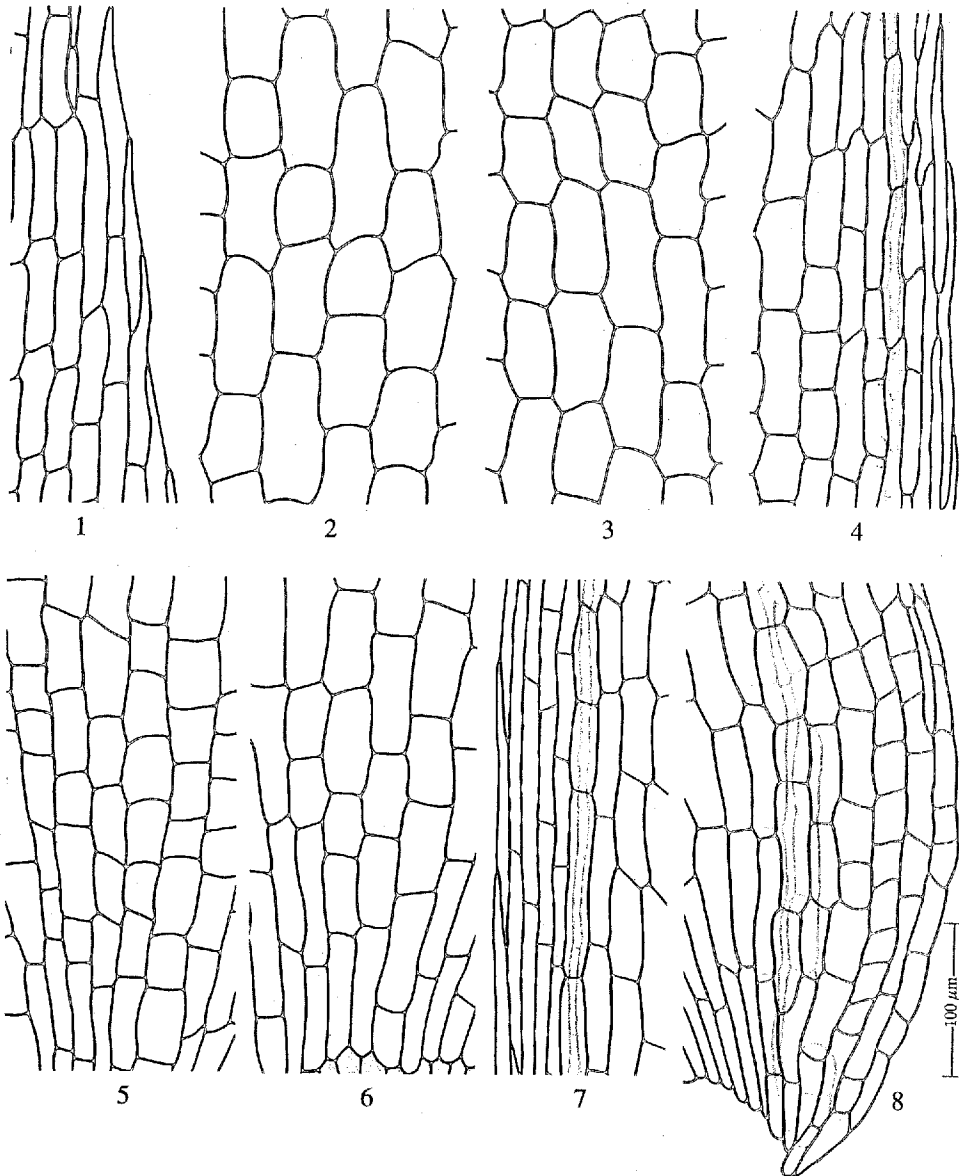


Figure LXXVII. *Leucobryum boninense* Sull. & Lesq. 1. Cells near leaf apex (adaxial view). 2-4. Median cells of leaf (2, abaxial view; 3, 4, adaxial view). 5-8. Basal cells of leaf (5, abaxial view; 6-8, adaxial view). All figures were drawn from holotype of *L. boninense* (FH).

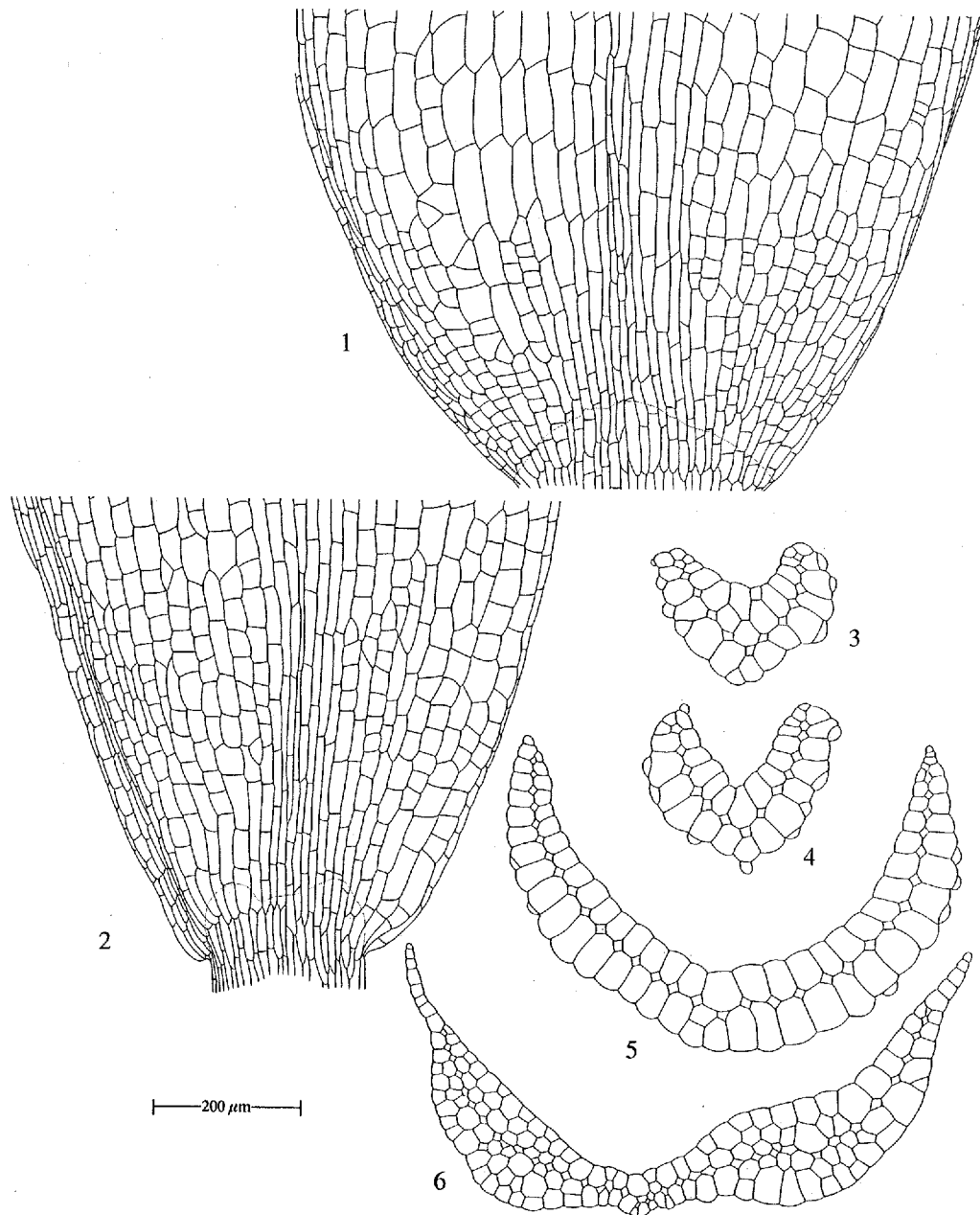


Figure LXXVIII. Leucobryum boninense Sull. & Lesq. 1, 2. Leaf bases (abaxial view). 3–6. Cross-sections of leaf (3, 4, apical; 5, median; 6, basal portions). Figs. 1, 3–6 were drawn from holotype of L. armatum (H); 2, from holotype of L. boninense (FH).

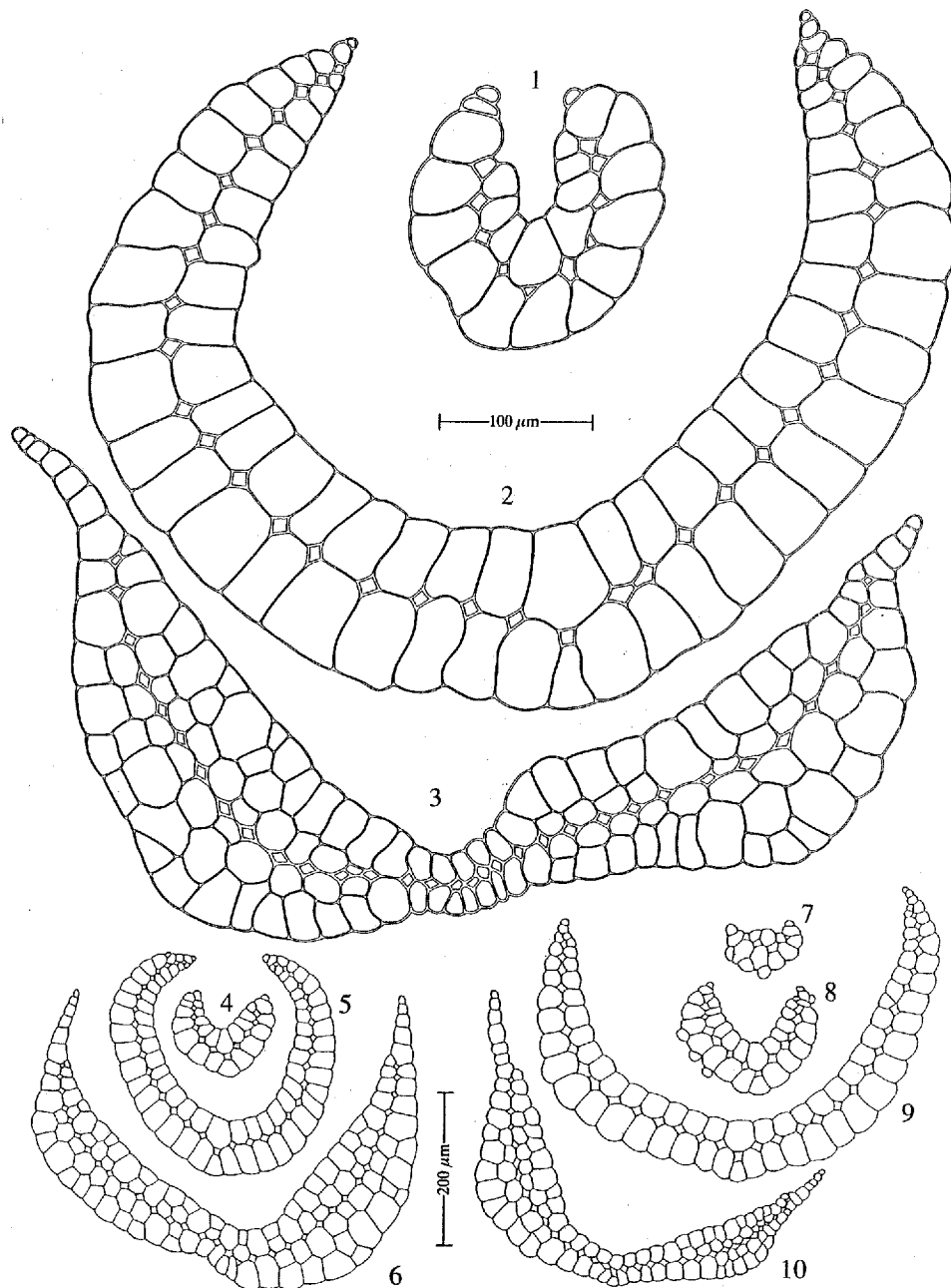


Figure LXXIX. *Leucobryum boninense* Sull. & Lesq. 1–10. Cross-sections of leaves (1, 4, 7, 8, apical; 2, 5, 9, median; 3, 6, 10, basal portions). Figs. 1–3 were drawn from holotype of *L. boninense* (FH); 4–6, from holotype of *L. salmonii* (PC); 7–9, from isotype of *L. scaberulum* (BM).

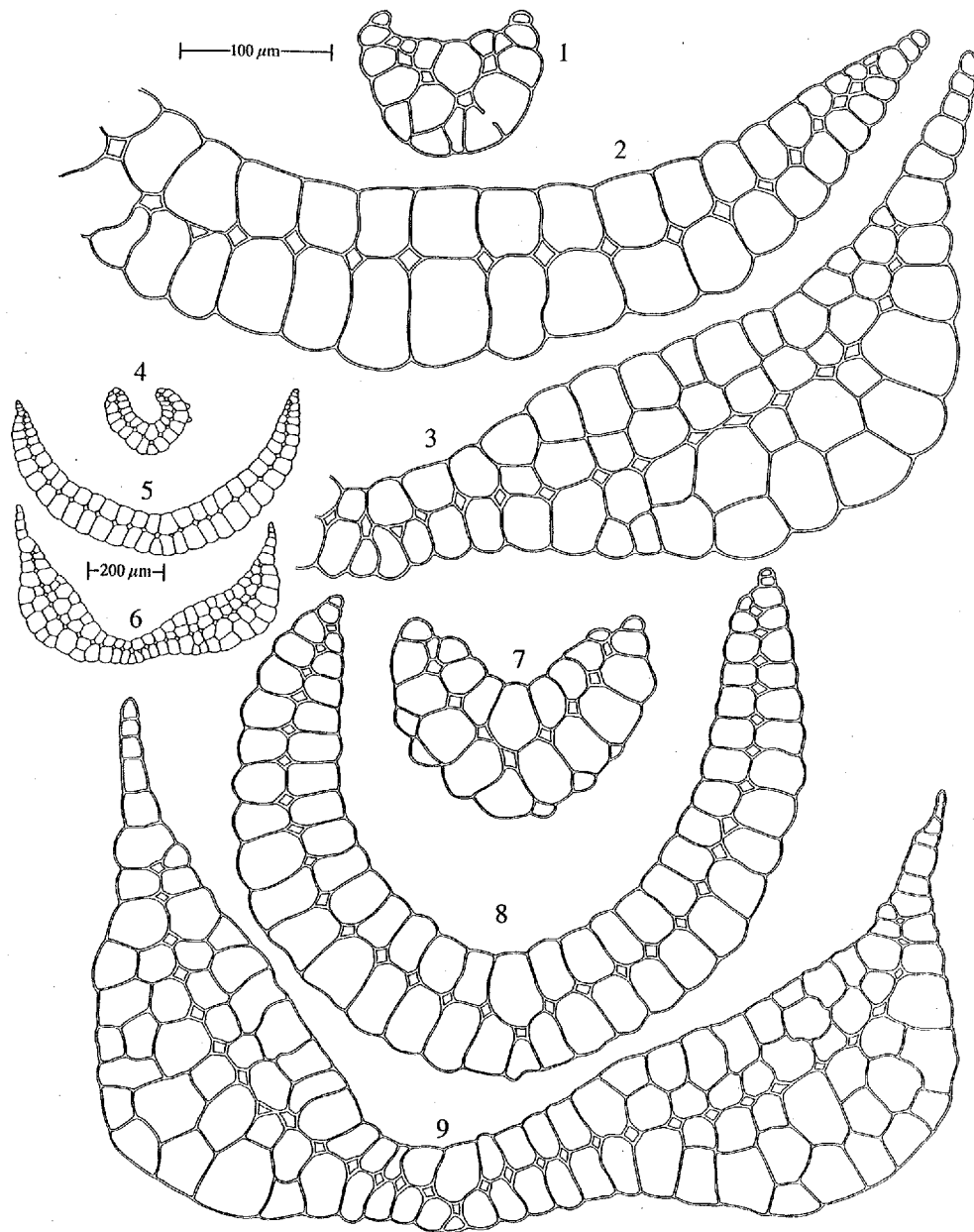


Figure LXXX. *Leucobryum boninense* Sull. & Lesq. 1-9. Cross-sections of leaves (1, 4, 7, apical; 2, 5, 8, median; 3, 6, 9, basal portions). Figs. 1-6 were drawn from holotype of *L. boninense* (FH); 7-9, from Lai 16511 (HIRO).



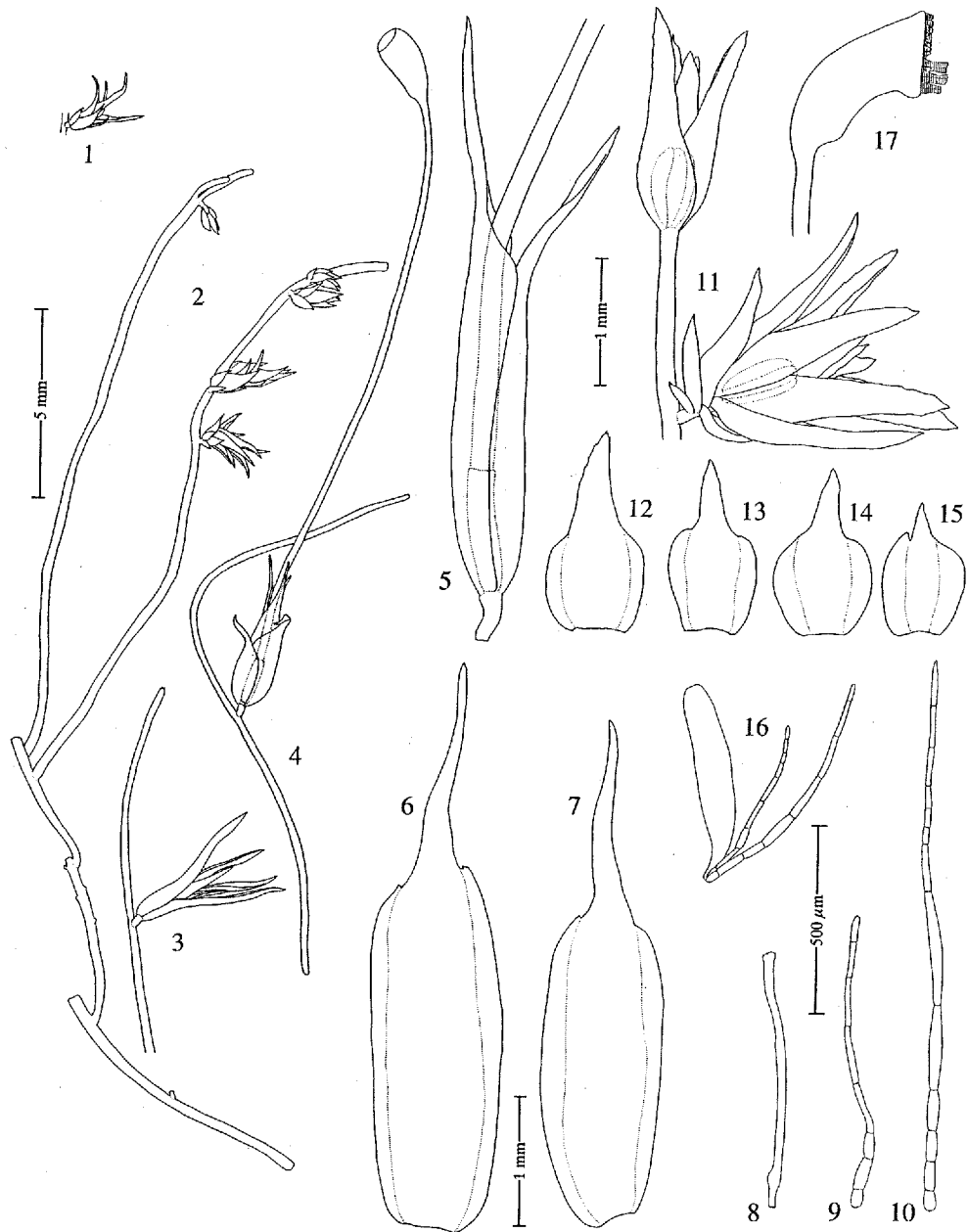


Figure LXXXI. *Leucobryum boninense* Sull. & Lesq. 1-5. Perichaetia. 6, 7. Inner perichaetial leaves. 8. Archegonium. 9, 10. Paraphyses. 11. perigonia. 12-15. Perigonial leaves [expanded; numbers show the order of perigonial leaves from the innermost leaf (number 15)]. 16. Antheridium. 17. Capsule. Fig. 1 was drawn from holotype of *L. salmonii* (PC); 2, from holotype of *L. armatum* (H); 3, from isotype of *L. scaberulum* (BM); 4, Furuki & Imura s. n. (Yamaguchi 8828, HIRO); 5-17, from holotype of *L. boninense* (FH).

boulders, 11 Jan. 1930. Herklots s. n. (in herb. Dixon, ref. no. 203) – holotype (BM).

Leucobryum nakaii Hor., Bot. Mag. Tokyo 49: 217. 2 (1935), syn. nov. Type: Japan, Bonin Islands, Hahajima, Mt. Chibusayama, Apr. 1934, Nakai s. n. – holotype (not seen).

Plants whitish green when dry, forming compact tufts or cushions. Stems to 50 mm long with leaves; central strand not differentiated in cross-sections of stems. Leaves erect spreading or slightly falcate secund, somewhat arranged in 5 rows; 4.1-7.4 x 0.9-1.4 mm, broadly to narrowly lanceolate, gradually narrowed to subtubulous point from oblong to ovate base, acute to bluntly mucronate, papillose prorate from the apex to  $\frac{3}{5}$  of the leaf length on abaxial surface; laminae and borders consisting of 5-8 rows of narrowly rectangular to linear cells near base, the differentiation between laminal cells and border cells indistinct; alar parts consisting of 5-6 rows of quadrate to rectangular cells; in cross-sections near leaf base leucocysts in 2-3 cell layers on both sides; abaxial leucocysts hardly decurrent on stems.

Dioicous. Male plants as large as female plants; perigonia bud-like, terminal on short or elongated lateral branches; dwarf male plants not observed. Perichaetia terminal on short lateral branches; inner perichaetial leaves around mature sporophytes 0.7-1.0 times longer than

ordinary leaves near the perichaetium; archegonia 0.6-0.8 mm long. Setae 15-16 mm long. Capsules inclined, ovoid to ellipsoid; urns 1.3-1.6 mm long, 0.6-0.9 mm wide.

Representative specimens examined: Japan, Bonin Islands, Chichijima Island, Mt. Chuo, Higashi-daira, 230 m alt., 12 July 1985, Imura & Furuki s. n., in herb. Yamaguchi 8828 (HIRO); Ryukyu Islands, Oknawa Island, Yona, 27 Mar. 1986, Nakatsubo s. n. (HIRO). Taiwan, Pingtung Co., Nanjenshan Reserve Area, 300 m alt., 29 Jan. 1985, Lai 16511 (HIRO). China, prov. Szechuan, in monte Go-lo-san prope Chungking, 700 m alt., Apr. 1940, Chen s. n., as Musci Sinici Exsiccati 1: 7 (NICH).

Habitat: On logs and rocks.

Distribution: Japan, Taiwan, China.

The present species is characterized by (1) papillose proration of apical parts of leaves on abaxial surface, and (2) perichaetia terminal on short lateral branches.

Some plants of the present species show weak proration of leucocysts which are restricted to apical part of leaves. Such plants frequently occurs in Japanese and Taiwanese populations. The plants with leaves with weakly prorated abaxial leucocysts are often confused with L. juniperoideum. However, L. juniperoideum is distinguished from L. boninense by (1) the perichaetia usually terminal on main stems, (2) smooth abaxial surface of apical parts of leaves, and (3)

broad laminal parts composed of 5-12 quadrate to rectangular cells and bordered by 2-3 rows of linear cells.

L. scabrum and L. aduncum are related to the present species, but differs in undulate and spinosely prorated leucocysts on abaxial surface of leaves.

Type specimen of L. nakaii collected from Bonin Islands (type locality of L. boninense) seems to be burned during the World War II. According to the original description and illustrations by Horikawa (1935), L. nakaii is identical with the present species, especially by the same character of inner perichaetial leaves smaller than ordinary leaves.

6. Leucobryum juniperoideum (Brid.) C. Müll. (Fig. XXII, XXV: B, XXVII, XXXI, LXXXII-XCIII, CXL: 2)

Linnaea 18: 689 (1845).

Basionym: Dicranum juniperoideum Brid., Bryol. Univ. 1: 409 (1826). Type: Teneriffa (without collector name) – syntype (B).

Leucobryum neilgherrense C. Müll., Bot. Zeit. 12: 556 (1854). Type: India, Neilgher, Perrottet s. n. – holotype (not seen).

Leucobryum holleanum Dozy & Molk., Bryol. Jav. 1: 17, t. 13 (1855). Type: Java, Holle s. n. (Herb. Lugd. Bat. 20. Ind. Or. no. 910.132-1639) – holotype (L).

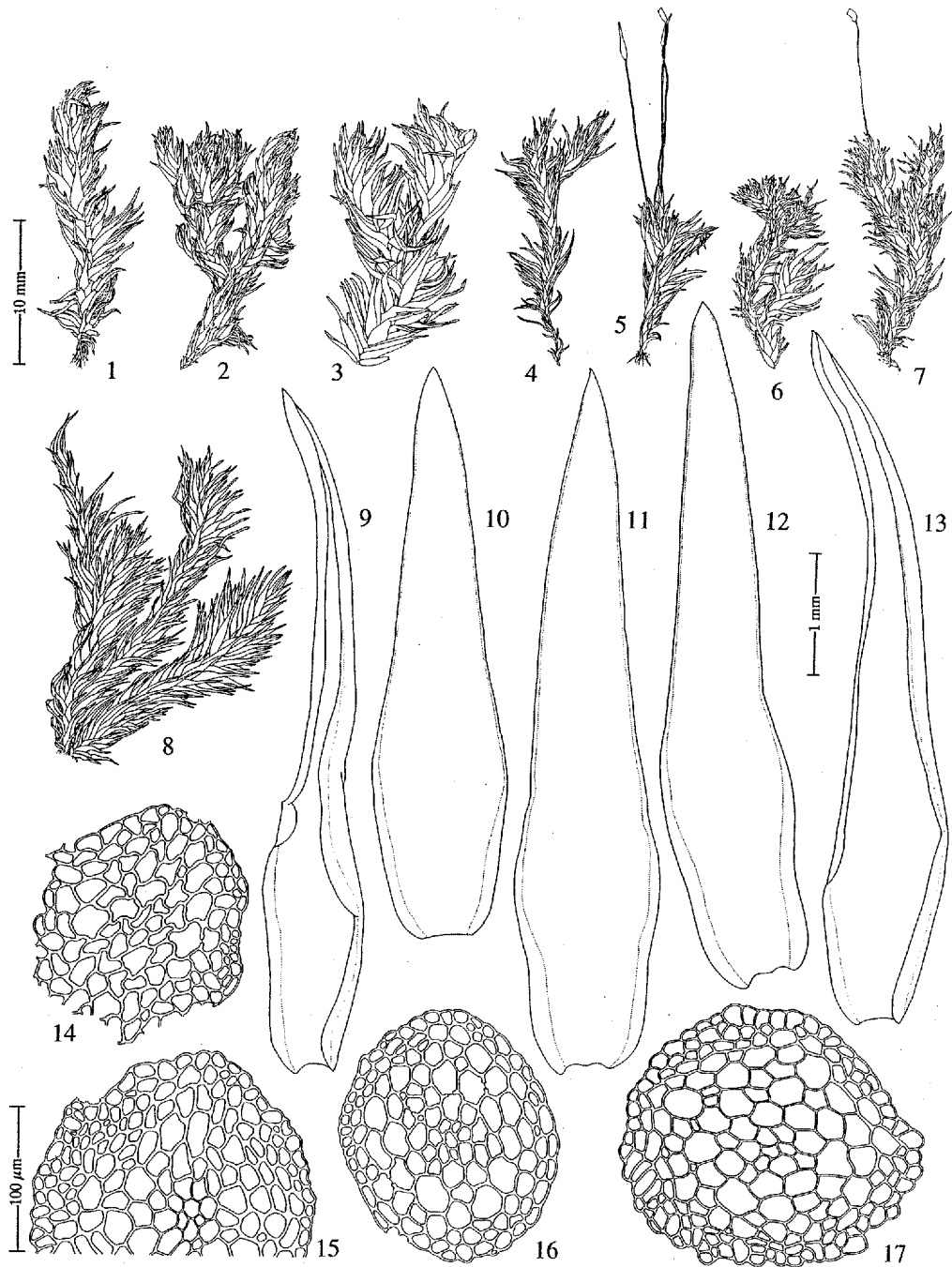


Figure LXXXII. *Leucobryum juniperoideum* (Brid.) C. Müll. 1–8. Plants (4, 6, male plants). 9–13. Leaves (10–12, expanded). 14–17. Cross-sections of stems. Figs. 1, 9, 10, 17 were drawn from syntype (Teneriffa) of *Dicranum juniperoideum* (B); 2, 16, from isotype of *L. textorii* (L); 3, 11, from holotype of *L. holleanum* var. *fragillifolium* (FH); 4, 5, 12, 13, 15, from holotype of *L. angustissimum* (H); 6, 7, from Noguchi 16753 (NICH); 8, 14, from holotype of *L. holleanum* (L).

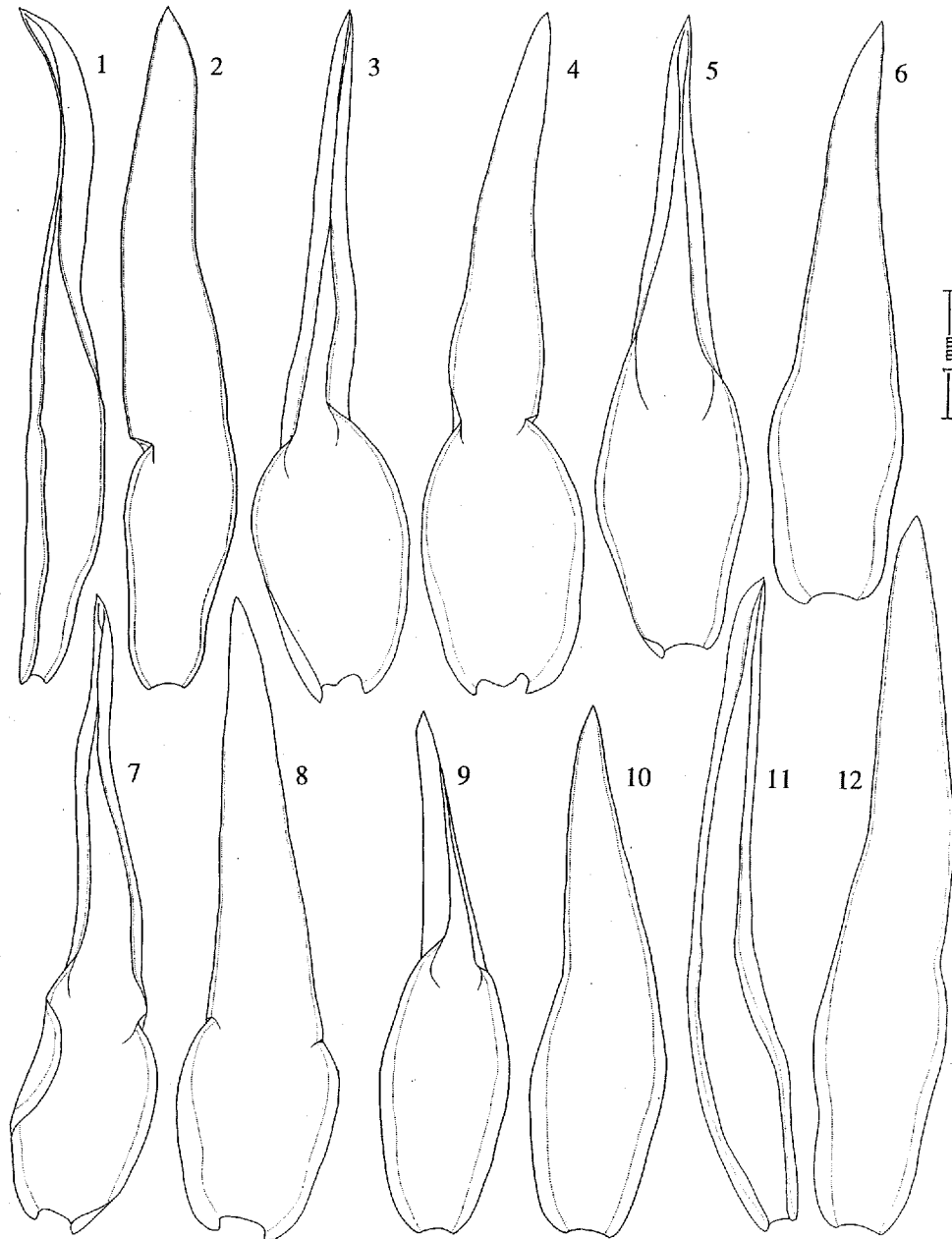


Figure LXXXIII. Leucobryum juniperoideum (Brid.) C. Müll. 1–12. Leaves (2, 4, 6, 8, 10, 12, expanded). Figs. 1, 2 were drawn from holotype of L. retractum (PC); 3, 4, from isotype of L. altiusculum (KYO); 5, 6, from holotype of L. holleanum (L); 7, 8, from isolectotype of L. humile (KYO); 9, 10, from isotype of L. rhizophyllum (MAK); 11, 12, from isotype of L. textorii (L).

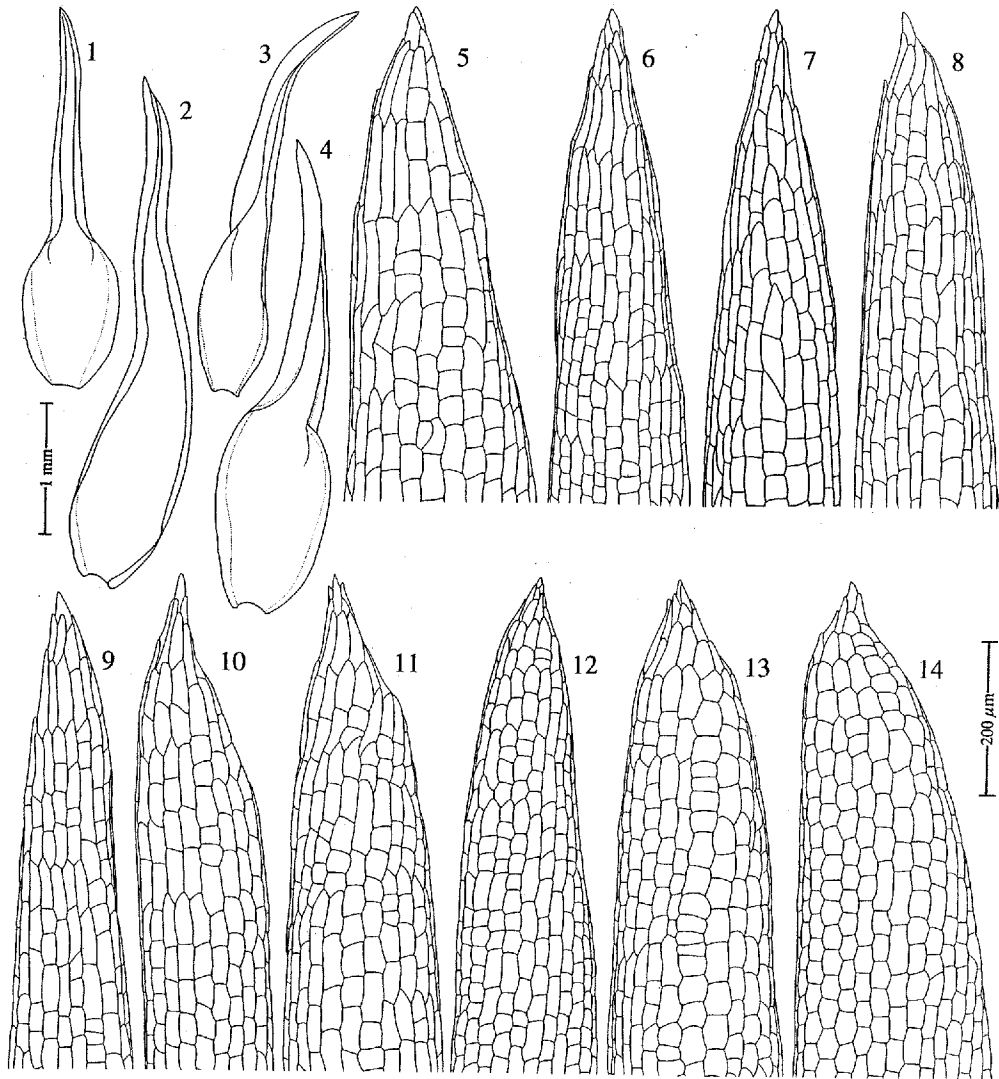


Figure LXXXIV. *Leucobryum juniperoideum* (Brid.) C. Müll. 1–4. Leaves. 5–14. Leaf apices. Figs. 1, 9 were drawn from isotype of *Ochrobryum japonicum* (KYO); 2, 6, from isolectotype of *L. brevicaule* (KYO); 3, from isotype of *L. ferriei* (BM); 4, 10, from isotype of *L. lacteorum* (KYO); 5, from syntype (Teneriffa) of *Dicranum juniperoideum* (B); 7, from holotype of *L. holleanum* (L); 8, from isotype of *L. altiusculum* (KYO); 11, from isolectotype of *L. humile* (KYO); 12, from isotype of *L. rhizophyllum* (MAK); 13, from isotype of *L. textorii* (L); 14, from holotype of *L. retractum* (PC).

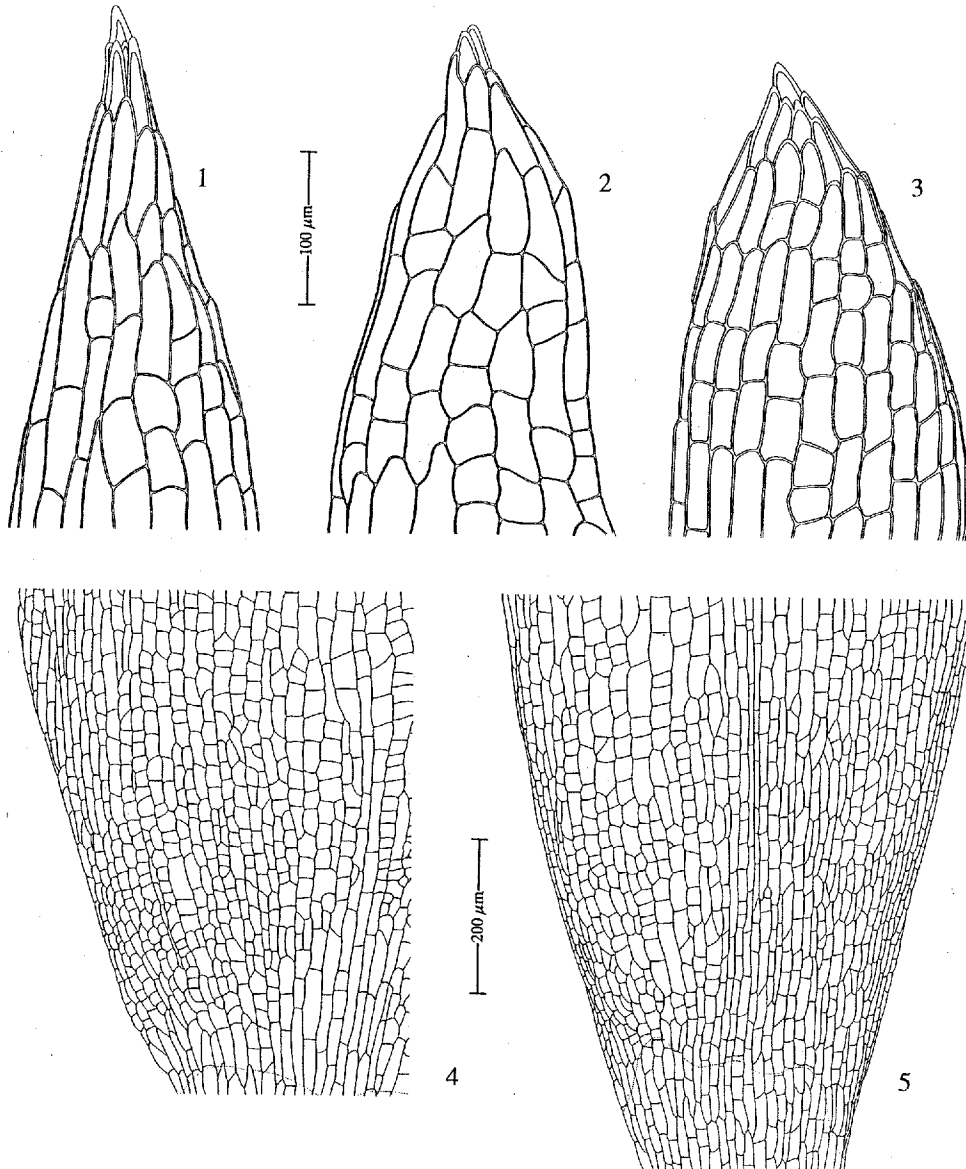


Figure LXXXV. *Leucobryum juniperoideum* (Brid.) C. Müll. 1–3. Leaf apices. 4, 5. Leaf bases (abaxial view). Fig. 1 was drawn from holotype of *L. holleanum* (L); 2, from isotype of *L. textorii* (L); 3, 4, from syntype (Teneriffa) of *Dicranum juniperoideum* (B); 5, from isotype of *L. rhizophyllum* (MAK).



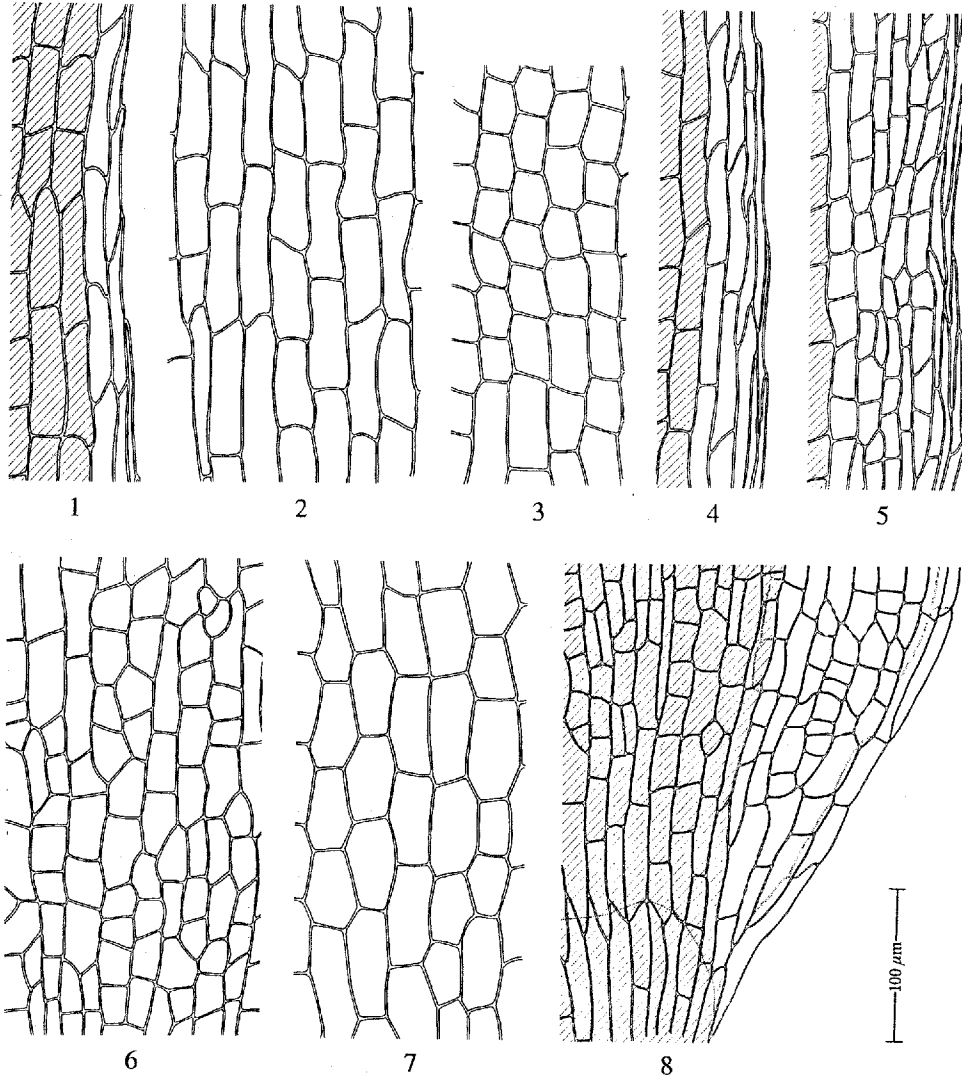


Figure LXXXVI. *Leucobryum juniperoideum* (Brid.) C. Müll. 1. Cells near leaf apex (abaxial view). 2-4. Median cells of leaf (2, 4, abaxial view; 3, adaxial view). 5-8. Basal cells of leaf (5, 6, 8, abaxial view; 7, adaxial view). All figures were drawn from syntype (Teneriffa) of *Dicranum juniperoideum* (B).

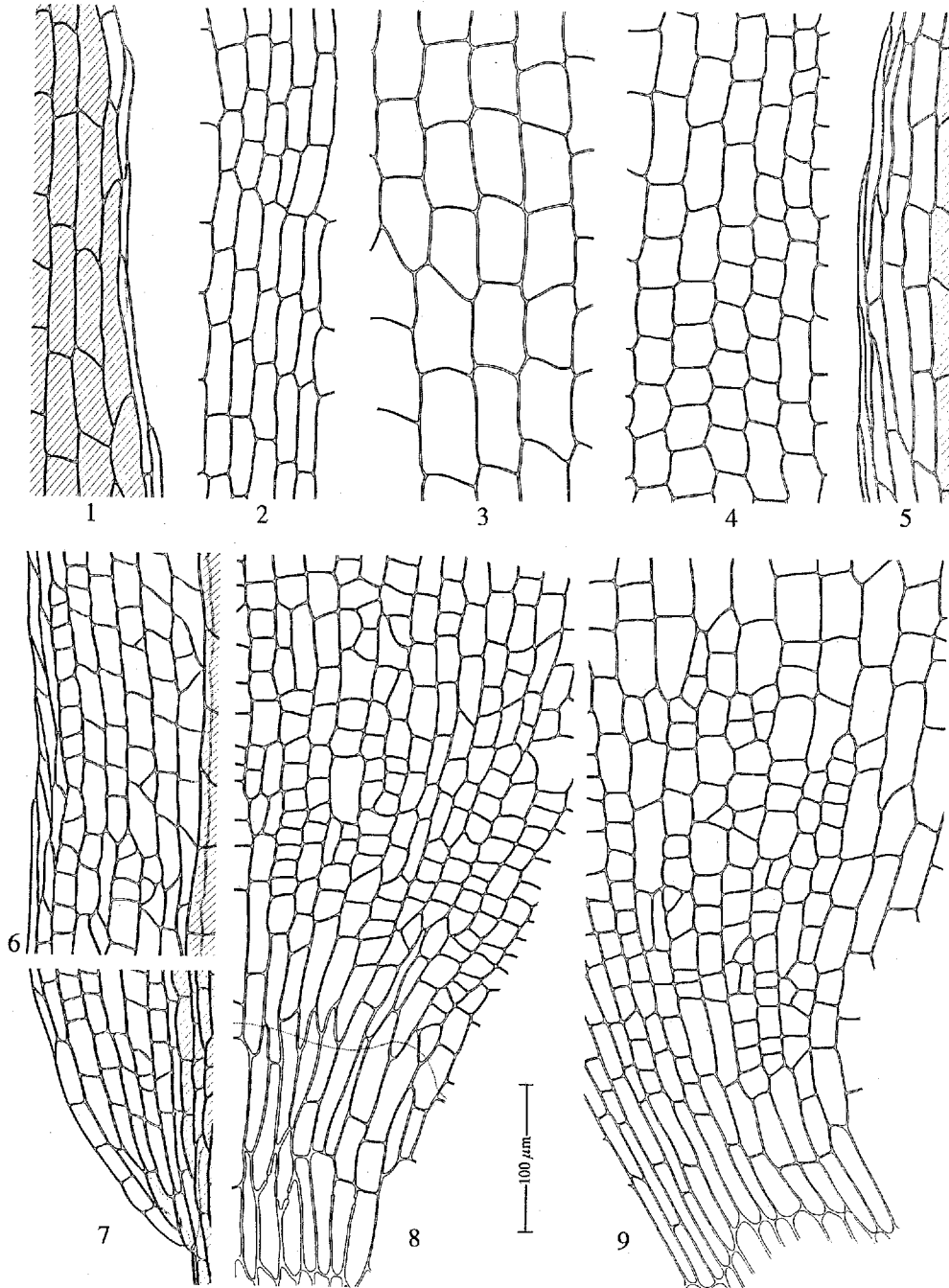


Figure LXXXVII. *Leucobryum juniperoideum* (Brid.) C. Müll. 1, 2. Cells near leaf apex (1, abaxial view; 2, adaxial view). 3-5. Median cells of leaf (3, 5, abaxial view; 4, adaxial view). 6-9. Basal cells of leaf (6-8, abaxial view; 9, adaxial view). All figures were drawn from holotype of *L. holleanum* (L).

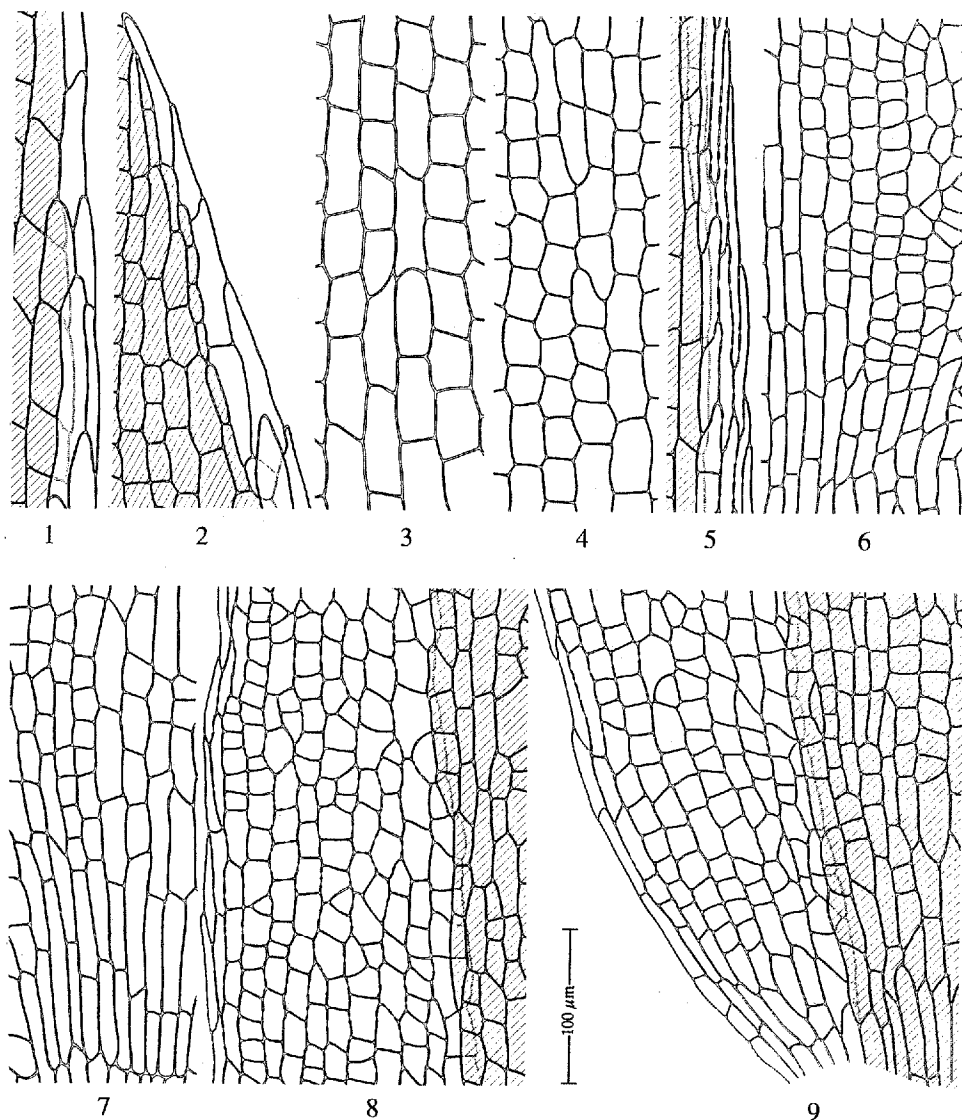


Figure LXXXVIII. Leucobryum juniperoideum (Brid.) C. Müll. 1, 2. Cells near leaf apex (1, abaxial view; 2, adaxial view). 3-5. Median cells of leaf (3, 5, abaxial view; 4, adaxial view). 6-9. Basal cells of leaf (6, 8, 9, abaxial view; 7, adaxial view). All figures were drawn from isotype of L. textorii (L).

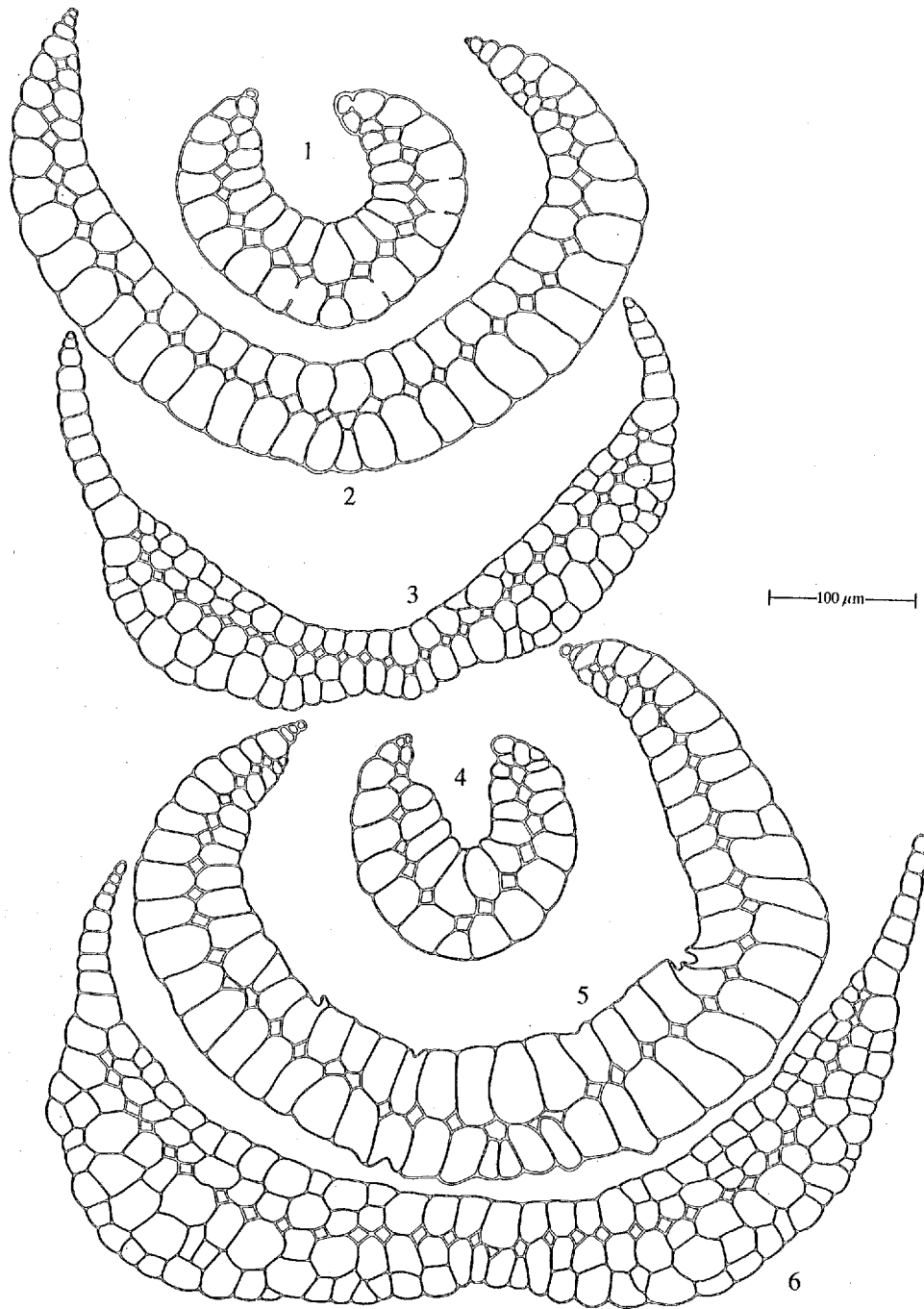


Figure LXXXIX. Leucobryum juniperoideum (Brid.) C. Müll. 1–6. Cross-sections of leaves (1, 4, apical; 2, 5, median; 3, 6, basal portions). Figs. 1–3 were drawn from isotype of L. textorii (L); 4–6, from syntype (Teneriffa) of Dicranum juniperoideum (B).

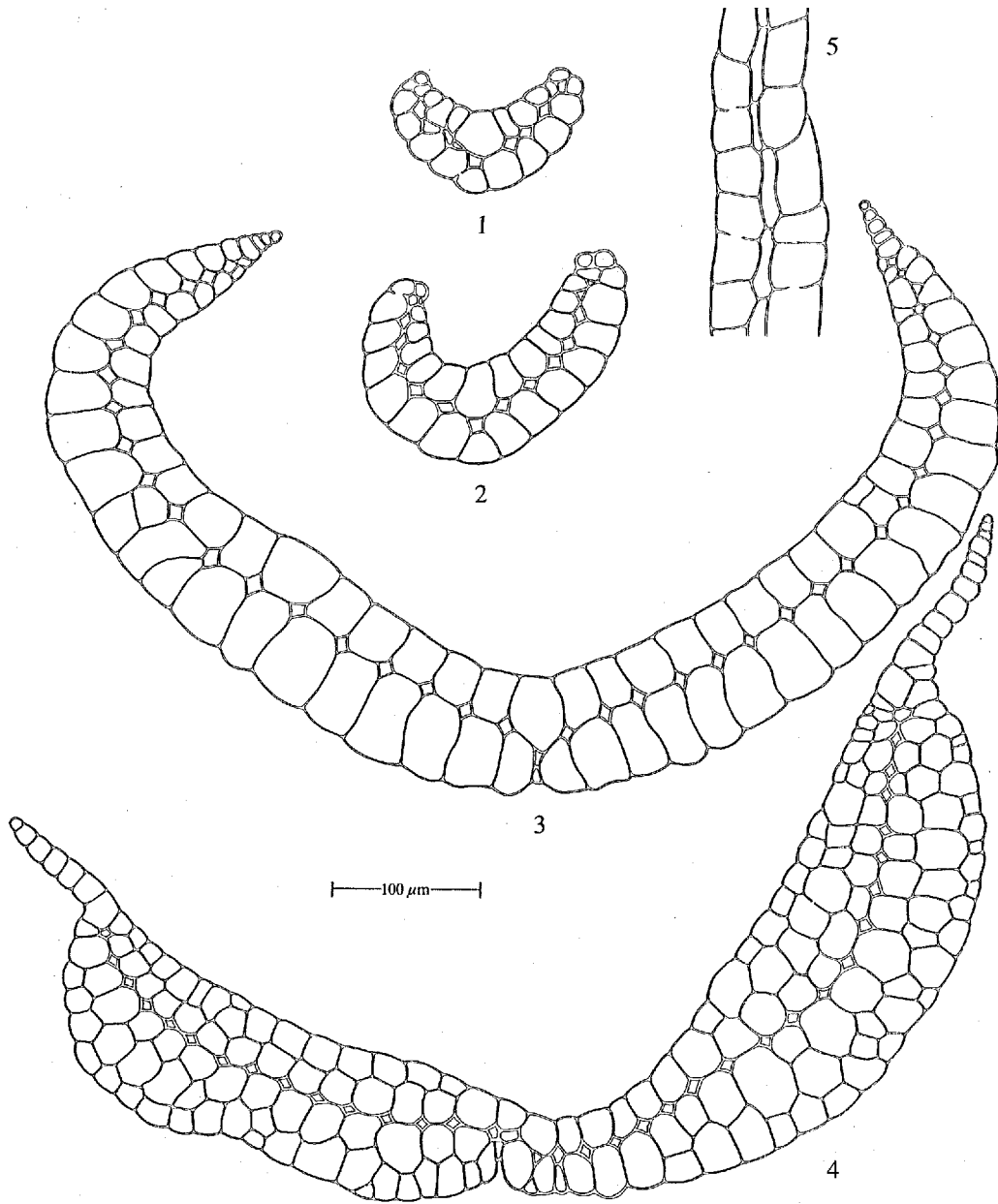


Figure XC. *Leucobryum juniperoideum* (Brid.) C. Müll. 1–4. Cross-sections of leaf (1, 2, apical; 3, median; 4, basal portions). 5. Longitudinal section of leaf near apex (abaxial side on the right side). All figures were drawn from holotype of *L. holleanum* (L).

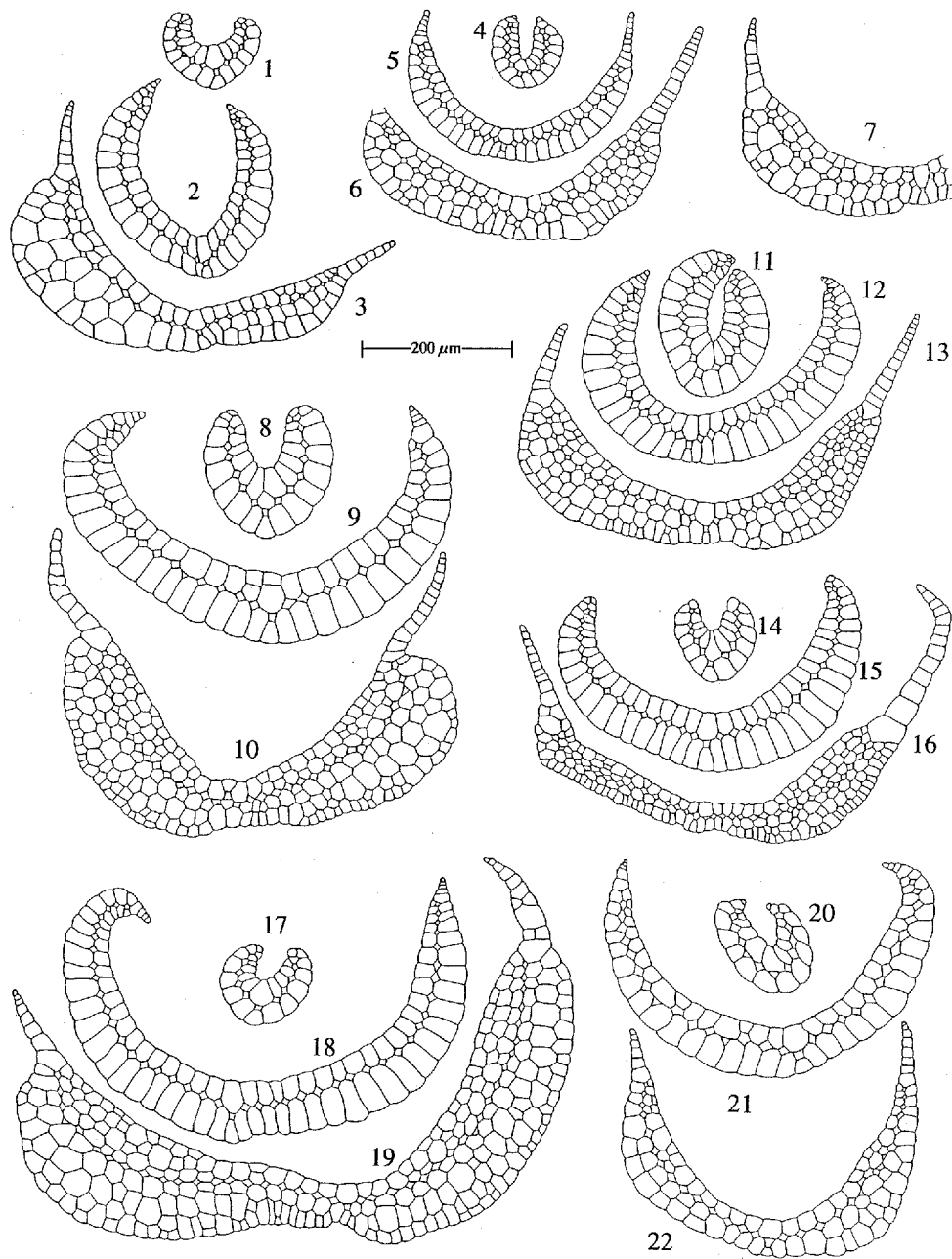


Figure XCI. *Leucobryum juniperoideum* (Brid.) C. Müll. 1–22. Cross-sections of leaves (1, 4, 8, 11, 14, 17, 20, apical; 2, 5, 9, 12, 15, 18, 21, median; 3, 6, 7, 10, 13, 16, 19, 22, basal portions). Figs. 1–3 were drawn from isotype of *L. ferriei* (BM); 4–6, from isotype of *Ochrobryum japonicum* (KYO); 7, from holotype of *L. retractum* (PC); 8–10, from isolectotype of *L. humile* (KYO); 11–13, from isotype of *L. rhizophyllum* (MAK); 14–16, from isolectotype of *L. brevicaulis* (KYO); 17–19, from isotype of *L. altiusculum* (KYO); 20–22, from isotype of *L. lacteorum* (KYO).

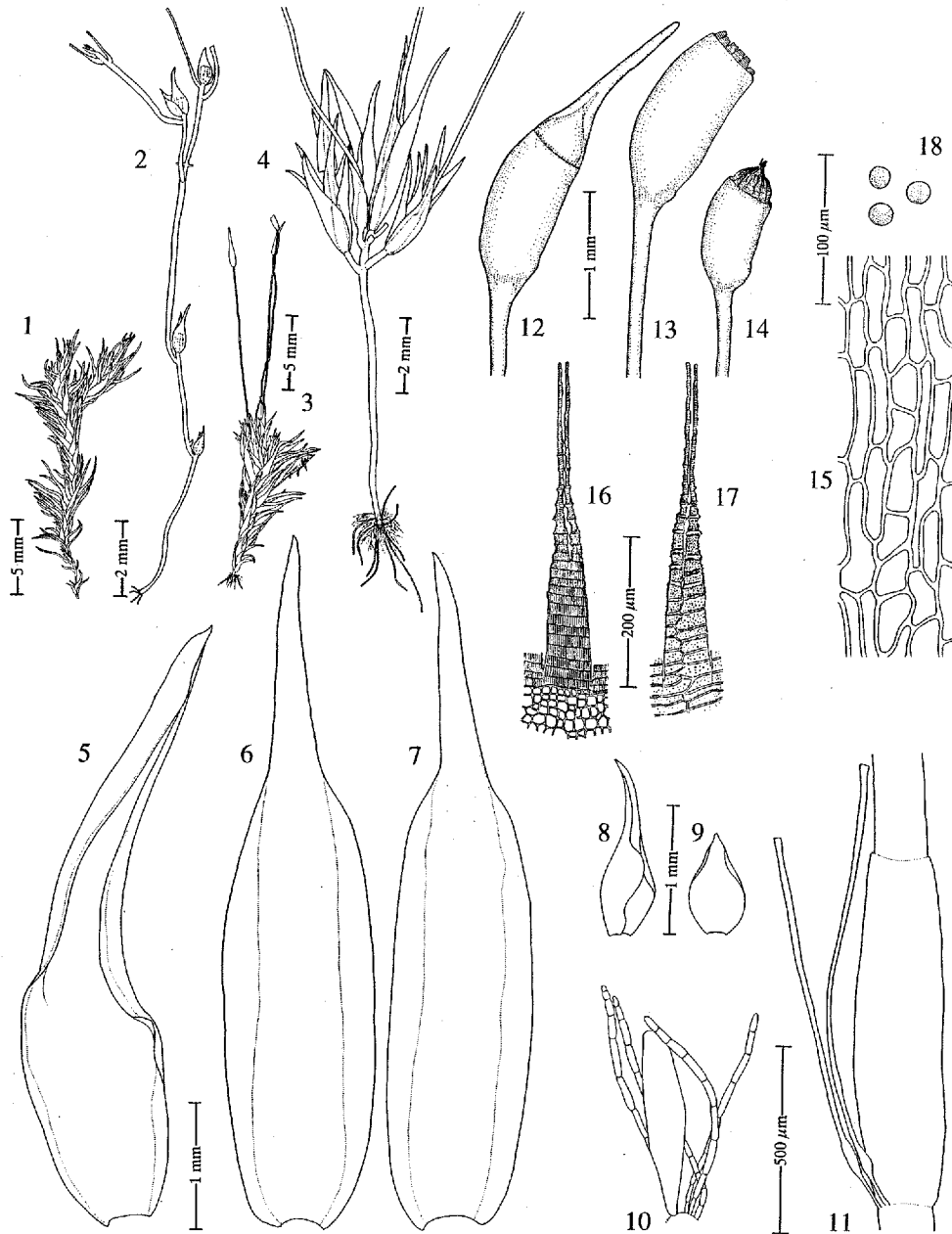


Figure XCII. *Leucobryum juniperoideum* (Brid.) C. Müll. 1. Male plant. 2. Branching of male plant 1, showing position of perigonia. 3. Female plant. 4. Branching of female plant 3, showing position of perichaetia. 5. Stem leaf. 6, 7. Inner perichaetial leaves (expanded). 8, 9. Inner perigonial leaves. 10. Antheridium. 11. Vaginula and archegonia. 12–14. Capsules. 15. Exothecial cells. 16, 17. Peristome teeth (16, dorsal view; 17, ventral view). 18. Spores. Figs. 1–11 were drawn from holotype of *L. angustissimum* (H); 12–18. Noguchi 16753 (NICH).

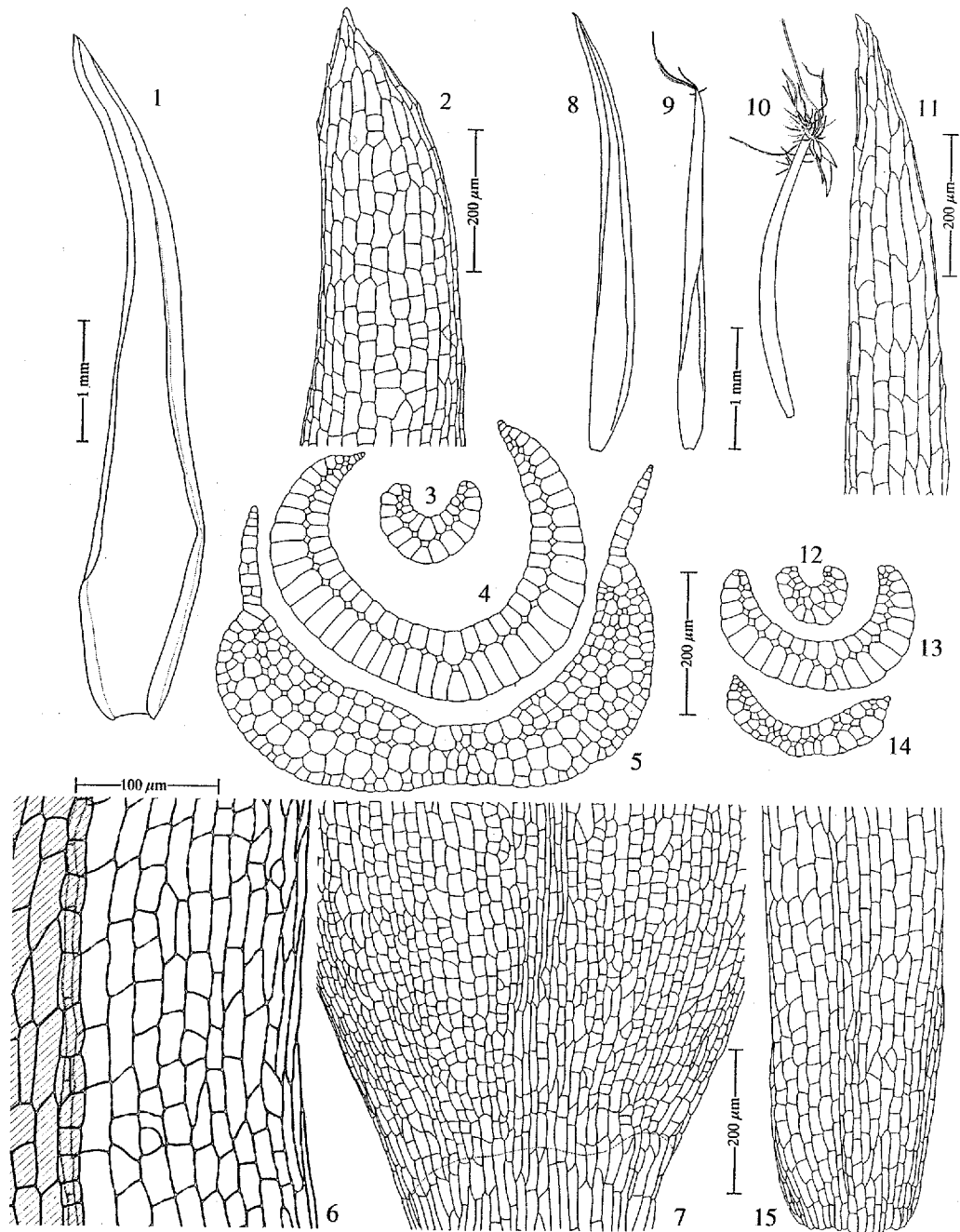


Figure XCIII. *Leucobryum juniperoideum* (Brid.) C. Müll. 1-7. Ordinary stem leaves. 8-15. Deciduous leaves. 1, 8-10. Leaves (9, with rhizoids; 10, with a bud). 2, 11. Leaf apices. 3-5, 12-15. Cross-sections of leaves (3, 12, apical; 4, 13, median; 5, 14, basal portions). 6. Basal cells of leaf (adaxial view). 7, 15. Leaf bases (abaxial view). All figures were drawn from holotype of *L. angustissimum* (H).



Leucobryum triviale C. Müll., Linnaea 36: 30 (1869),  
syn. nov. Type: "E Calcutta forsan ex sikkim habeo. In  
Khasiya et alibi haud rarum videtur" – syntypes (not seen).

Leucobryum retractum Besch., Ann. Sc. Nat. Bot. sér. 7,  
17: 334 (1893), syn. nov. Type: Japan, Yokoska, Savatier  
109 – holotype (PC).

Ochrobryum japonicum Besch., J. de Bot. 11: 151 (1897)  
= Leucobryum japonicum (Besch.) Card. in Broth., Nat. Pfl.  
1(3): 346 (1901). Type: Japan, forêt de Mimmaya, 9 July  
1894, Faurie 14045 – isotype (KYO).

Leucobryum altiusculum Besch., J. de Bot. 12: 285  
(1898). Type: Japan, Kominato, 9 Dec. 1885, Faurie 60 –  
holotype (PC), isotype (KYO).

Leucobryum brevicaule Besch., J. de Bot. 12: 285  
(1898). Type: Japan, cascades d'Osaka, 28 Nov. 1893, Faurie  
11289 – isolectotype (KYO).

Leucobryum humile Broth. ex Besch., J. de Bot. 12: 286  
(1898). Type: Japan, Mayebara, 7 Nov. 1893, Faurie 11128 –  
isolectotype (KYO).

Leucobryum lacteorum Besch., J. de Bot. 12: 286 (1898).  
Type: Japan, Akan, 3 Aug. 1893, Faurie 10745 – isotype  
(KYO).

Leucobryum textorii Besch., J. de Bot. 12: 288 (1898).  
Type: Japan, Textor s. n. – holotype (PC).

Leucobryum holleanum var. fragilifolium Fl., Hedwigia 38 (Beibl.): 128 (1899), syn. nov. Type: Java, Tjibodas im Berggarten auf einem gefälltem Baumstamm in ausgebreiteten Polstern, 1450 m alt., 20 July 1898, Fleischer s. n. (Musci Frond. Archipelagi indici ser. I, no. 6) – holotype (FH), isotype (HIRO).

Leucobryum ferriei Card. in Ren. & Card., Bull. Soc. R. Bot. Belg. 41(1): 28 (1905). Type: Japan, Omura, 15 Jan. 1898, Ferrie s. n. (det. Cardot, no. 155; in herb. Levier) – isotypes (BM, FI).

Leucobryum neilgherrense var. minus Card., Beih. Bot. Centralbl. 19(2): 97 (1905), syn. nov. Type: Taiwan, Taitum, Faurie 50 – holotype (not seen).

Leucobryum rhizophyllum Warnst., Hedwigia 57: 81, f. 17 (1915). Type: Japan, Prov. Idsu, Badeort Yugashima, in schattigen Wäldern an faulenden Baumstämmen am 26. April 1914, Sakurai 567 – isotype (MAK).

Leucobryum angustissimum Broth., Symb. Sin. 4: 28 (1929), syn. nov. Type: China, Hunan, den ganz verwitterten Stirnchnitt eines Cunninghamia-Strunkes im Walde ober Tungdjiapai bei Hsikwangschan im Bezirke Hsinhwa ganz überziehend, wtp. St., 700 m alt., 2 Sept. 1918, Handel-Mazzetti 12597 – holotype (H).

Plants whitish tinged with brown when dry, forming compact cushions or tufts. Stems to 35 mm long with leaves;

central strand not differentiated in cross-sections of stems, but sometimes with weak central area which composed of small cells with colored thin walls. Leaves erect spreading; 2.9-5.7 x 0.6-1.3 mm, lanceolate, acute to bluntly mucronate, gradually narrowed to subtubulous point from oblong to ovate base, smooth on abaxial surface, weakly scabrous at tips due to minutely projected leucocysts; laminae consisting of 5-12 rows of quadrate to rectangular cells near base, bordered by 2-3 rows of linear cells, laminae consisting of 2-3 rows of rectangular cells extended beyond mid leaf; in cross-sections near leaf base leucocysts in 2-4 cell layers on adaxial side and 3-4 cell layers on abaxial side at the thickest part, the central parts hollowed, consisting of 2 layered leucocysts, the thickest parts 1.8-3.0 times thicker than the central parts; abaxial leucocysts hardly decurrent on stems.

Dioicous. Male plants dimorphous; dwarf male plants small, usually growing on tomentum enclosed by perichaetial leaves, or detached from perichaetia and epiphytic on stem leaves of female plants; normal male plants as large as female plants, independent, perigonia small, usually terminal on stems and subfloral innovations. Perichaetia terminal on stems and subfloral innovations; inner perichaetial leaves around mature sporophytes 1.0-1.8 times longer than ordinary leaves near the perichaetia; archegonia

1.2-1.6 mm long. Setae 5-17 mm long. Capsules inclined, ovoid to ellipsoid; urns 0.8-1.5 mm long, 0.5-0.8 mm wide. Apices of peristome teeth divided to the middle, ca. 0.45 mm long, ca. 0.07 mm wide at base. Spores 15-16  $\mu$ m in diameter.

Representative specimens examined: Russia, Far East, the southern part, the bay Plastun, 4 Oct. 1974, Bardunov s. n. (NICH 352366). Japan, Honshu, Koya, 26 Nov. 1893, Faurie 11267 - isoparatype of L. brevicaulis (KYO); Kyushu, Nagasaki, Mar. 1895, Faurie 15292 - isoparatype of L. humillimum (KYO); Kyushu, Unzen, 5 Mar. 1895, Faurie 15336 - isoparatype (KYO); Kyushu, Nagasaki, 9 Mar. 1895, Faurie 15450 - isoparatype of L. humillimum (KYO); Honshu, Mie-ken, Minamimuro-gun, Kiho-cho, Onodani, 70 m alt., 26 Dec. 1965, Nakajima s. n., in herb. Noguchi 16753 (NICH); Honshu, Hiroshima-ken, Hiba-gun, Shimoyukawa, Mt. Shitomi, 760 m alt., 30 Aug. 1980, Une 3545 (HIRO); Honshu, Hiroshima-ken, Saeki-gun, Yuki-cho / Yoshiwa-mura, Iwaidani Valley, 500-600 m alt., 24 Aug. 1976, Iwatsuki 12012 (NICH); Textor s. n., labeled as Leucobryum glaucum  $\beta$  minus C. Müll. (L). Korea, Mt. Soyo, 200-300 m alt., 18 Oct. 1959, Hong 1365 (HIRO). Taiwan, Nantou-hsien, Luku-hsiang, Chitou, 1100-1400 m alt., 30 May 1984, Yamaguchi et al. 6573 (HIRO). China, Western Hubei Province, Metasequoia Region of Lichuan Xian (Hsien), Vicinity of Hongwanxi on the E side of the valley, 30°10'N,

108°45'E, 1100-1350 m alt., 7 Oct. 1980, 1980 Sino-Amer. Exped. no. 2074 (HIRO). India, Madras State, Madura District, Palni Hills, Kodaikanal and surrounding region, Shembaganur, 1923, Foreau s. n. (L). Sri Lanka, Nuwara District, Hakgala Gardens and hakgala Forest, 19 Feb. 1978, Ruinard 19/116 (L). Sumatra, Brastagi-Tonkkeh, summit of Delangsikut, 1500 m alt., 19 June 1952, Wijk 1617 (L). Java, Prov. Preanger, in Cinchoneto "Daradjat" prope Garut, 1730 m alt., 12 Feb. 1894, Shiffner 10336 (L). New Guinea, div. Hollandia, Baliem, Wiligimaeu, 1600 m alt., 29 June 1961, Versleegh s. n. mixed with 12562BW (L).

Habitat: On soil, rocks and tree trunks.

Distribution: Europe, Macaronesia, Madagascar, Turkey, Caucasus, Japan, Korea, Taiwan, China, Himalaya, India, Sri Lanka, Myanmar, Tahiland, Philippines, Borneo, Sulawesi, Sumatra, Java, New Guinea.

The present species is characterized by (1) abaxially smooth leaf apices, (2) broad laminae which consist of 5-12 rows of quadrate to rectangular cells near base and bordered by 2-3 rows of linear cells, and (3) perichaetia terminal on stems and subfloral innovations.

In L. juniperoideum the central area of stems are sometimes weakly differentiated as a group of small cells, but the walls of the central small cells are more or less tinged with brown and different from the central strand such

as that of L. humillimum. L. humillimum is closely related to the present species, but differs in having the distinct central strand of stems which is composed of hyaline and thin-walled cells, and distinctly mucronate leaf apices.

L. glaucum is also closely related to the present species, but differs in having indistinctly hollowed central parts in cross-sections of leaf bases, which are composed of (2-) 3-4 layered of leucocysts.

I could not locate type specimens of L. triviale and L. neilgherrense var. minus. L. triviale were treated as synonym of L. neilgherrense by Renauld and Cardot (1905). According to the detailed original description of L. triviale by Müller (1869), it seems to be identical with L. juniperoideum. Original description of L. neilgherrense var. minus by Cardot (1905) was very brief and only showed smaller sized plants compared with L. neilgherrense, I consider that L. neilgherrense var. minus is also identical with the present species based on the diagnostic characters mentioned by Cardot (1905).

7. Leucobryum humillimum Card. (Fig. XXXIV, XCIV-C, CXLI:

2)

Mem. Soc. Nat. Cherbourg 32: 15, f. 29 (1901).

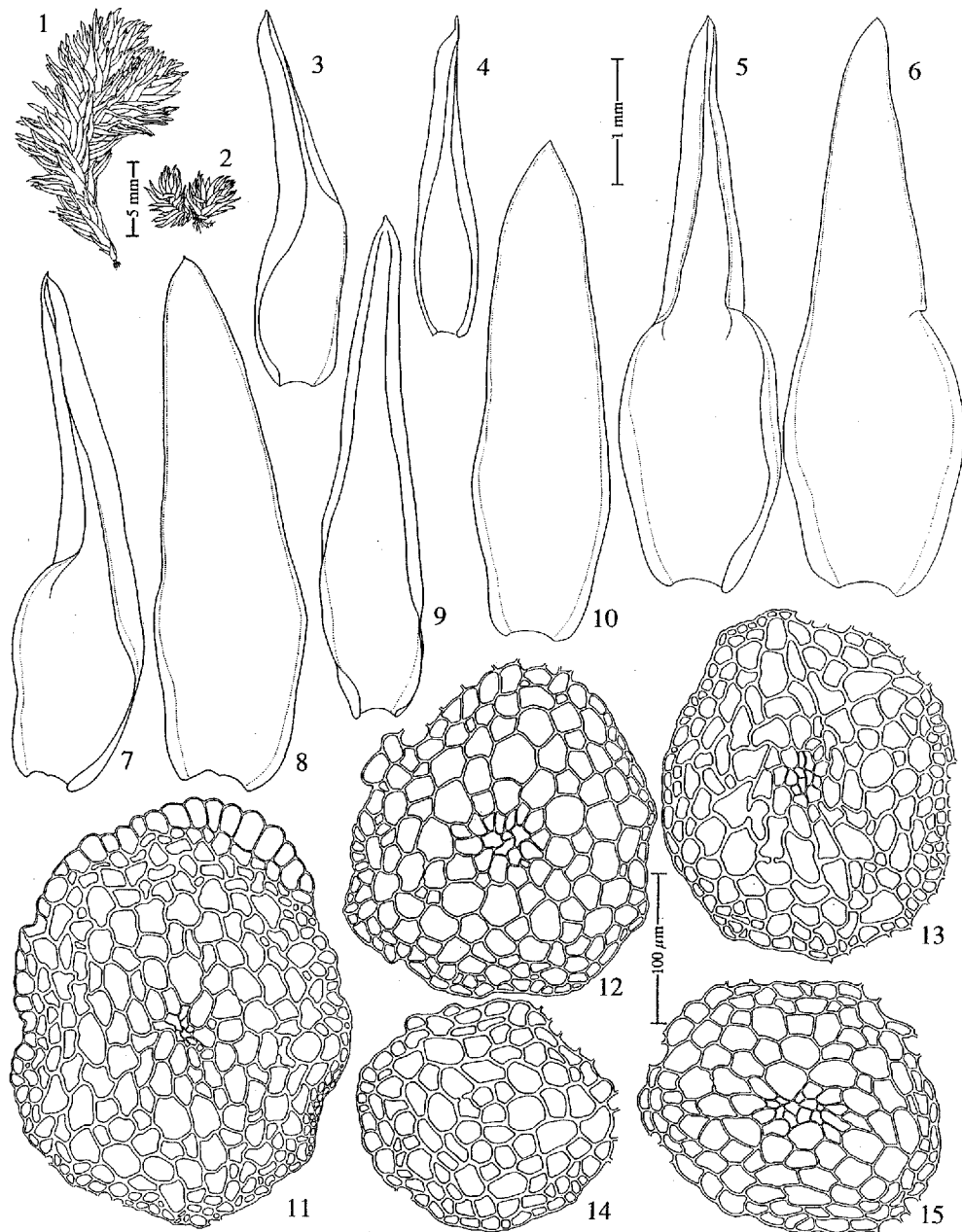


Figure XCIV. *Leucobryum humillimum* Card. 1, 2. Plants. 3–10. Leaves (6, 8, 10, expanded). 11–15. Cross-sections of stems. Fig. 1 was drawn from isotype of *L. galeatum* (KYO); 2–4, 15, from Thwaites 82 labeled as *Schistomitrium cucullatum* (NY); 5, 6, 11, from isosyntype (Faurie 11245) of *L. wichurae* (KYO); 7, 8, from lectotype of *L. cucullifolium* (PC); 9, 10, 12, from isotype of *L. galeatum* (BM); 13, from hb. Cardot 105, determined as *L. mittenii* by Bescherelle (PC); 14, from isotype of *L. mittenii* (BM).

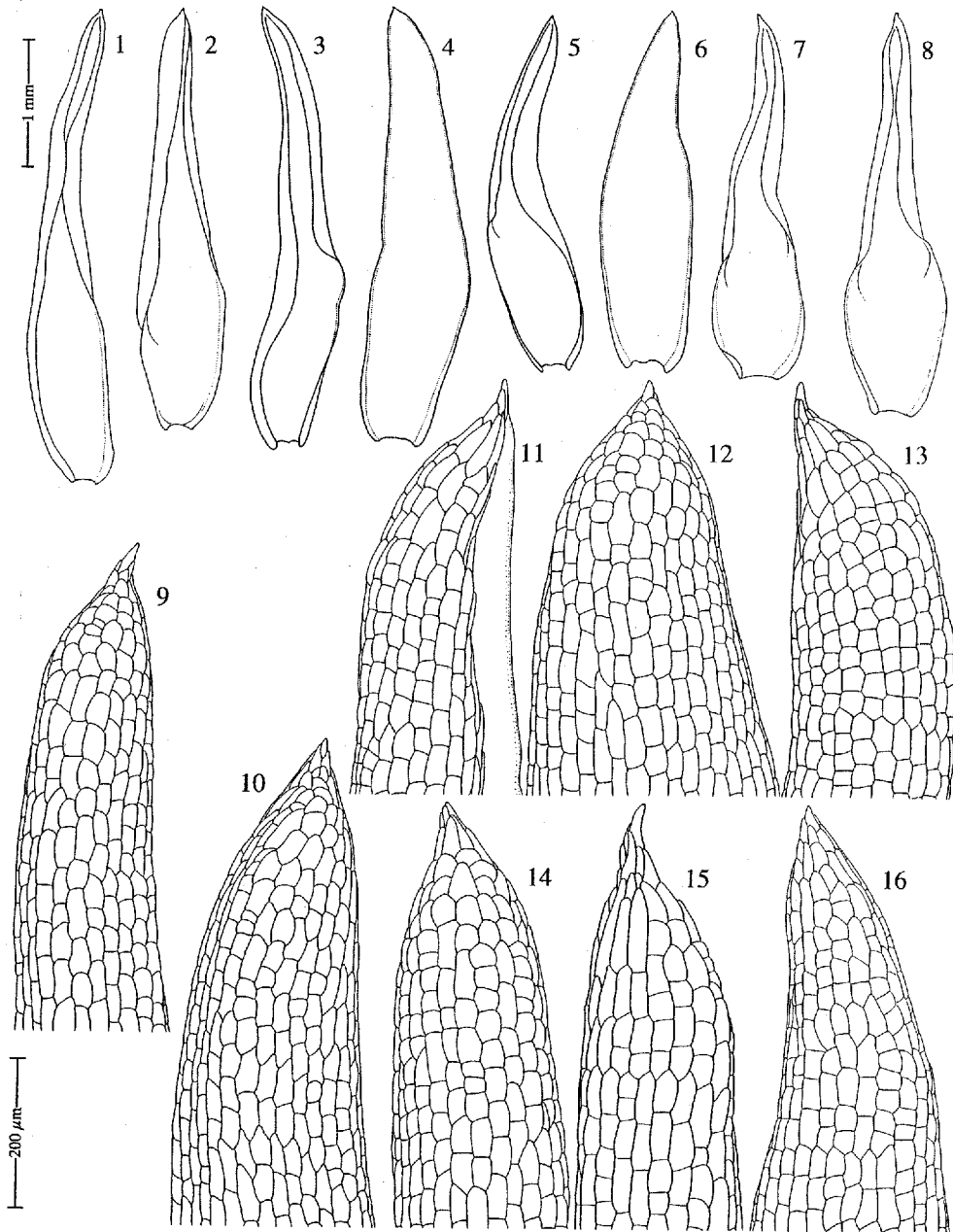


Figure XCV. *Leucobryum humillimum* Card. 1–8. Leaves (4, 6, expanded). 9–16. Leaf apices (11, 13, lateral view). Figs. 1, 2, 11, 14 were drawn from isotype of *L. mittenii* (BM); 3–6, 9, 10, from holotype of *Ochrobryum wightii* (PC); 7, 8, 15, from hb. Cardot 105, determined as *L. mittenii* by Bescherelle (PC); 12, from lectotype of *L. cucullifolium* (PC); 13, from isotype of *L. galeatum* (BM); 16, from isosytype (Faurie 11245) of *L. wichurae* (KYO).



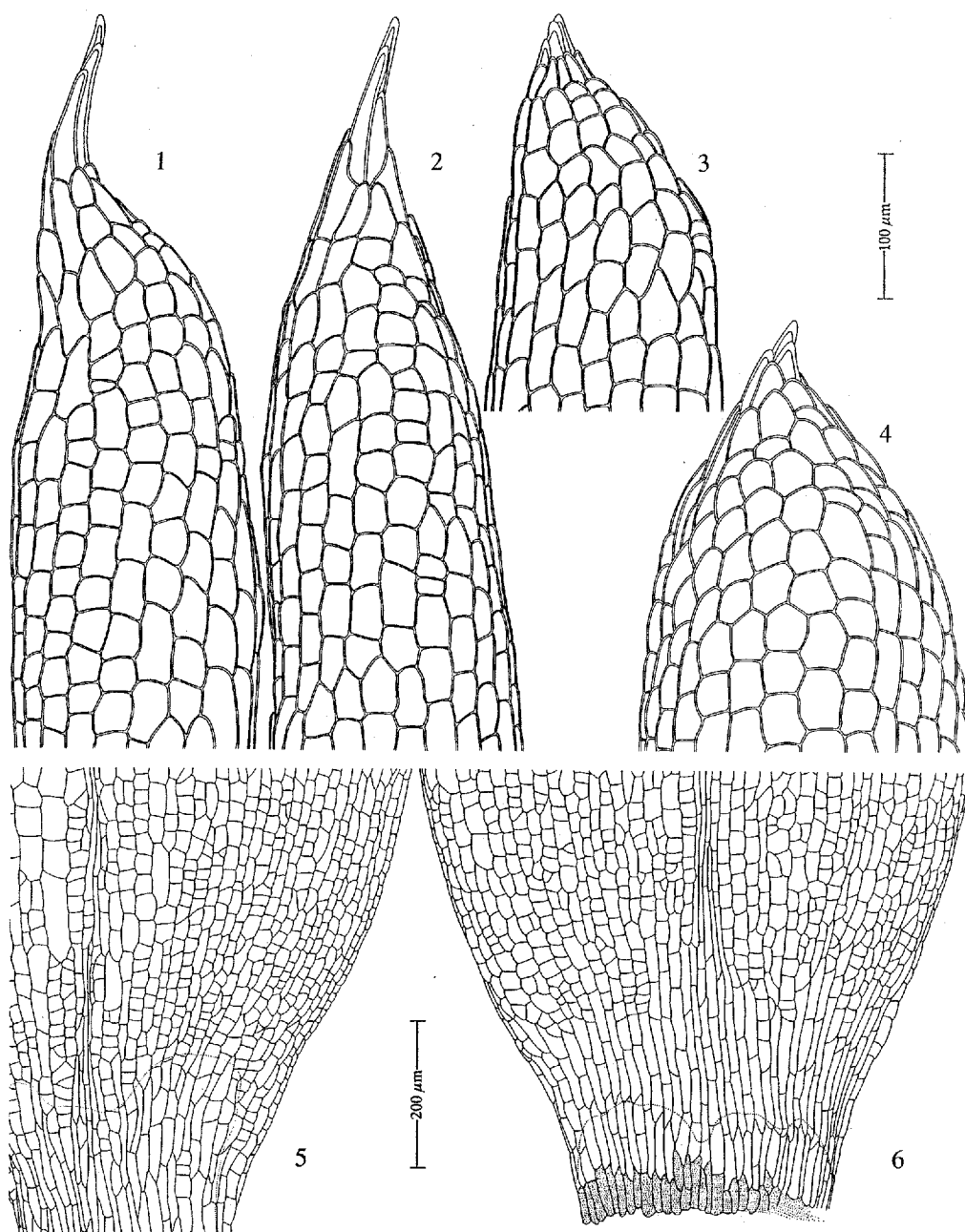


Figure XCVI. *Leucobryum humillimum* Card. 1-4. Leaf apices (1, 3, lateral view). 5, 6. Leaf bases (abaxial view). Figs. 1-3 were drawn from Thwaites 82 labeled as *Schistomitrium cucullatum* (NY); 4, from isotype of *L. galeatum* (BM); 5, from isosytype (Faurie 11245) of *L. wichurae* (KYO); 6, from lectotype of *L. cucullifolium* (PC).

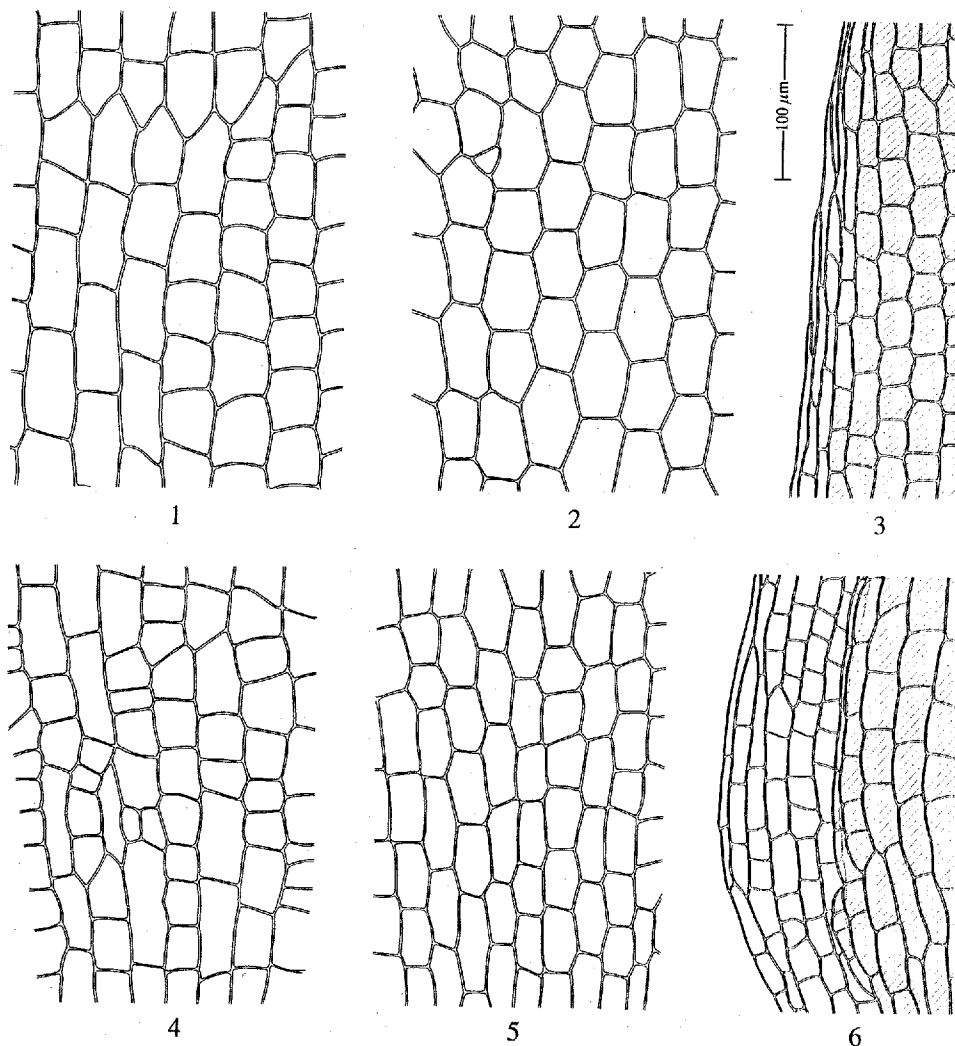


Figure XCVII. Leucobryum humillimum Card. 1-3. Median cells of leaf (1, 3, abaxial view; 2, adaxial view). 4-6. Basal cells of leaf (4, 6, abaxial view; 5, adaxial view). All figures were drawn from Thwaites 82 labeled as Schistomitrium cucullatum (NY).

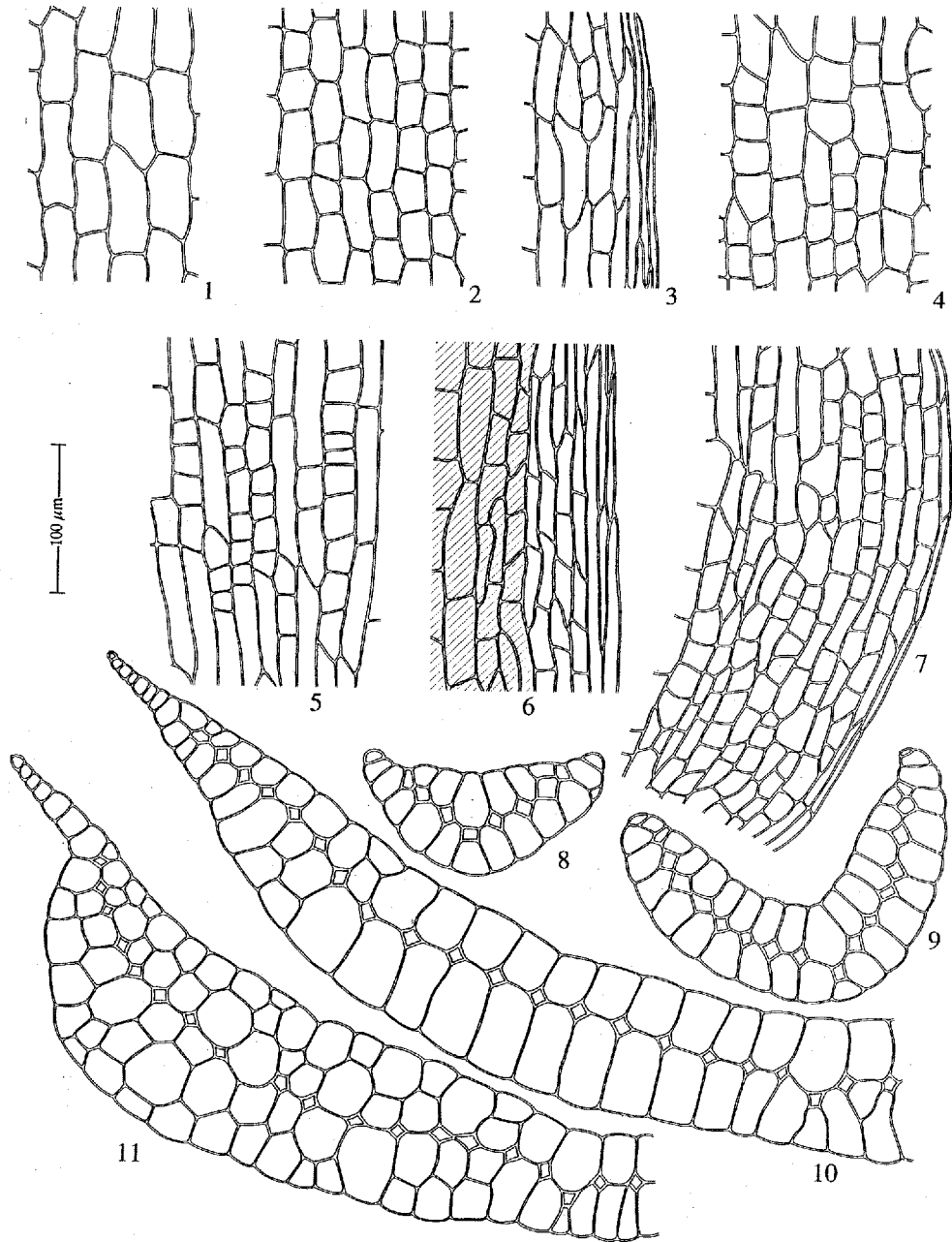


Figure XCVIII. *Leucobryum humillimum* Card. 1-3. Median cells of leaf (1, 3, abaxial view; 2, adaxial view). 4-7. Basal cells of leaf (4, 6, 7, abaxial view; 5, adaxial view). 8-11. Cross-sections of leaf (8, 9, apical; 10, median; 11, basal portions). All figures were drawn from isotype of *L. galeatum* (BM).

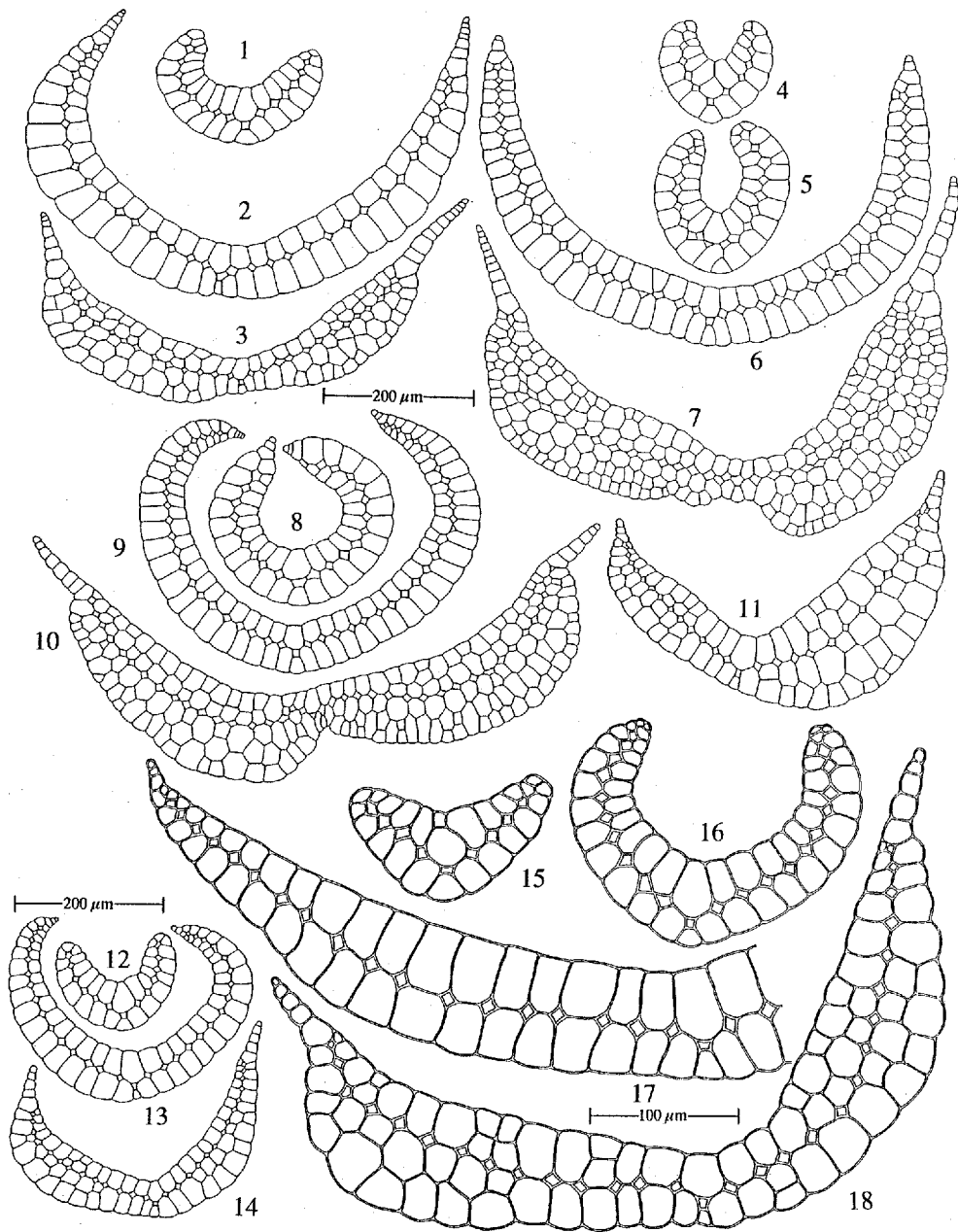


Figure XCIX. *Leucobryum humillimum* Card. 1–18. Cross-sections of leaves (1, 4, 5, 8, 12, 15, 16, apical; 2, 6, 9, 13, 17, median; 3, 7, 10, 11, 14, 18, basal portions). Figs. 1–3 were drawn from isotype of *L. mittenii* (BM); 4–7, from isosytype (Faurie 11245) of *L. wichurae* (KYO); 8–10, from lectotype of *L. cucullifolium* (PC); 11–14, from holotype of *Ochrobryum wightii* (PC); 15–18, from Thwaites 82 labeled as *Schistomitrium cucullatum* (NY).

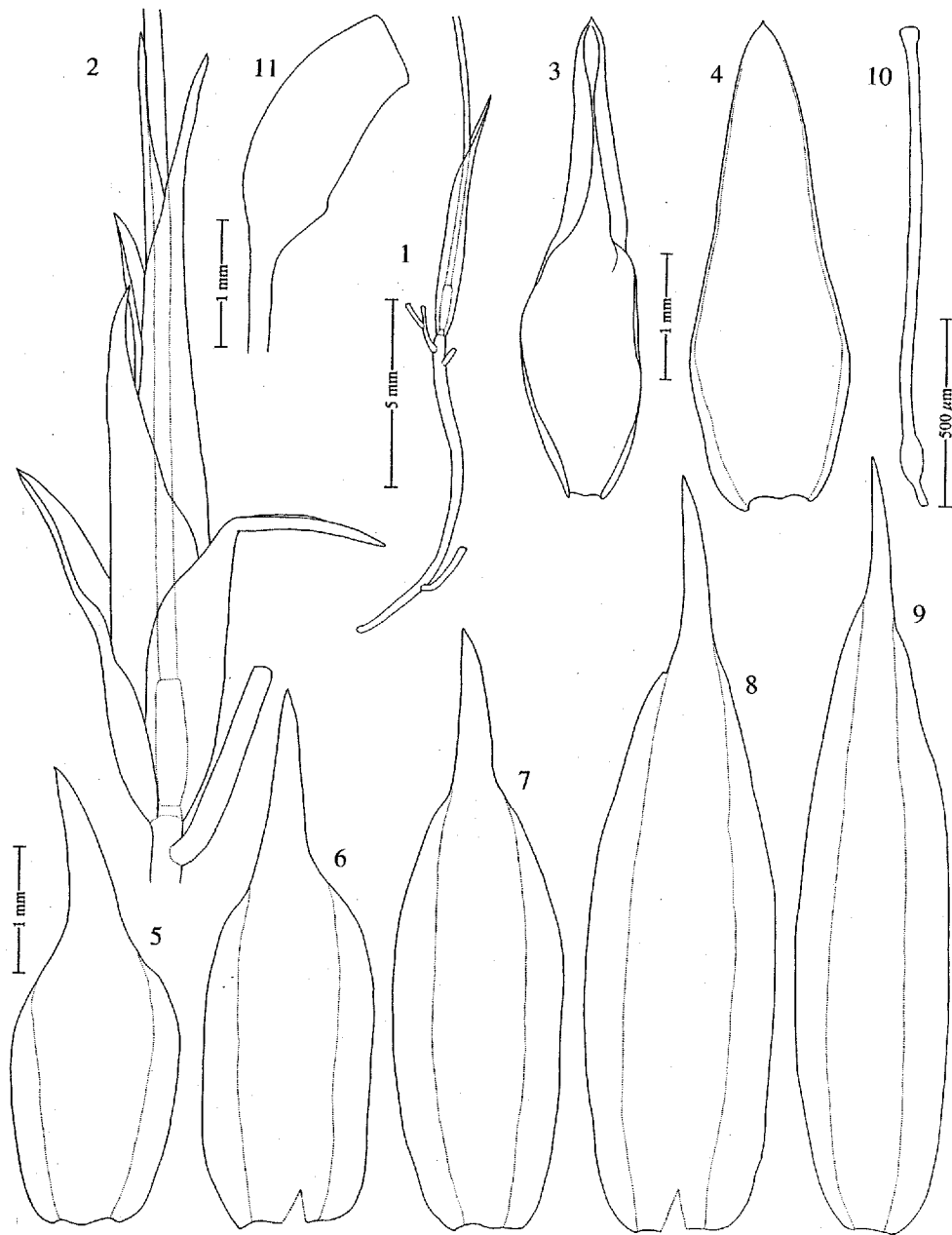


Figure C. *Leucobryum humillimum* Card. 1, 2. Perichaetia. 3, 4. Stem leaves near perichaetium 1 (4, expanded). 5-9. Perichaetial leaves from perichaetium 1 [expanded; numbers show the order of perichaetial leaves from the innermost leaf (number 9)]. 10. Archegonium. 11. Capsule. All figures were drawn from Nishimura 1514 (HIRO).

Basionym: Ochrobryum wightii Besch., J. de Bot. 11: 149, f. 6 (1897). Type: India, Madras, Wight s. n. – holotype (PC).

Leucobryum galeatum Besch., J. de Bot. 12: 286 (1898) = Leucobryum neilgherrense var. galeatum (Besch.) Dix., Hong Kong Natural. Suppl. 2: 7 (1933), syn. nov. Type: China, Hongkong, 19 Mar. 1895, Faurie 15472 – isotypes (BM, KYO).

Leucobryum mittenii Besch., J. de Bot. 12: 287 (1898), syn. nov. Type: India, Mt. Khasia, Hooker and Thomson et Thomson 1247 – isotype (BM).

Leucobryum wichurae Broth. ex Besch., J. de Bot. 12: 288 (1898), syn. nov. Type: Japan, Kochi, 22 Nov. 1893, Faurie 11245 – isosyntype (KYO).

Leucobryum cuculliphyllum Fl., Musci Fl. Buitenzorg 1: 152 (1904), syn. nov. Type: Sri Lanka, bei Wattescalle an morscher Rinde, 900-1200 m alt., Feb. 1898, Fleischer s. n. (Musci Frond. Archipelagi Indici ser. VI, no. 259) – isotype (HIRO).

Leucobryum cucullifolium Card. in Ren. & Card., Bull. Soc. R. Bot. Belg. 41(1): 30 (1905), syn. nov. Type: India, Sikkim-Himalaya, prope Kurseong, Punkabari, 16 Dec. 1899, Decoly and Schaul s. n. (in herb. Levier) – lectotype (PC).

Ochrobryum propaguliferum Dix., Not. R. Bot. Gard. Edinburgh 19: 281, f. 1 (1938) = Leucobryum propaguliferum (Dix.) Robinson, Bryologist 68: 91 (1965), syn. nov. Type:

Sri Lanka, base of Hunasgiriya, under rock, 29 Sept. 1928, Alston 1895 - holotype (BM).

Plants whitish tinged with brown when dry, forming compact cushions. Stems to 30 mm long with leaves; central strand well differentiated in cross-sections of stems, composed of small, hyaline and thin-walled cells. Leaves imbricate to erect spreading; 2.7-4.5 x 0.7-1.5 mm, broadly lanceolate or oblong, distinctly mucronate at apex, sometimes with a spinous apical cell, gradually narrowed to subtubulous point from oblong to ovate base, smooth on abaxial surface; apical cells nearly quadrate on abaxial surface; laminae consisting of 4-8 rows of quadrate to rectangular cells near base, bordered by 2-3 rows of linear cells; in cross-sections near leaf base leucocysts in 2-3 cell layers on both sides; abaxial leucocysts hardly decurrent on stems.

Dioicous. Male plants dimorphous; dwarf male plants small, usually growing on tomentum enclosed by perichaetial leaves; normal male plants as large as female plants, perigonia small, terminal on stems of subfloral innovations. Perichaetia terminal on main stems or subfloral innovations; inner perichaetial leaves around mature sporophytes 1.4-1.6 times longer than ordinary leaves near the perichaetia; archegonia ca. 1.3 mm long. Setae 7-10 mm long. Capsules

inclined, ovoid to ellipsoid; urns 0.7-1.3 mm long, 0.4-0.6 mm wide.

Representative specimens examined: Japan, Honshu, Hiroshima-ken, Ootake-shi, a valley of north of Arashitaniyama, 180-250 m alt., 4 Aug. 1977, Nishimura 1514 (HIRO). Korea, Mt. Chii, 700 m alt., 16 Aug. 1960, Hong 2080 (HIRO). China, Kwangtung, Fengkai, Nov. 1980, Li 1369 (NICH). Himalaya, without definit locality and collector name, in Hb. Roy. Kew 1875, no. 105, labeled as Leucobryum mittenii Besch. (BM). Nepal, in montibus circa Khatmandu, Feb.-Apr. 1900, Rana s. n. (in herb. Levier, Leucobryum laticuspes Broth., nov. spec. in sched.) – paratype of L. cucullifolium (PC). India, Wight s. n. (in herb. Dixon, ref. no. 52) – paratype of Ochrobryum propaguliferum (BM). Sri Lanka, Hatton, on rock near Hambantotuoya, 17 Mar. 1929, Alston 2607 – paratype of Ochrobryum propaguliferum (BM); Thwaites 82, labeled as Schistomitrium cucullatum T. et M. – original specimen of S. cucullatum Twait. & Mitt., nom. nud. (NY).

Habitat: On soil and rocks.

Distribution: Japan, Korea, China, Himalaya, India, Sri Lanka.

The present species is characterized by (1) distinctly differentiated central strand of stem, (2) mucronate leaf apices which sometimes have spinous apical cells, and (3)



nearly quadrate cells on abaxial surface of apical parts of leaves.

In mature plants the present species always have well differentiated central strand of stem. However, in some cases, such as in juvenile condition, the central strand is hardly differentiated (Fig. XCIV: 14). When the central strand is not differentiated, the present species is differentiated from other Asian species of Leucobryum, except for L. imbricatum, by conspicuous mucronate leaf apices.

Most of the Asian species of Leucobryum produce deciduous leaves, especially in L. humillimum (Fig. XXXIV). L. mittenii and L. propaguliferum were described based on the formation of deciduous leaves as one of the diagnostic characters.

8. Leucobryum imbricatum Broth. (Fig. CI-CIII, CXLI: 9)

Rec. Bot. Surv. India 1: 314 (1899). Type: India, Coorg, on tree trunks in dry open jungle near Verajpet, Mar. 1898, Walker 292 - lectotype (H).

Plants whitish tinged with brown when dry, forming compact cushions. Stems to 30 mm long with leaves; central strand well differentiated in cross-sections of stems. Caducous leaves highly differentiated, linear, twisted or bent, forming a cluster of gemmae at shoot apex enclosed by

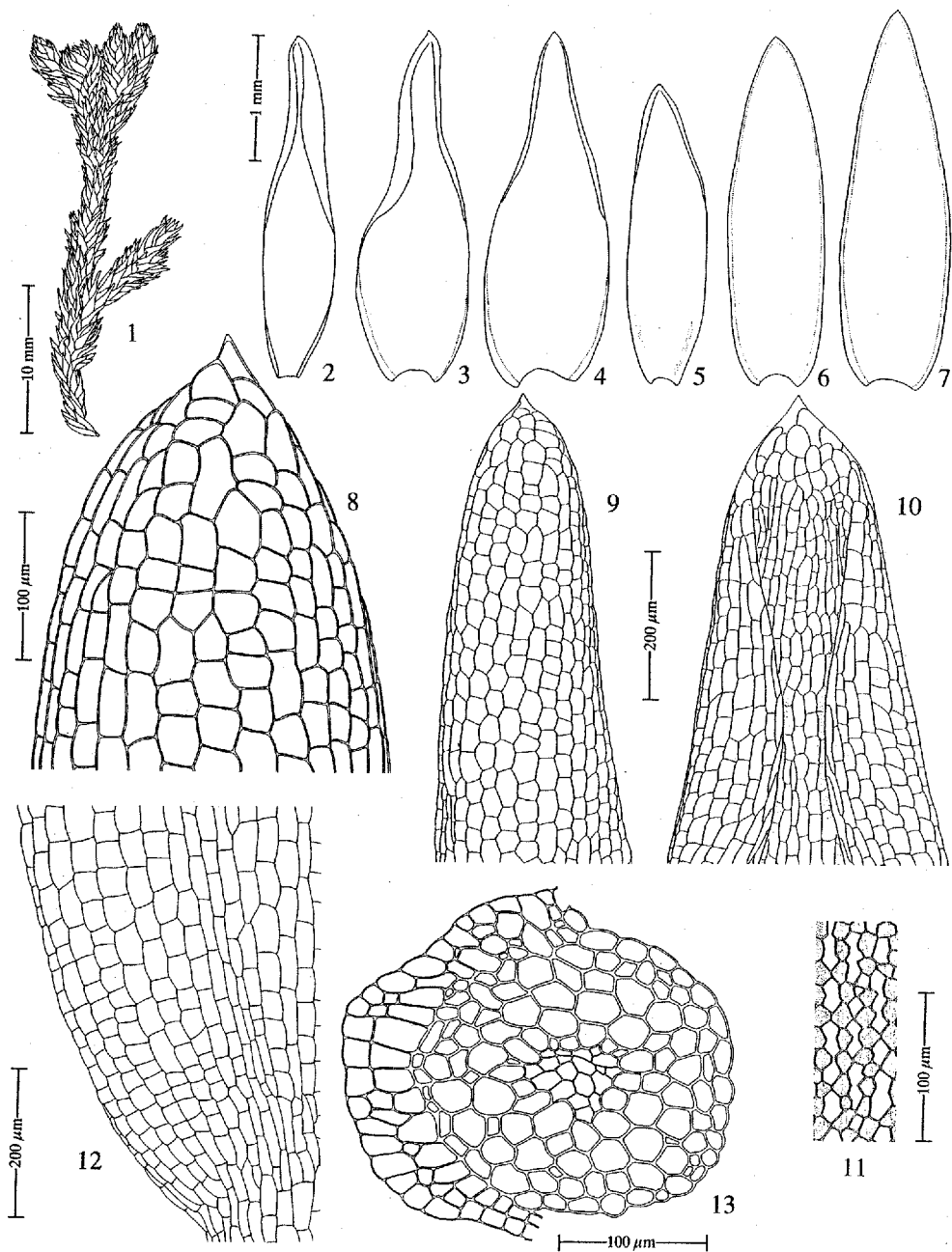


Figure Cl. *Leucobryum imbricatum* Broth. 1. Plant. 2-7. Leaves (6, 7, expanded). 8-10. Leaf apices (10, adaxial view). 11. Chlorocysts near the leaf apex. 12. Leaf base (abaxial view). 13. Cross-section of stem. All figures were drawn from lectotype of *L. imbricatum* (H).

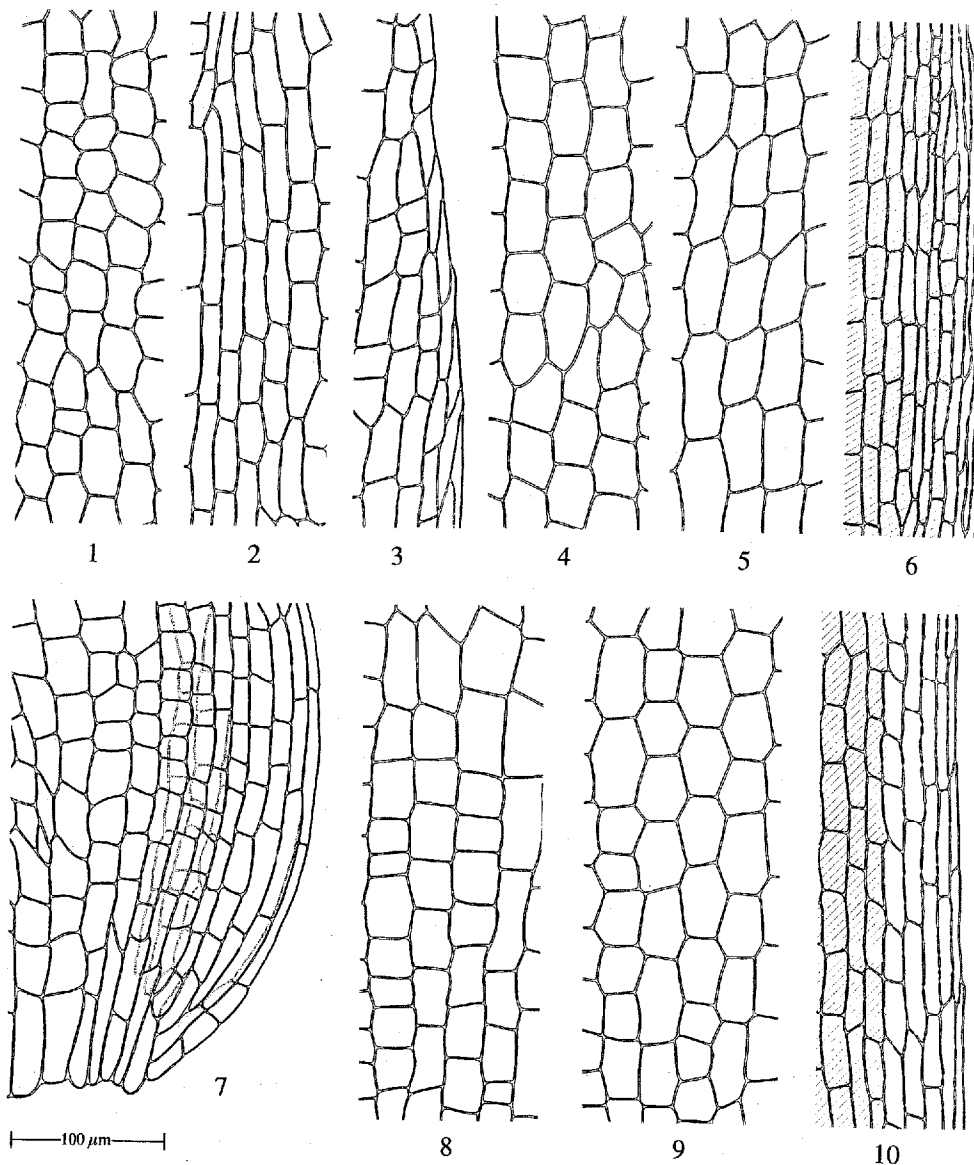


Figure CII. *Leucobryum imbricatum* Broth. 1-3. Cells near leaf apex (1, 3, abaxial view; 2, adaxial view). 4-6. Median cells of leaf (4, abaxial view; 5, 6, adaxial view). 7-10. Basal cells of leaf (7, 8, abaxial view; 9, 10, adaxial view). All figures were drawn from lectotype of *L. imbricatum* (H).

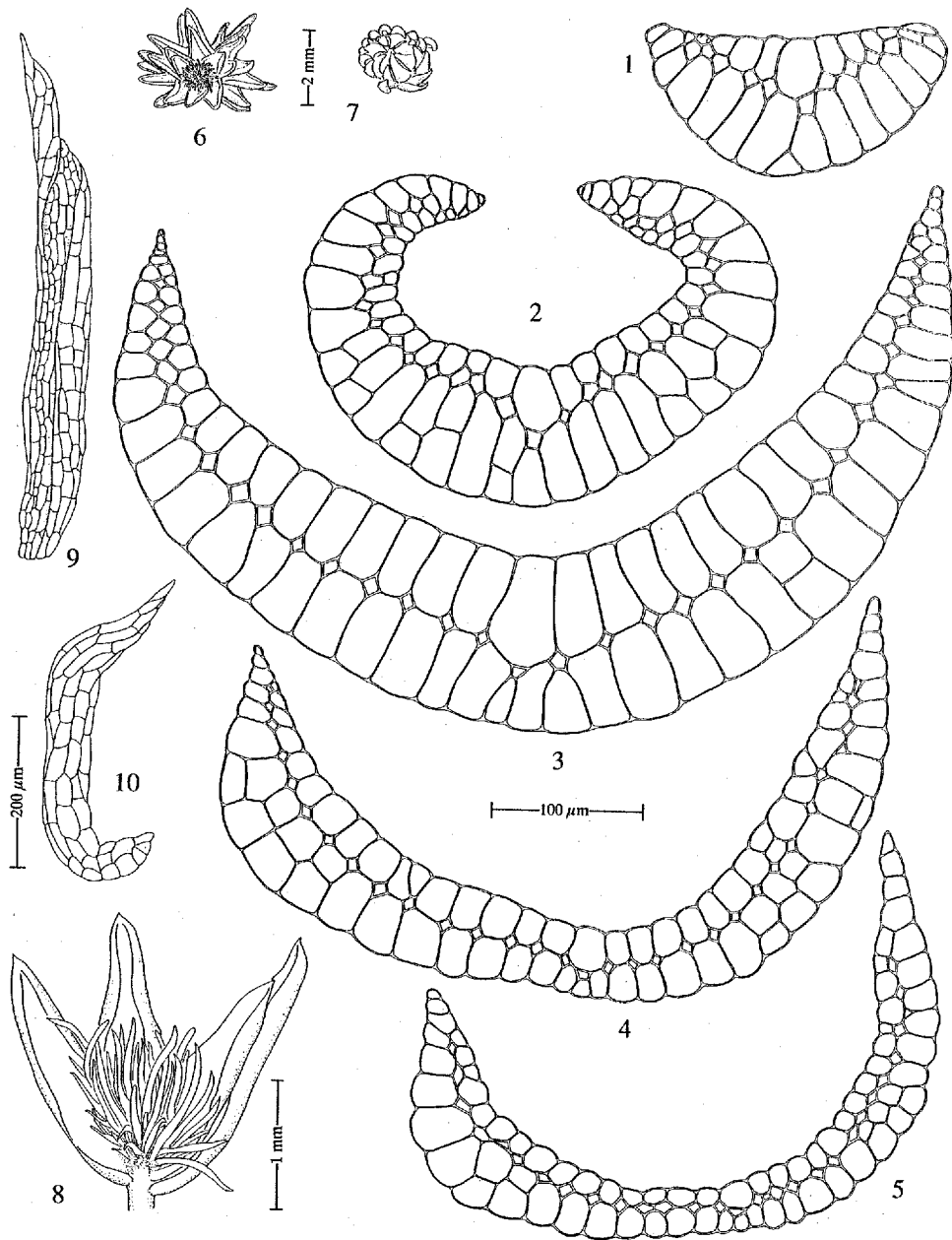


Figure CIII. *Leucobryum imbricatum* Broth. 1-5. Cross-sections of leaf (1, 2, apical; 3, median; 4, 5, basal portions). 6-8. Shoot apices (6, wet condition; 7, dry condition). 9, 10. Gemmae. All figures were drawn from lectotype of *L. imbricatum* (H).

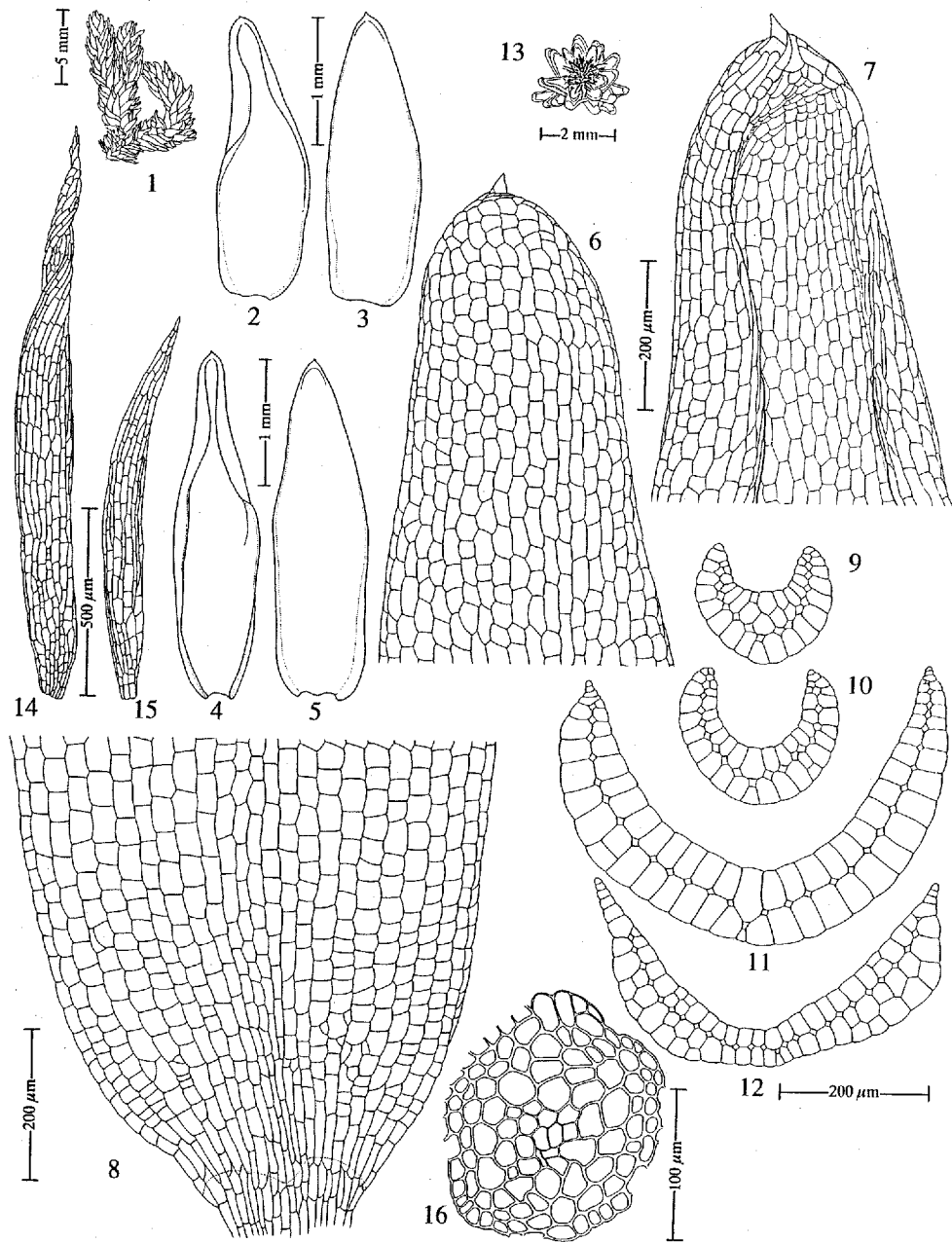


Figure CIV. *Leucobryum incurvifolium* C. Müll. 1. Plant. 2-5. Leaves (3, 5, expanded). 6, 7. Leaf apices (7, adaxial view). 8. Leaf base (abaxial view). 9-12. Cross-sections of leaf (9, 10, apical; 11, median; 12, basal portions). 13. Shoot apex, when dry. 14, 15. Gemmae. 16. Cross-section of stem. All figures were drawn from isotype of *L. incurvifolium* (FH).

stem leaves when dry. Leaves closely imbricated; 2.4-2.8 x 0.6-1.0 mm, broadly lanceolate to oblong, mucronate, with a hyaline conical cell at apex, abruptly narrowed to subtubulous or broadly channeled point from ovate base, smooth on abaxial surface; abaxial leucocysts on abaxial surface at apical part nearly quadrate; laminae and borders consisting of 3-5 rows of narrowly rectangular to linear cells near base, the differentiation between laminal cells and border cells indistinct; in cross-sections near leaf apex leucocysts in 1 cell layer on adaxial side and 1-2 cell layers on abaxial side, the adaxial layer conspicuously thinner than the abaxial layer (Fig. CIII: 2); chlorocysts at apical part well visible from adaxial side because of the thin layered adaxial leucocysts, roundish polygonal, forming a network composed of bead-like chlorocysts; in cross-sections near leaf base leucocysts in 1-2 cell layers on both sides, somewhat hypercentric; abaxial leucocysts hardly decurrent on stems.

Sexual organs and sporophytes not observed.

Representative specimens examined: India, Coorg, Murnad, on tree trunks in dry open places, Dec. 1897, Walker 107 - paratype of L. imbricatum (BM).

Habitat: On tree trunks in dry open sites.

Distribution: Endemic to S. India.

The present species is characterized by (1) well differentiated central strand of stem, (2) mucronate leaf apex with a hyaline conical cell, (3) abaxial leucocysts (1-2 cell layer) thicker than adaxial leucocysts (1 cell layer) at apical part of leaf in cross-section, and (4) highly differentiated caducous leaves (gemmae).

L. humillimum is similar to the present species in general appearance, but differs in having homostrosic leucocysts and centric position of chlorocysts at apical part of leaf in cross-section and absence of specialized gemmae.

L. incurvifolium C. Müll. (Fig. CIV) from Central America is closely related to the present species, having specialized gemmae at shoot apices, differentiated central strand of stems and mucronate leaf apices with a hyaline point. However, adaxial leucocysts (1-2 cell layer) of L. incurvifolium thicker than abaxial leucocysts (1 cell layer) in cross-section at apical part of leaf (Fig. CIV: 9).

9. Leucobryum glaucum (Hedw.) Ångstr. in Fries (Fig. XXIII, CV-CIX, CXL: 1)

Summ. Veg. Scand. 1: 94 (1846).

Basionym: Dicranum glaucum Hedw., Spec. Musc.: 135 (1801). Type: "In sylvis uliginosis, pinetis, ericetis, pratisque paludosis caespitose vitam degit, totius Europae

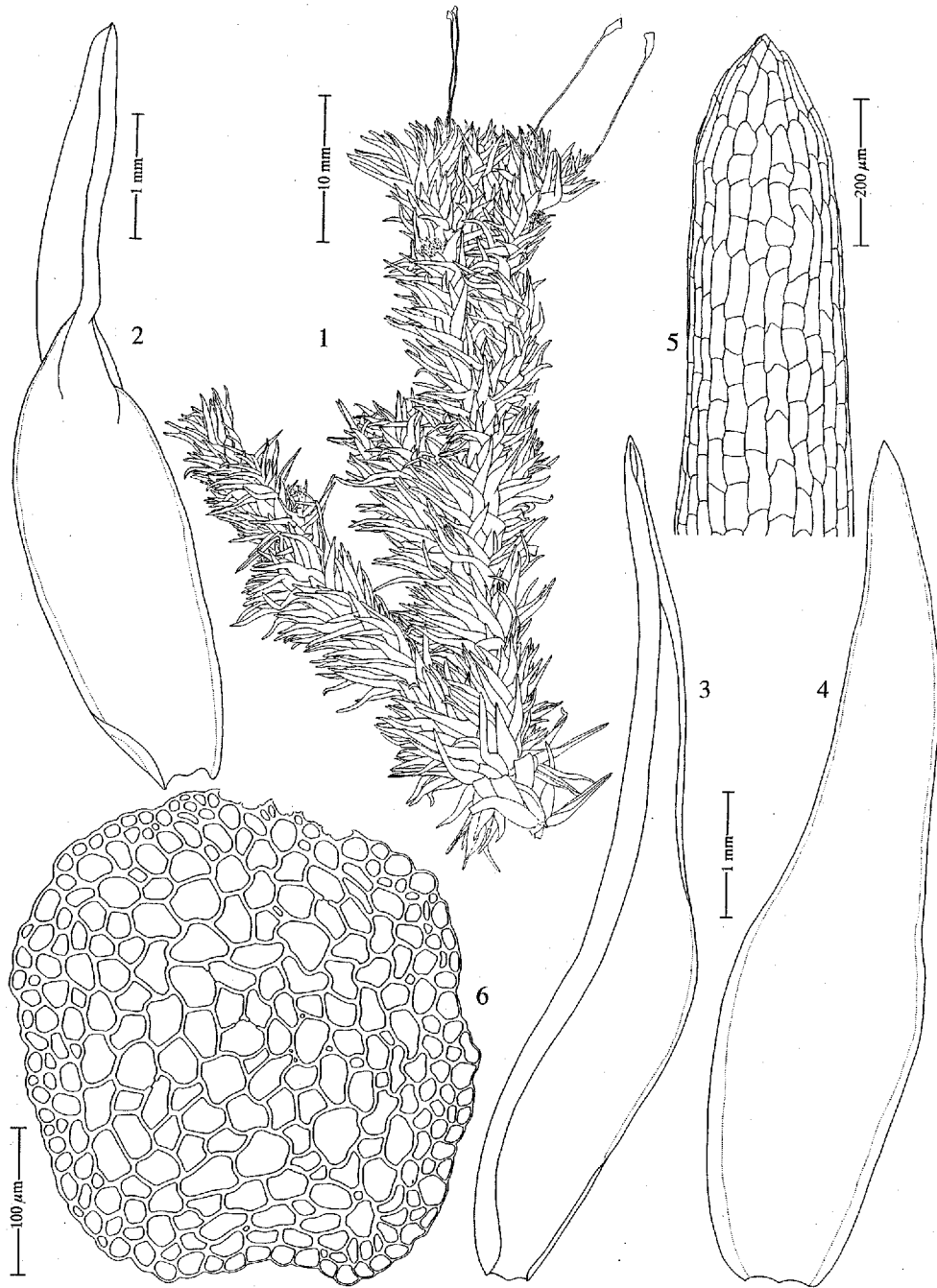


Figure CV. *Leucobryum glaucum* (Hedw.) Ångstr. in Fries. 1. Plant. 2-4. Leaves (4, expanded). 5. Leaf apex. 6. Cross-section of stem. Figs. 1, 2, 5 were drawn from Europe, Sept. 1797, s. n. (B); 3, 4, 6 from Zanten 3319 (NICH).



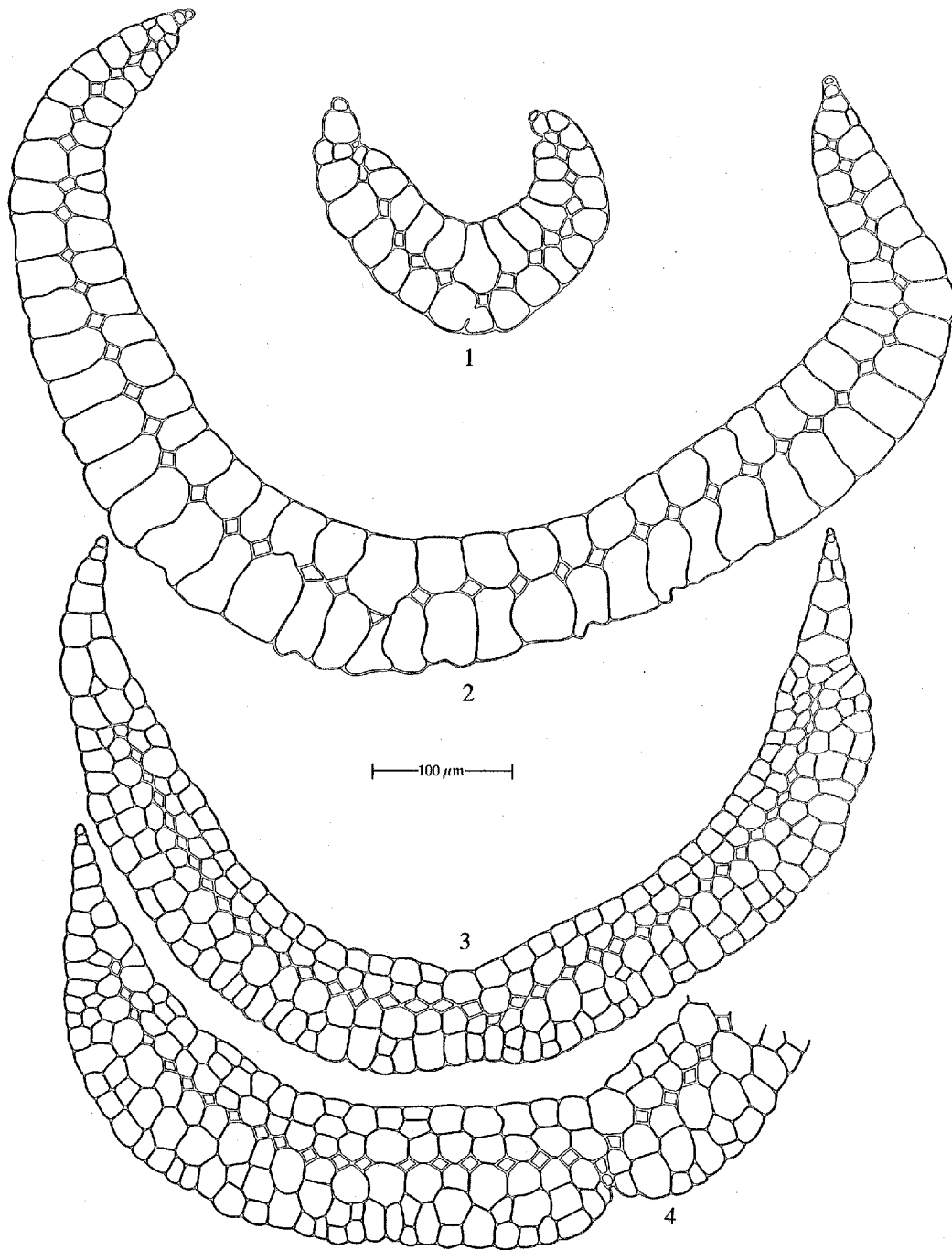


Figure CVI. *Leucobryum glaucum* (Hedw.) Ångstr. in Fries. 1–4. Cross-sections of leaf (1, apical; 2, median; 3, 4, basal portions). All figures were drawn from Europe, Sept. 1797, s. n. (B).

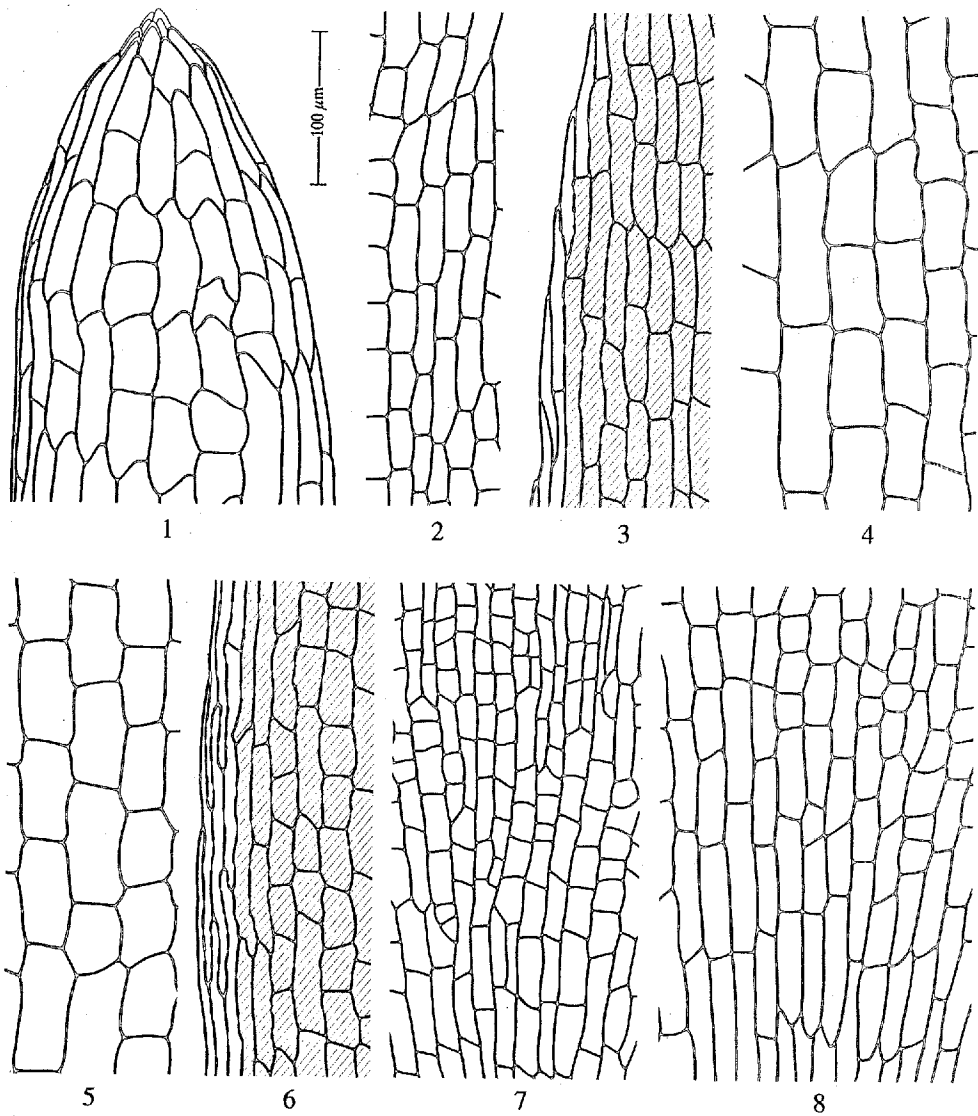


Figure CVII. *Leucobryum glaucum* (Hedw.) Ångstr. in Fries. 1–3. Cells near leaf apex (1, abaxial view; 2, 3, adaxial view). 4–6. Median cells of leaf (4, abaxial view; 5, 6, adaxial view). 7, 8. Basal cells of leaf (7, abaxial view; 8, adaxial view). All figures were drawn from Europe, Sept. 1797, s. n. (B).

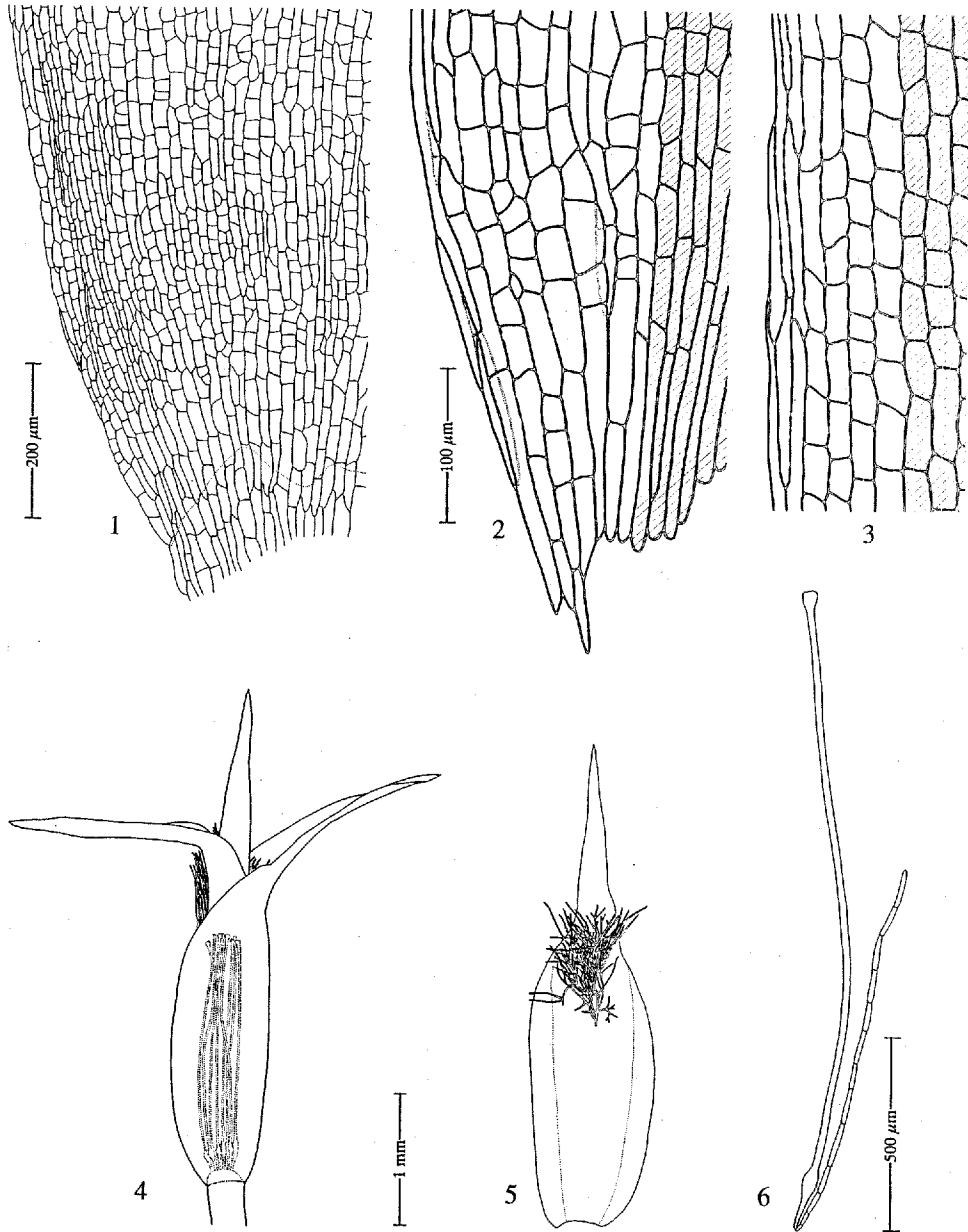


Figure CVIII. *Leucobryum glaucum* (Hedw.) Ångstr. in Fries. 1. Leaf base (abaxial view). 2, 3. Basal cells of leaf (adaxial view). 4. Perichaetium. 5. Inner perichaetial leaf (expanded) showing formation of tomentum on abaxial side. 6. Archegonium. Figs. 1-3 were drawn from Europe, Sept. 1797, s. n. (B); 4-6, from Zanten 3319 (NICH).

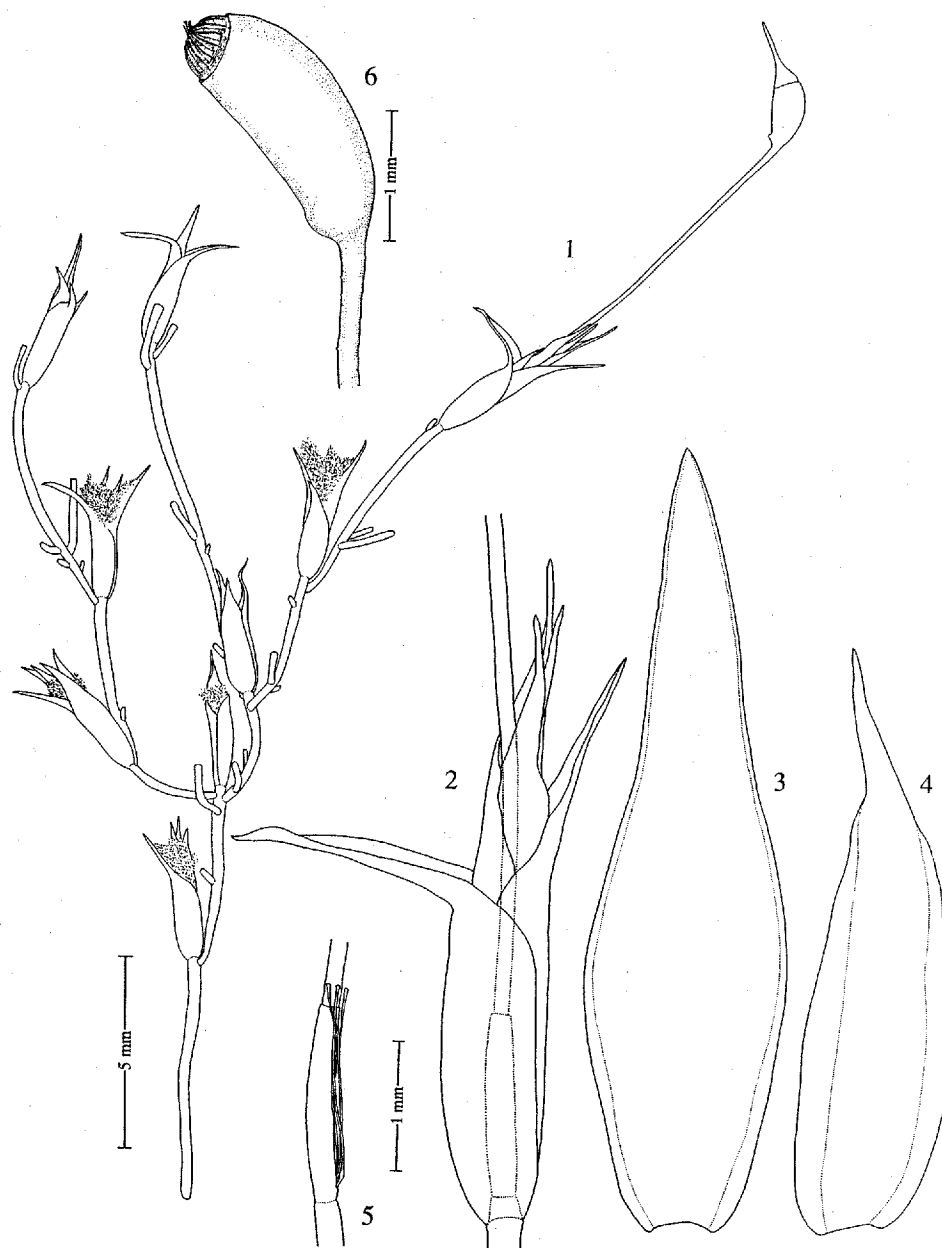


Figure CIX. *Leucobryum glaucum* (Hedw.) Ångstr. in Fries. 1. Branching showing position of perichaetia. 2. Perichaetium. 3. Stem leaf (expanded) near perichaetium. 4. Inner perichaetial leaf (expanded) from perichaetium. 5. Vaginula and Archegonia. 6. Capsule. All figures were drawn from Zanten 3319 (NICH).

et Americae septemtrionalis nec non Jamaicae incola" --  
syntypes (not seen).

Plants whitish green when dry, forming tufts or cushions. Stems to 50 mm long with leaves; central strand not differentiated in cross-sections of stems. Leaves erect spreading; 5.9-6.8 x 1.3-1.6 mm, lanceolate, gradually narrowed to subtubulous point from oblong base, acute to bluntly mucronate, smooth on abaxial surface; laminae consisting of 4-7 rows of quadrate to rectangular cells near base, bordered by 2-3 rows of linear cells, the laminal area composed of rectangular cells extended to mid leaf; in cross-sections near leaf base leucocysts in 2-3 cell layers on both sides at the thickest part, the central part indistinctly hollowed, in (2-) 3-4 layers of leucocysts, the thickest part 1.2-1.6 times thicker than the central part; abaxial leucocysts hardly decurrent on stems.

Dioicous. Dwarf male plants usually growing on tomentum enclosed by perichaetial leaves; independent normal male plants not observed. Perichaetia terminal on main stems and subfloral innovations; inner perichaetial leaves around mature sporophytes 0.7-0.8 times longer than ordinary leaves near the perichaetia; archegonia 1.7-1.8 mm long. Setae 8-11 mm long. Capsules inclined, ovoid to ellipsoid; urns ca. 1.6 mm long, ca. 0.8 mm wide.

Representative specimens examined: Japan, Hokkaido, Kushiro-shicho, Wakoto side of Lake Kussharo, 120 m alt., 30 Sept. 1985, Furuki 6177 (HIRO). Japan, Honshu, Iwate-ken, Mt. Hayachine, 1800 m alt., 29 Aug. 1967, Komizuuchi and Ishizuka 23 (HIRO). Japan, Honshu, Gunma-ken, Nikko National Park, Mt. Shibutsu, 1880 m alt., 23 Aug. 1955, Kurachi 2023 (NICH). Europe, without definite locality, labeled as "In dem kleinen ... buch auf dem Boden mit Mlütchen im ... September 1797" (B). Netherlands, Prov. of Gelderland, Speulder forest near Putten, 26 Feb. 1966, Zanten 3319 (NICH).

Habitat: Usually on humus near damp sites, occasionally on soil, rotten logs, stumps, or on tree base in moist forests.

Distribution: Japan. Widely distributed throughout temperate to cool temperate regions in N. Hemisphere.

L. glaucum shows similar appearance with L. juniperoideum, but is differentiated from L. juniperoideum by (1) laminae consist of 4-7 rows of quadrate to rectangular cells near base, (2) indistinctly hollowed central parts in cross-sections near leaf bases which are composed of (2-) 3-4 layers of leucocysts, and (3) short perichaetial leaves 0.7-0.8 times longer than ordinary leaves near the perichaetium when sporophytes are matured.

L. glaucum usually grows on moist humus near damp sites, while L. juniperoideum grows on soil, rocks, logs and tree base in Japan. Different growing habitats of these two species are also reported in Europe by Bonnot (1964), Crundwell (1972) and Blackstock (1987).

10. Leucobryum bowringii Mitt. (Fig. XXIV, XXV: C, XXVIII, XXIX, XXXII, CX-CXXII, CXLII: 1)

J. Linn. Soc. Bot. Suppl. 1: 26 (1859). Type: Sri Lanka, Gardner 1279 - lectotype (NY).

Ochrobryum ceylanicum Besch., J. de Bot. 11: 148 (1897) = Leucobryum ceylanicum (Besch.) Card., Mem. Soc. Sc. Nat. Cherbourg 32: 15, f. 27 (1901), syn. nov. Type: Sri Lanka, Central Province, Thwaites 81 - holotype (PC), isotype (BM).

Leucobryum yamatense Besch., J. de Bot. 12: 288 (1898). Type: Japan, Yamato, Mt. Kasuga, 15 July 1883, Okubo s. n. - isotype (NICH).

Leucobryum nagasakense Broth., Hedwigia 38: 208 (1899). Type: Japan, Nagasaki, 20 Jan. 1861, Wichura 1416c - holotype (H).

Leucobryum brotheri Card. in Ren. & Card., Bull. Soc. R. Bot. Belg. 41(1): 36 (1905). Type: Java, Sri Lanka, Hantanna Dschungl bei Peradenniya, 1500 m alt., Feb. 1898, without collector name (Musci Frond. Archipelagi Indici ser. I, no. 7, Leucobryum bowringii Mitt. in sched.) - isosytype

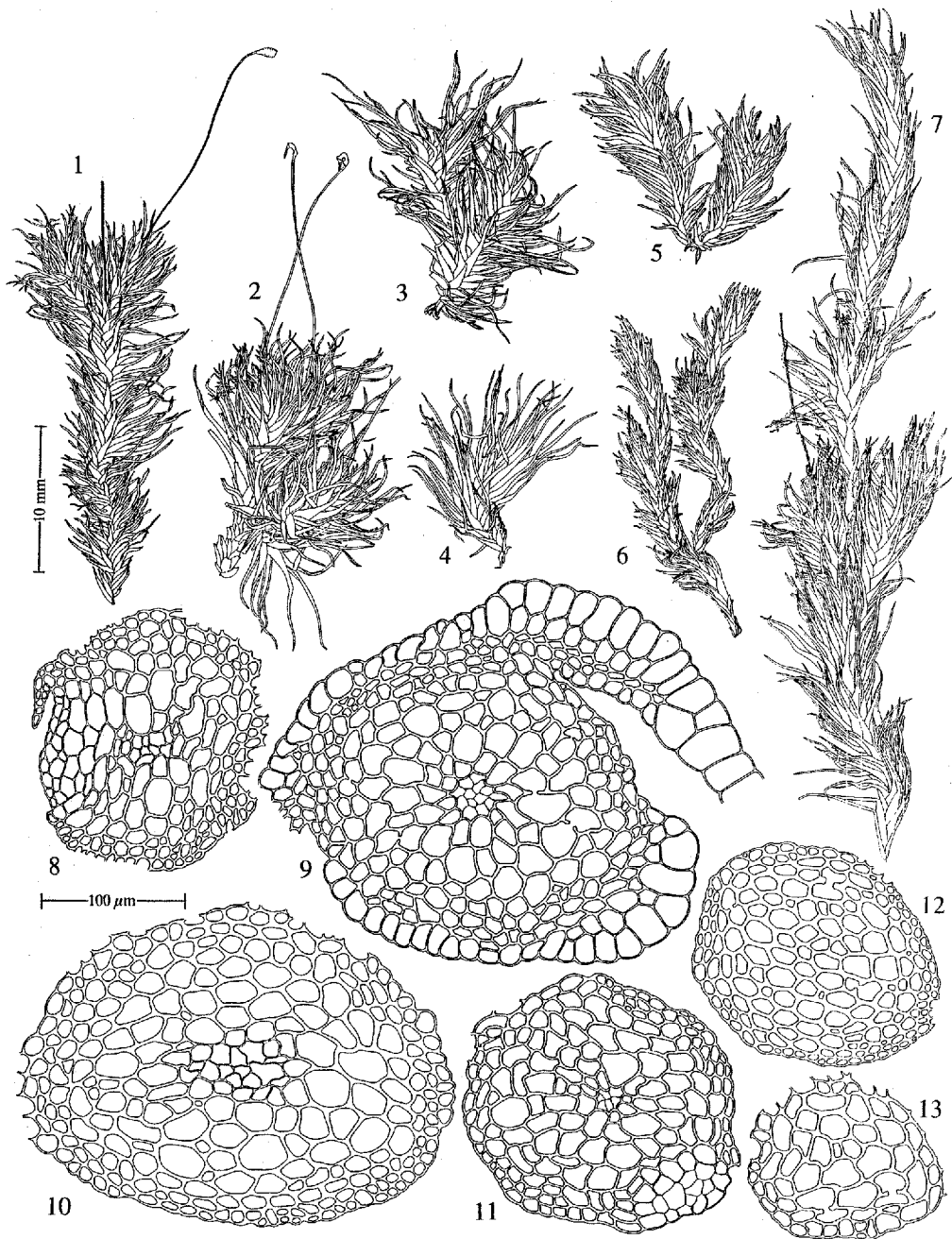


Figure CX. *Leucobryum bowringii* Mitt. 1-7. Plants. 8-13. Cross-sections of stems. Figs. 1, 8 were drawn from lectotype of *L. bowringii* (NY); 2, 3, from Yamaguchi 9313 (HIRO); 4, from Faurie 62 labeled as *L. bowringii* f. *brevifolium* (KYO); 5, 13, from isosytype (Wright s. n.) of *L. stenobasis* (FI); 6, 12, from isosytype (Gollan s. n.) of *L. stenobasis* (FI); 7, from Noguchi 26323 (NICH); 9, from holotype of *L. subsericeum* (BM); 10, from holotype of *L. nagasakense* (H); 11, from isotype of *Ochrobryum ceylanicum* (BM).



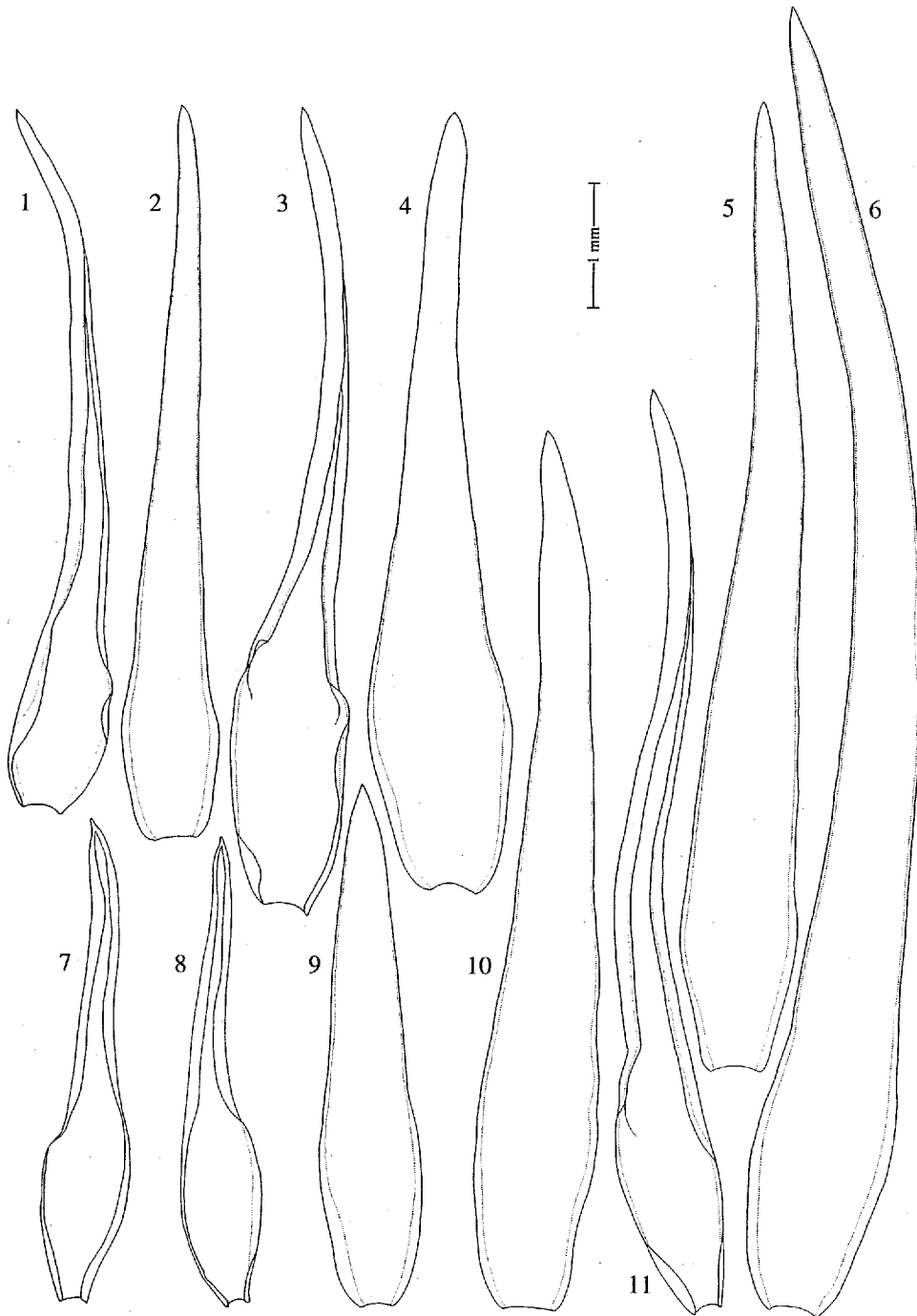


Figure CXI. Leucobryum bowringii Mitt. 1-11. Leaves (2, 4, 5, 6, 9, 10, expanded). Figs. 1, 2 were drawn from lectotype of L. bowringii (NY); 3, 4, from Faurie 62 labeled as L. bowringii f. brevifolium (KYO); 5, from Fleischer s. n., Musci Archipelagi Indici 4: 152, labeled as L. angustifolium var. macrophyllum (FH); 6, from Yamaguchi 9313 (HIRO); 7-9, from isotype of Ochrobryum ceylanicum (BM); 10, 11, from isotype of L. confine (KYO).

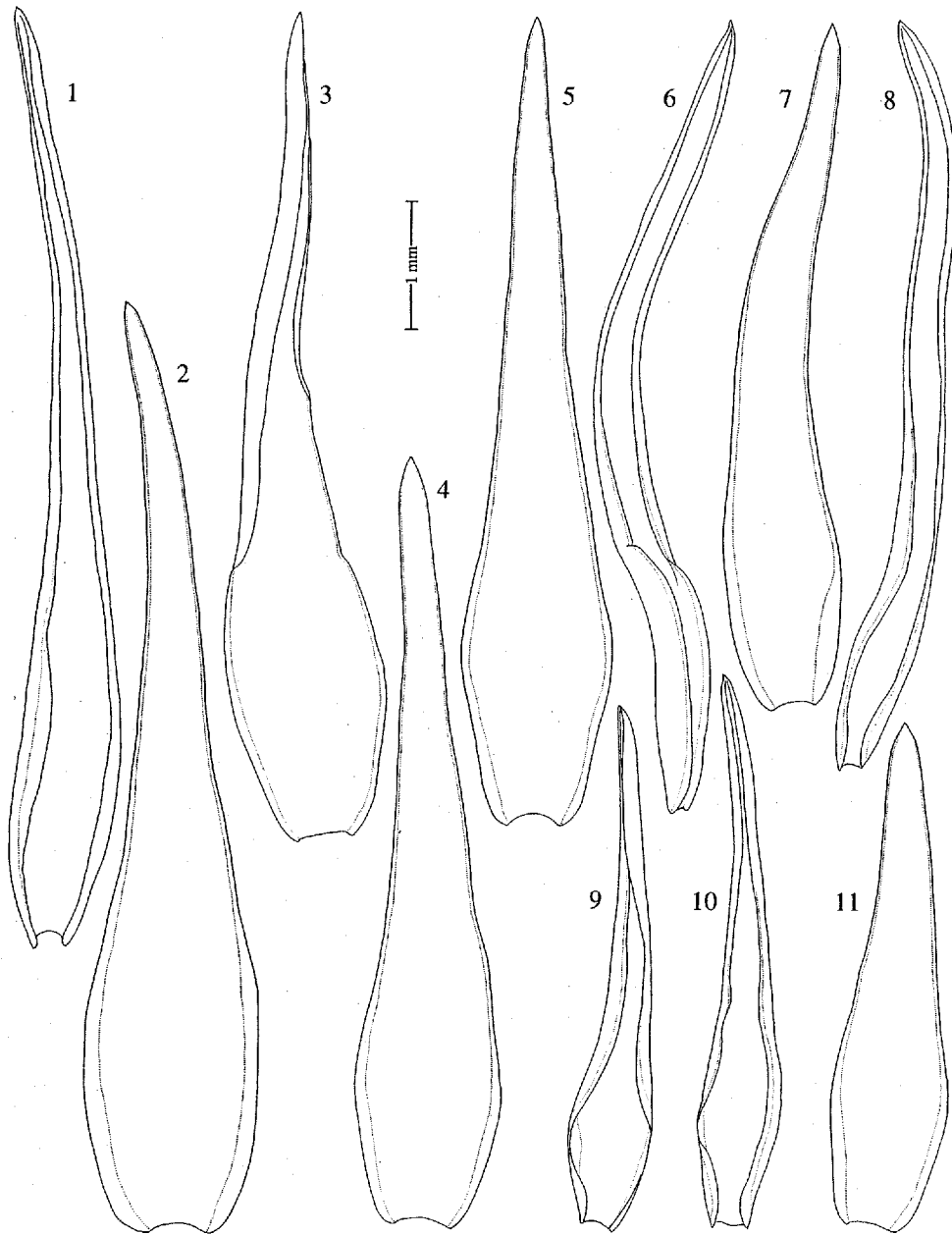


Figure CXII. *Leucobryum bowringii* Mitt. 1–11. Leaves (2, 4, 5, 7, 11, expanded). Figs. 1, 2, were drawn from holotype of *L. nagasakense* (H); 3, 4, from isotype of *L. yamatense* (NICH); 5, from holotype of *L. subsericeum* (BM); 6–8, from isosyntyne (Wright s. n.) of *L. stenobasis* (FI); 9–11, from isosyntyne (Gollan s. n.) of *L. stenobasis* (FI).

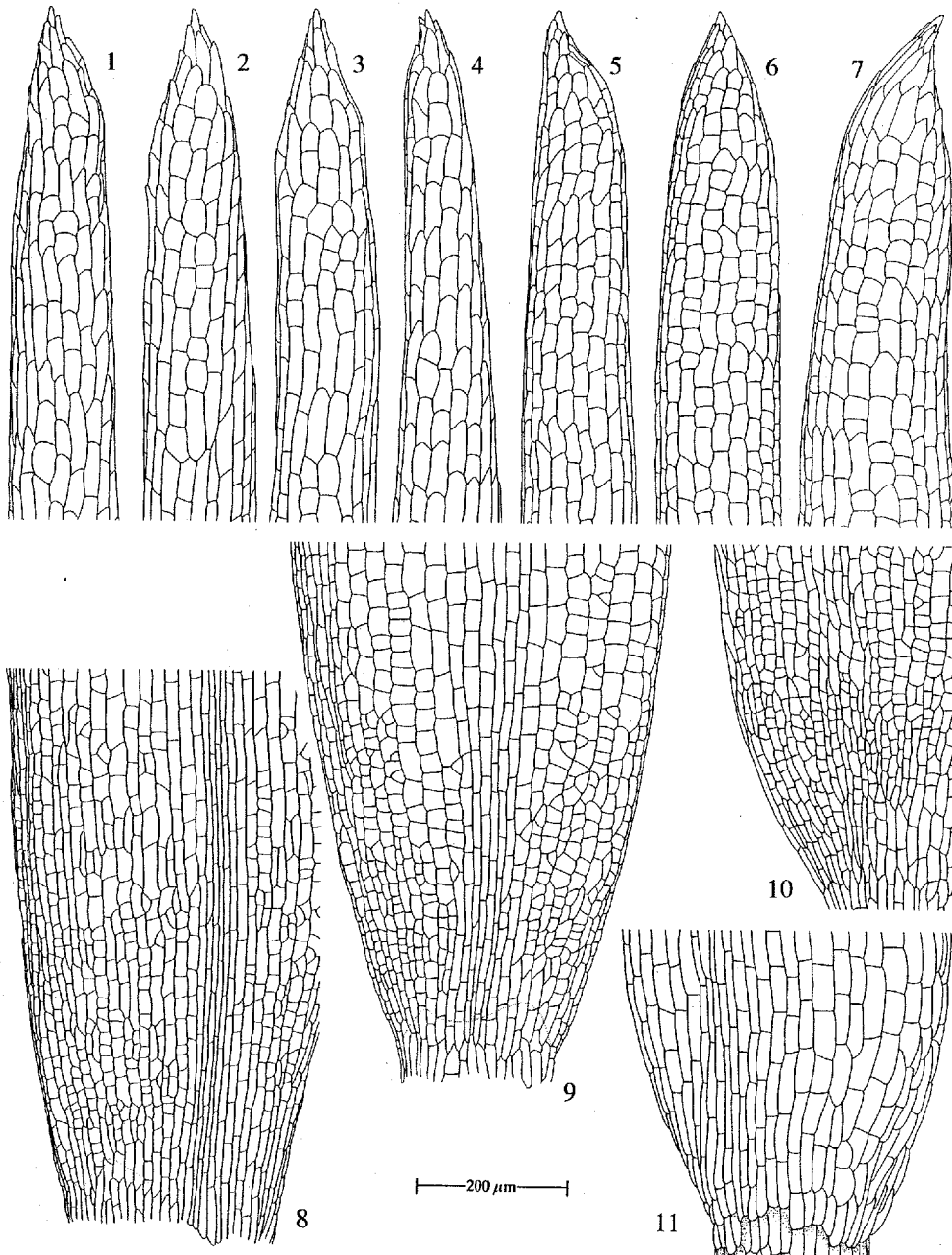


Figure CXIII. *Leucobryum bowringii* Mitt. 1-7. Leaf apices. 8-11. Leaf bases (abaxial view). Fig.1 was drawn from Faurie 62 labeled as *L. bowringii* f. *brevifolium* (KYO); 2, 3, from isotype of *L. yamatense* (NICH); 4, from isotype of *L. confine* (KYO); 5, 6, 8, from isosytype (Gollan s. n.) of *L. stenobasis* (FI); 7, 9, from isosytype (Wright s. n.) of *L. stenobasis* (FI); 10, from isotype of *Ochrobryum ceylanicum* (BM); 11, from lectotype of *L. bowringii* (NY).

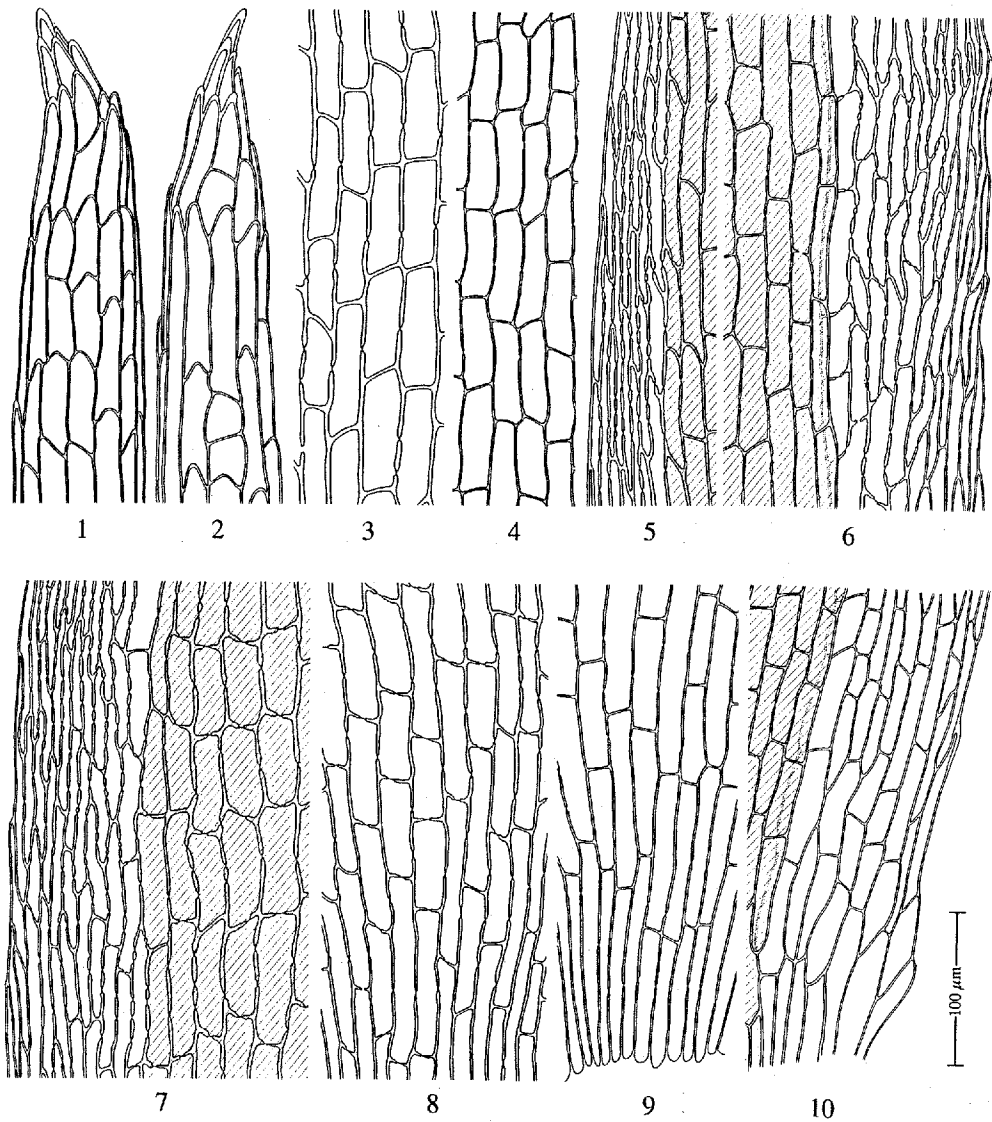


Figure CXIV. *Leucobryum bowringii* Mitt. 1, 2. Leaf apices. 3–5. Median cells of leaf (3, 5, abaxial view; 4, adaxial view). 6–10. Basal cells of leaf (7, 8, abaxial view; 6, 9, 10, adaxial view). All figures were drawn from lectotype of *L. bowringii* (NY).

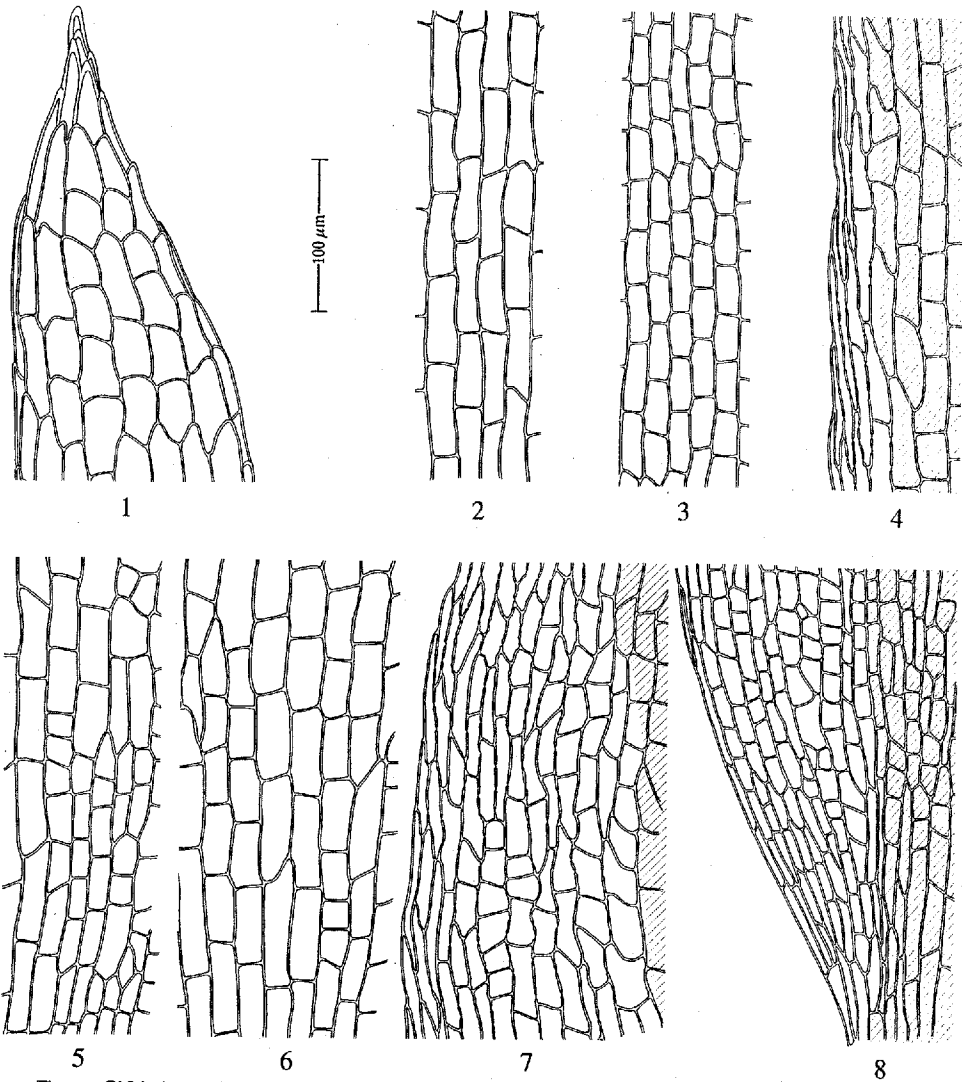


Figure CXV. *Leucobryum bowringii* Mitt. 1. Leaf apex. 2-4. Median cells of leaf (2, 4, abaxial view; 3, adaxial view). 5-8. Basal cells of leaf (5, 7, 8, abaxial view; 6, adaxial view). All figures were drawn from isotype of *Ochrobryum ceylanicum* (BM).

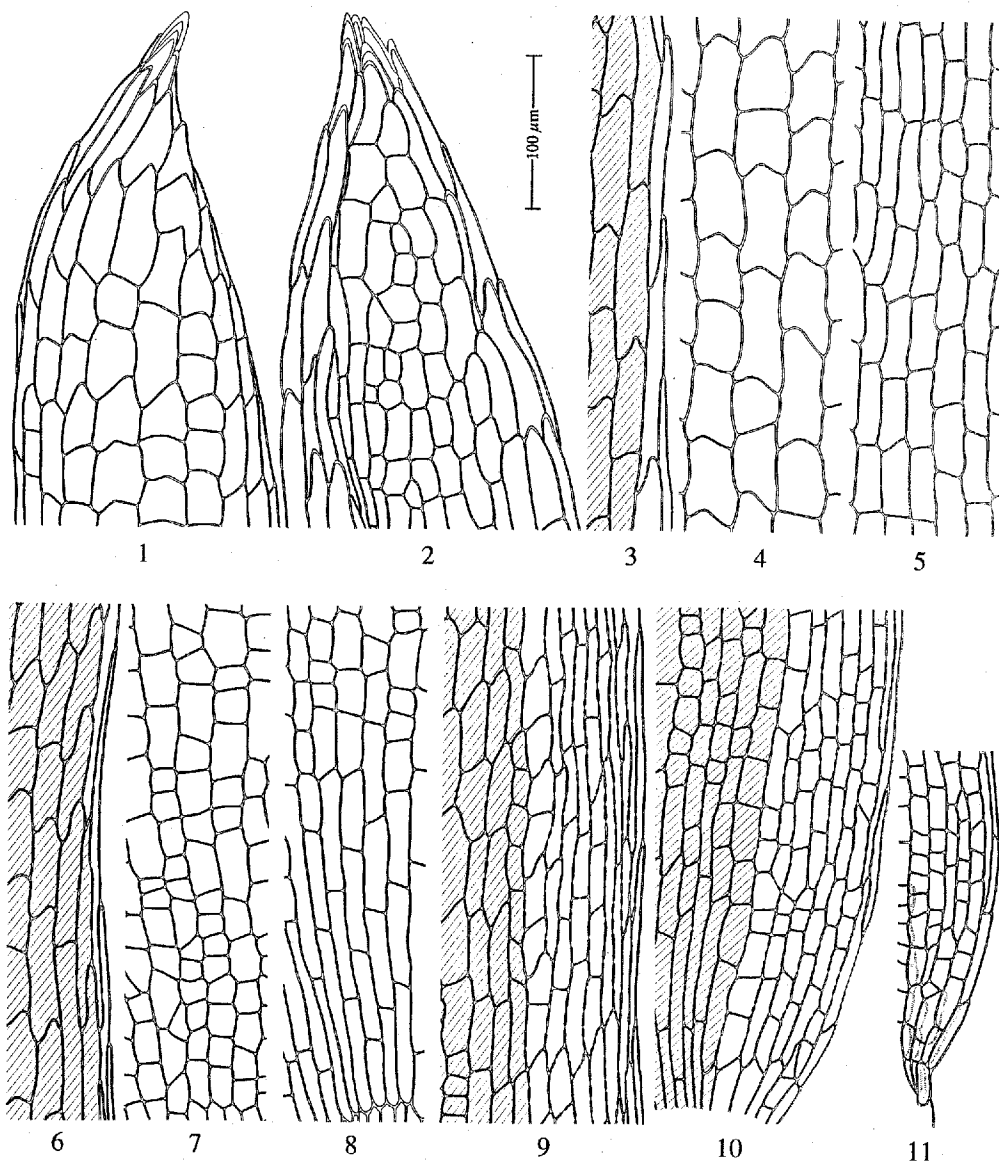


Figure CXVI. *Leucobryum bowringii* Mitt. 1, 2. Leaf apices (2, adaxial view). 3. Cells near leaf apex (abaxial view). 4-6. Median cells of leaf (4, 6, abaxial view; 5, adaxial view). 7-11. Basal cells of leaf (7, 11, abaxial view; 8-10, adaxial view). All figures were drawn from isosyntype (Wright s. n.) of *L. stenobasis* (FI).

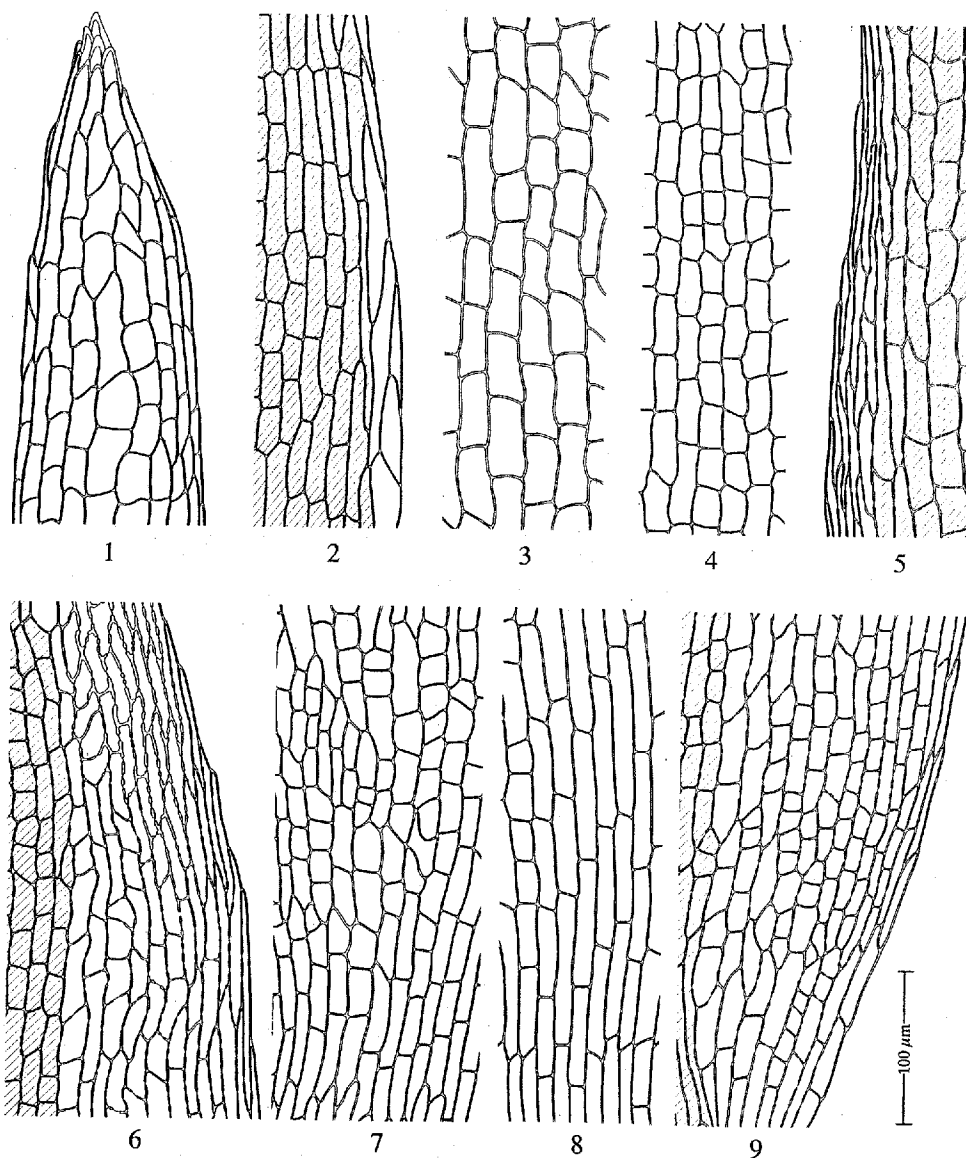


Figure CXVII. *Leucobryum bowringii* Mitt. 1. Leaf apex. 2. Cells near leaf apex (adaxial view). 3-5. Median cells of leaf (3, 5, abaxial view; 4, adaxial view). 6-9. Basal cells of leaf (7, abaxial view; 6, 8, 9, adaxial view; 6, from shoulder part). All figures were drawn from isosyntype (Gollan s. n.) of *L. stenobasis* (F).

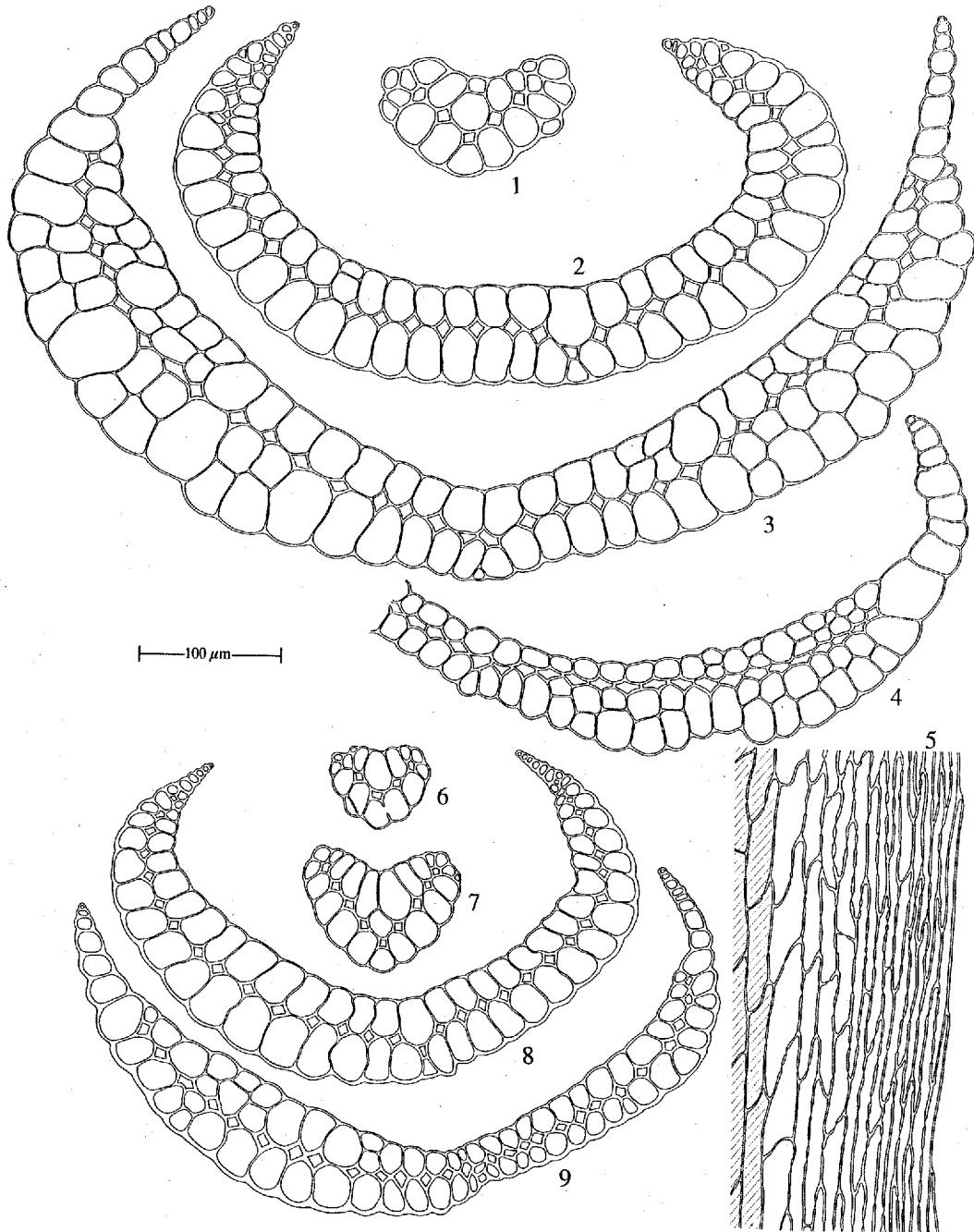


Figure CXVIII. *Leucobryum bowringii* Mitt. 1-4, 6-9. Cross-sections of leaves (1, 6, 7, apical; 2, 8, median; 3, 4, 9, basal portions). 5. Basal cells of leaf (abaxial view). Figs. 1-5 were drawn from holotype of *L. nagasakense* (H); 6-9, from lectotype of *L. bowringii* (NY).



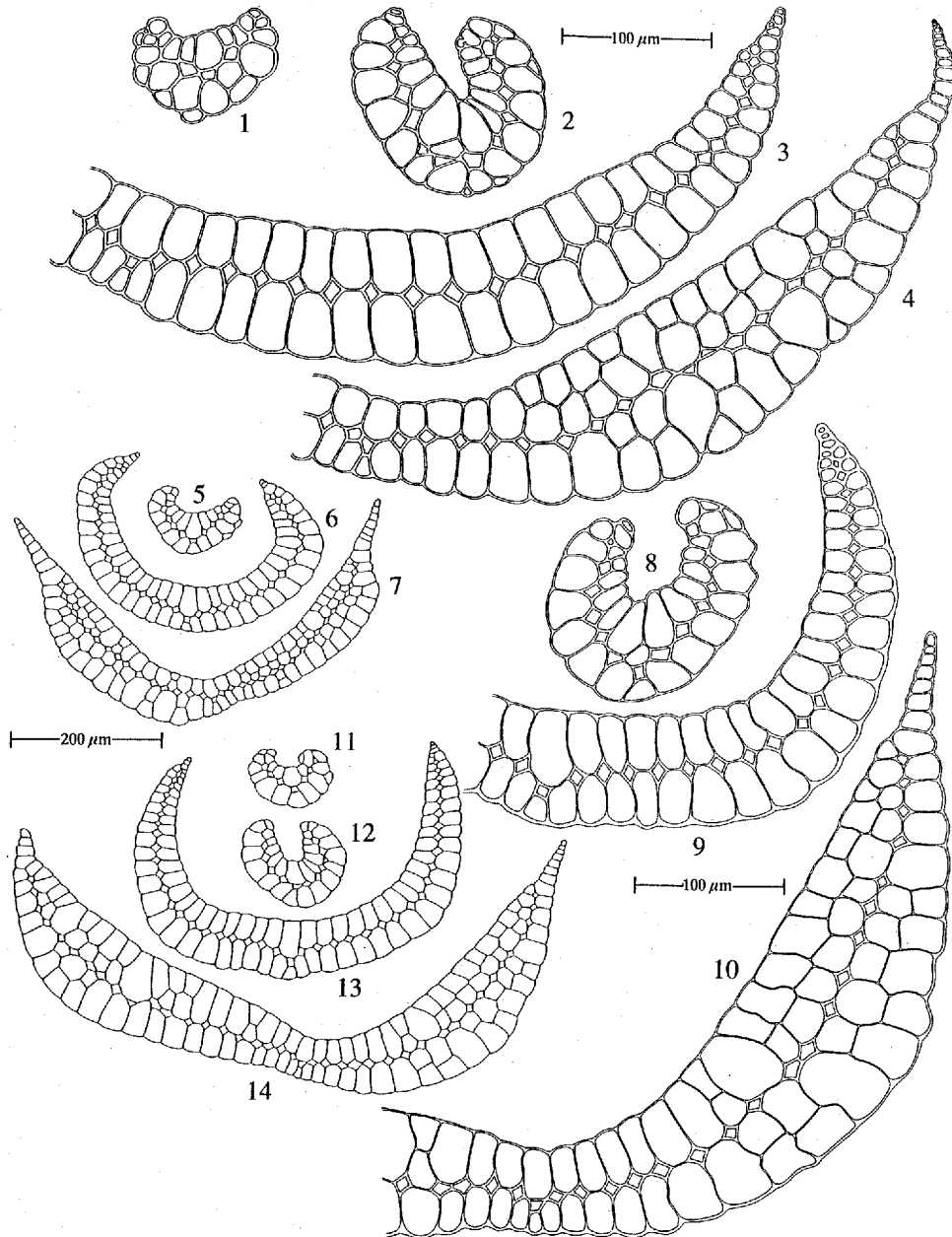


Figure CXIX. *Leucobryum bowringii* Mitt. 1-14. Cross-sections of leaves (1, 2, 5, 8, 11, 12, apical; 3, 6, 9, 13, median; 4, 7, 10, 14, basal portions). Figs. 1-4 were drawn from holotype of *L. subsericeum* (BM); 5-7, from isotype of *L. confine* (KYO); 8-14, from isotype of *L. yamatense* (NICH).

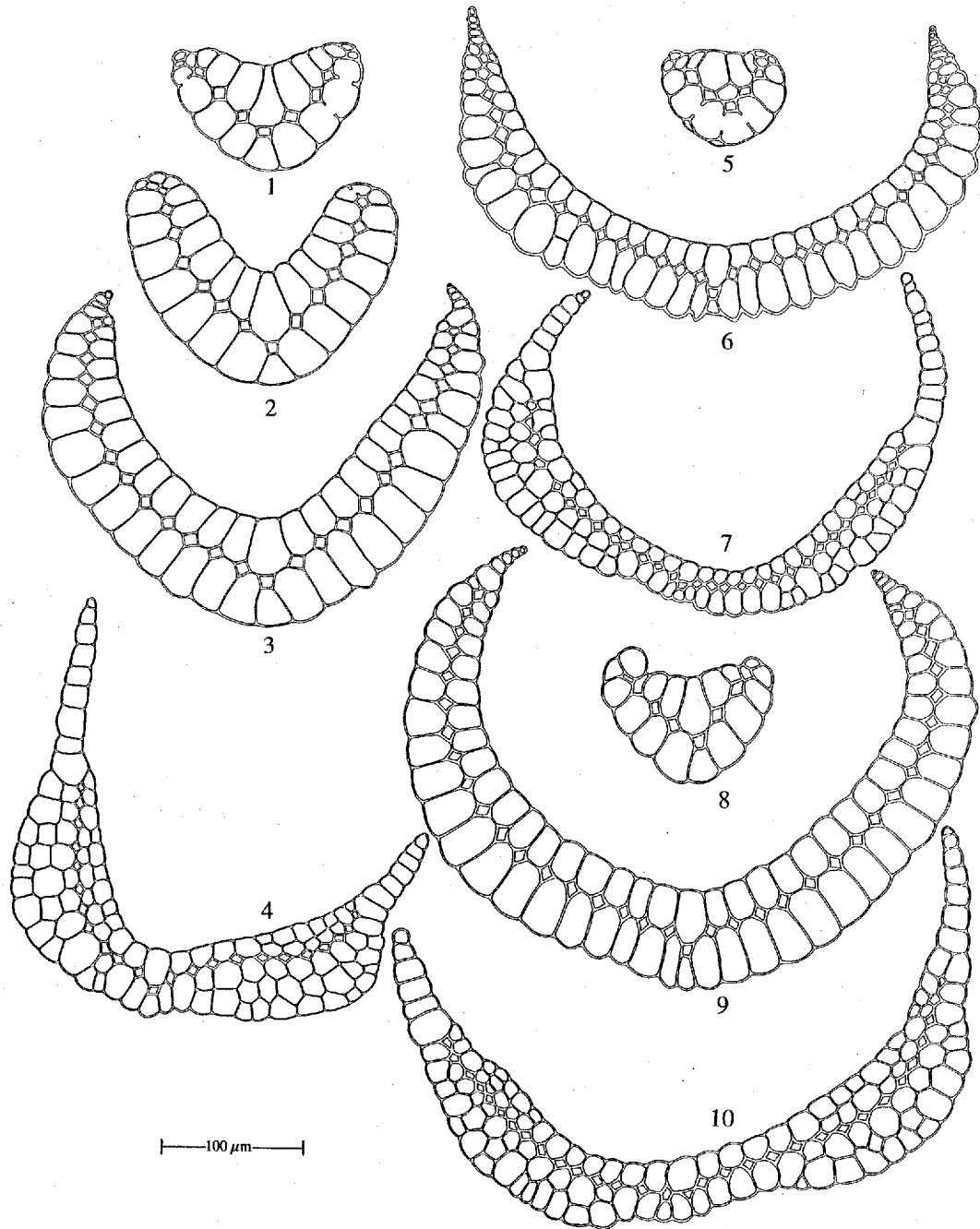


Figure CXX. *Leucobryum bowringii* Mitt. 1-10. Cross-sections of leaves (1, 2, 5, 8, apical; 3, 6, 9, median; 4, 7, 10, basal portions). Figs. 1-4 were drawn from isosyntype (Wright s. n.) of *L. stenobasis* (Fl); 5-7, from isosyntype (Gollan s. n.) of *L. stenobasis* (Fl); 8-10, from isotype of *Ochrobryum ceylanicum* (BM).

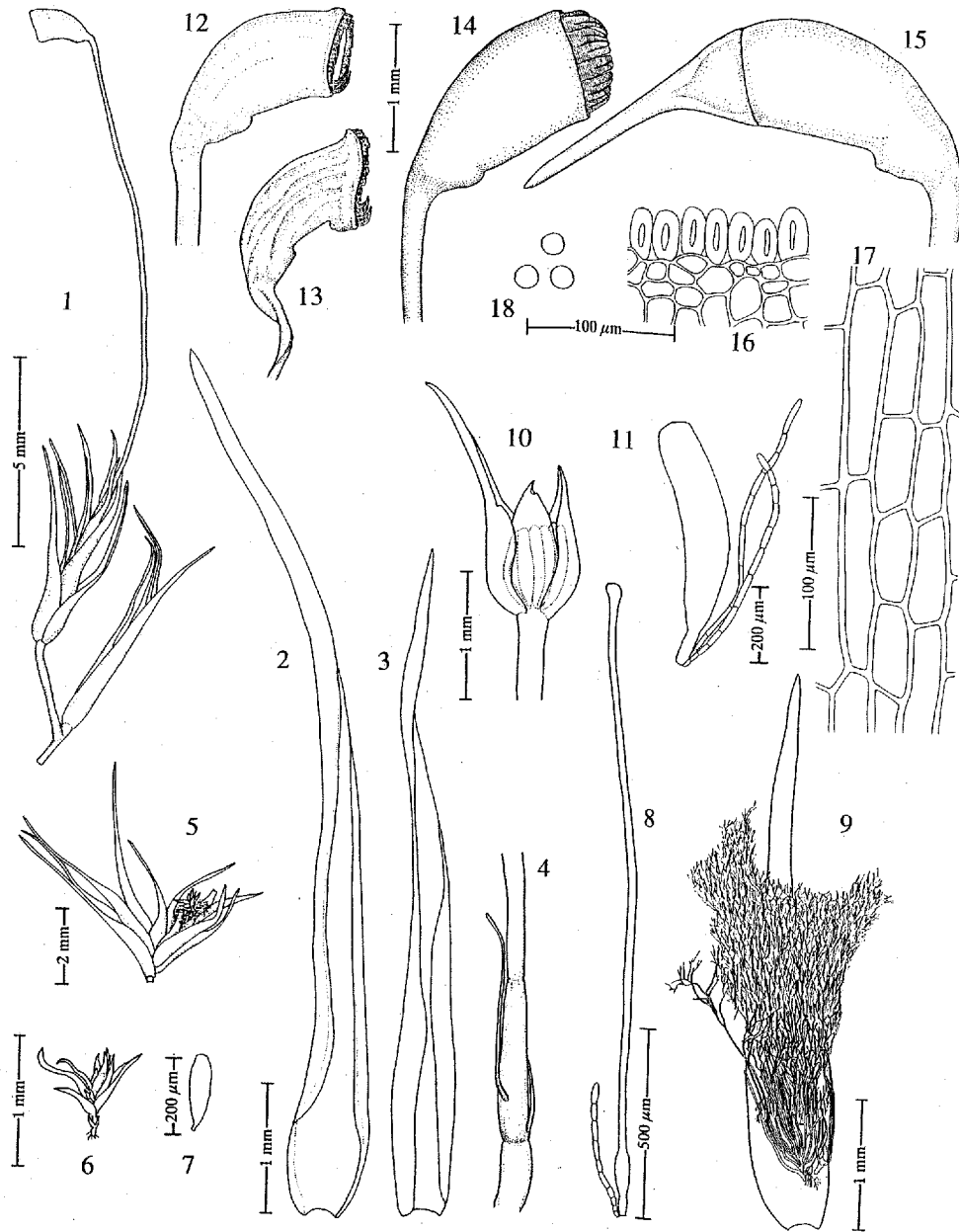


Figure CXXI. *Leucobryum bowringii* Mitt. 1. Perichaetium with sporophyte. 2. Stem leaf near perichaetium 1. 3. Inner perichaetial leaf from perichaetium 1. 4. Vaginula and archegonia. 5. Dwarf male plant growing on tomentum enclosed by perichaetial leaves. 6. Dwarf male plant. 7. Antheridium of dwarf male plant. 8. Archegonium. 9. Inner perichaetial leaf showing formation of tomentum on abaxial side. 10. Perigonium of normal male plant. 11. Antheridium of normal male plant. 12–15. Capsules. 16. Annulus. 17. Exothecial cells. 18. Spores. Figs. 1–7, 12, 13 were drawn from lectotype of *L. bowringii* (NY); 8, 10, 11, 15, from Yamaguchi 9313 (HIRO); 9, 14, 16–18, from Yamada 572 (NICH).

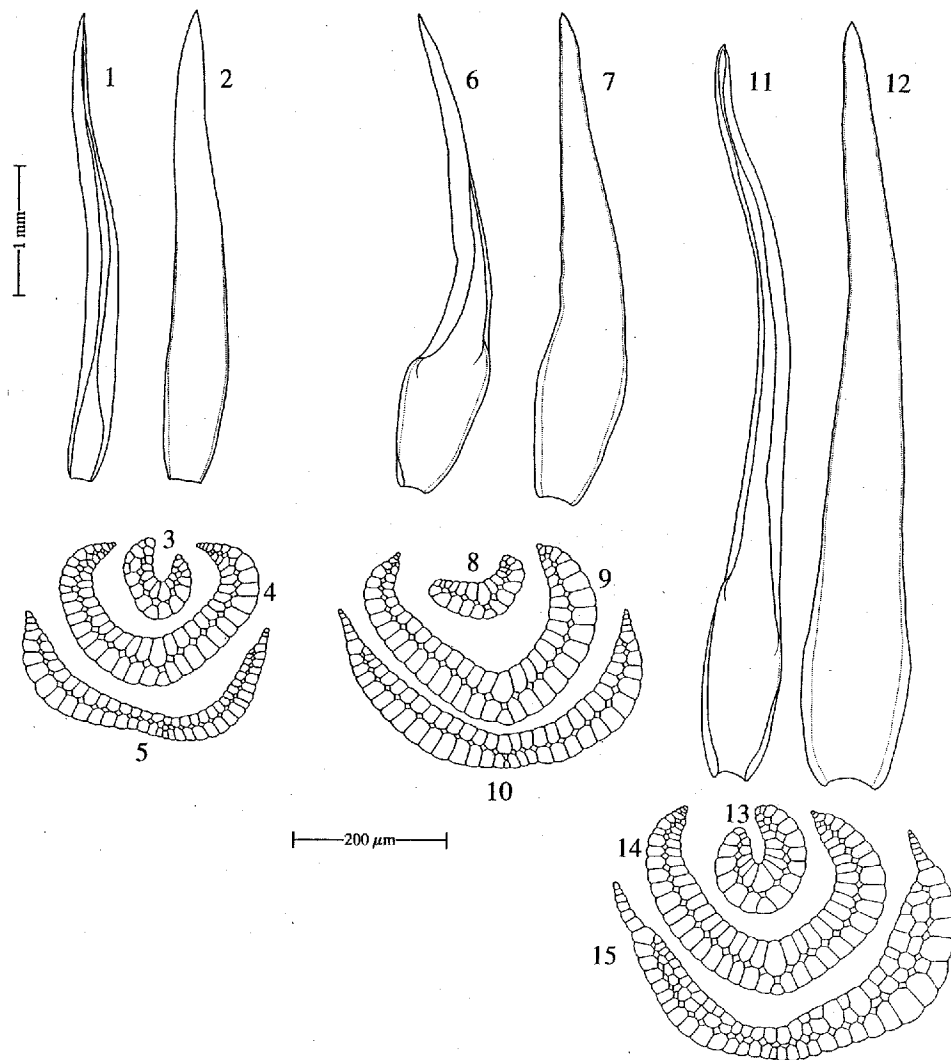


Figure CXXII. *Leucobryum bowringii* Mitt. 1–5. Deciduous leaves. 6–10. Ordinary leaves from branch. 11–15. Ordinary leaves from stem. 1, 2, 6, 7, 11, 12. Leaves (2, 7, 12, expanded). 3–5, 8–10, 13–15. Cross-sections of leaves (3, 8, 13, apical; 4, 9, 14, median; 5, 10, 15, basal portions). All figures were drawn from holotype of *L. deciduum* (PC).

(HIRO). Java, am Megamendong (Gedeh) an Bäumen, 1500 m alt., 25 Mar. 1899, Fleischer s. n. (Musci Archipelagi Indici ser. IV, no. 152, Leucobryum angustifolium Wils. n. var. macrophyllum Fl. in sched.) – isosyntype (HIRO).

Leucobryum deciduum Card. in Ren. & Card., Bull. Soc. R. Bot. Berg. 41(1): 42 (1905), syn. nov. Type: Vietnam, Tonkin, Dorr s. n. (in herb. Bescherelle, Leucobryum fragile Besch. in sched.) – holotype (PC).

Leucobryum stenobasis Card. in Ren. & Card., Bull. Soc. R. Bot. Belg. 41(1): 31 (1905), syn. nov. Type: India, N. W. Himalaya, below Kidarkanta, 9-10,000 ft. alt., 26 May 1881, Gollan s. n. – isosyntype (FI). Sri Lanka, Hinidoon Kanda hills, Oct. 1901, Wright 22 – isosyntype (FI).

Leucobryum confine Card., Beih. Bot. Centralbl. 19(2): 97, f. 4 (1905). Type: Taiwan, Kushaku, 6 June 1903, Faurie 111 – isotype (KYO).

Leucobryum subsericeum Dix., Hong Kong Natural. Suppl. 2: 6, f. 2a (1933), syn. nov. Type: China, Kwangtung, Canton, White Cloud Mountain, 800 ft. alt., 26 Dec. 1930, Herklots s. n. (in herb. Dixon, ref. no. 302 B) – holotype (BM).

Plants whitish tinged with yellow when dry, usually lustrous, forming tufts. Stems to 60 mm long with leaves; central strand well differentiated in cross-sections of stems. Leaves erect to widely spreading, flexuose and

contorted above, 3.7-11.0 x 0.7-1.4 mm, lanceolate to linear lanceolate, acute, gradually narrowed to subtubulous point from oblong base, smooth on abaxial surface, weakly scabrous at tips due to minutely projecting leucocysts; laminae consisting of 5-9 rows of quadrate to rectangular cells near base, bordered by 2-3 rows of linear cells; laminae and borders near leaf shoulders consisting of 7-12 rows of narrowly rectangular to linear cells with thick and porous walls, the differentiation between laminal cells and border cells indistinct; abaxial leucocysts of costae usually thick-walled (Fig. CXIV: 3, 4); in cross-sections near leaf base leucocysts in 1-2 (-3) cell layers on both sides; abaxially exposed walls of leucocysts usually thick-walled in cross-sections (Fig. CXVIII: 1-4, 6-9); abaxial leucocysts hardly decurrent on stems.

Dioicous. Male plants dimorphous; dwarf male plants small, usually growing on tomentum enclosed by perichaetial leaves, often detached from tomenta and growing on or among female shoots; normal male plants independent, as large as female plants; perigonia small, bud-like, terminal on main stems and subfloral innovations. Perichaetia terminal on main stems and subfloral innovations, rarely on elongated lateral branches; inner perichaetial leaves around mature sporophytes 0.5-0.9 times longer than ordinary leaves near the perichaetia; archegonia 1.2-1.8 mm long. Setae 10-20 mm

long. Capsules horizontal to inclined, ovoid to ellipsoid; urns 1.1-1.8 mm long, 0.6-1.1 mm wide. Annulus of 1 row of cells. Apices of peristome teeth divided to 2/3 of the length, ca. 0.73 mm long, ca. 0.12 mm wide at base. Spores 15-20  $\mu\text{m}$  in diameter.

Representative specimens examined: Japan, Japan, Honshu, Mie-ken, Ise Grand Shrine, Naigû, Nanzan, 12 Feb. 1961, Yamada 572 (NICH); Hoshu, Mie-ken, Watarai-gun, Omiya-cho, Takihara Shrine, 7 Jan. 1962, Yamada 729 (NICH); Kyushu, Yakushima Island, 400 m alt., June 1931(?), Kuwahara 841 (NICH); Ryukyu Islands, Okinawa Island, Mt. Yonaha, 210 m alt., 5 May 1986, Yamaguchi 9313 (HIRO). Taiwan, Taitum, 7 May 1903, Faurie 62 - duplicated original specimen of Leucobryum bowringii var. brevifolium Card., nom. nud. (KYO). China, Kwangtung, Ting-Wu Shan, 27 June 1980, Lin 104b (NICH); Hongkong, victoria Peak, Findlay Road, ca. 400 m alt., 13 June 1975, Touw 18898 (L). India, Mt. Khasia, Hooker and Thomson 1272, 1275 - paratypes of L. bowringii (NY). Sri Lanka, Kandy District, Knuckles, approach from Lebanon Estate, 12 Feb. 1978, Ruinard 12/98 (L). Thailand, Udawn, sandstone masive Phu(Mt.) Krading, 16°50'N 101°45'E, 1150-1200 m alt., 15 Jan. 1966, Touw 11074 (L). Cambodia, Province de Kampot, Poporkvil, ca. 1000 m alt., 4-6, Dec. 1964, Kira et al. 97 (HIRO). Vietnam, Prov. Hoa-binh, Montes Nui Bieu, 400 m alt., 5 Jan. 1966, Pócs 3147/a

(NICH). Philippines, Luzon, summit of Mt. Maquiling, 1000 m alt., 16 Dec. 1930, Herklots s. n., in herb. Dixon ref. no. 417a (L). Borneo, W Kalimantan, Gunung Palung nature Reserve, on Air Putih River, 20 km SE of Telukmelano, 1°15'S 110°05'E, 300-400 m alt., 17 Apr. 1985, Mori & Mitchell 17924 (L). Sulawesi, Mt. Roroka Timbu, summit, 0°30'S 119°30'-120°30'E, 2200 m alt., 15 May 1979, Balgooy 3357 (L). Sumatra, Mt. Korinchi, ravine of Sungai Kering, 2000 m alt., July 1956, Meijer B8853 (L). Java, Prov. Batavia, in monte Megamendong, ca. 1400 m alt., 5 Jan. 1894, Schiffner 10334 (L). Seram, Kecamatan Seram Utara, Sawai, Manusela National Park, along a trail between Wae Niniyoa and Wae Puo, ca. 1000 m alt., 3°00-03'S 129°14'E, 22 Jan. 1985, Akiyama 9634 (KYO, HIRO). New Guinea, Milne Bay District, Mt. Garatun, 4500 ft. alt., 11 June 1973, Cruttwell 60 (L). Solomon Islands, 20 July 1970, Robbins 4298 (L).

Habitat: On soil, humus, rocks and logs.

Distribution: Japan, Taiwan, China, Himalaya, India, Sri Lanka, Thailand, Cambodia, Vietnam, Malay Peninsula, Philippines, Borneo, Sulawesi, Sumatra, java, Seram, New Guinea, Solomon Islands.

The present species is characterized by (1) well differentiated central strand of stems, (2) lanceolate to linear lanceolate and usually lustrous leaves, (3) abaxial leucocysts with outer thick walls, (4) thick-walled laminal



and border cells at leaf shoulders, (5) perichaetia usually terminal on main stems or subfloral innovation, and (6) long archegonia up to 1.8 mm long.

The central strand of stems is sometimes weak or absent in juvenile plants of the present species. Plants of type specimens of L. stenobasis seem to be juvenile and have no central strand in stems (Fig. CX: 12, 13), but they are identical with L. bowringii because they have thick-walled marginal cells of leaves.

L. sumatranum is closely related to the present species, but differs in having long leaves (10.0-18.0 mm) and perichaetia terminal on short lateral branches.

L. sericeum is also similar to the present species in general appearance, but clearly differentiated in having scabrous abaxial surface of leaves and perichaetia usually terminal on short lateral branches.

11. Leucobryum sumatranum Broth. ex Fl. (Fig. CXXIII, CXXIV, CXLII: 5)

Musci Fl. Buitenzorg 1: 149 (1904). Type: Sumatra, Tindjaulaet, 3000 ft. alt, Nov. 1891, Micholitz 63 - holotype (FH), isotype (BM).

Leucobryum pulchrum Broth., Mitteil. Inst. Allg. Bot. Hamburg 7: 118 (1928). Type: Borneo, Bukit Raja, 1400 m

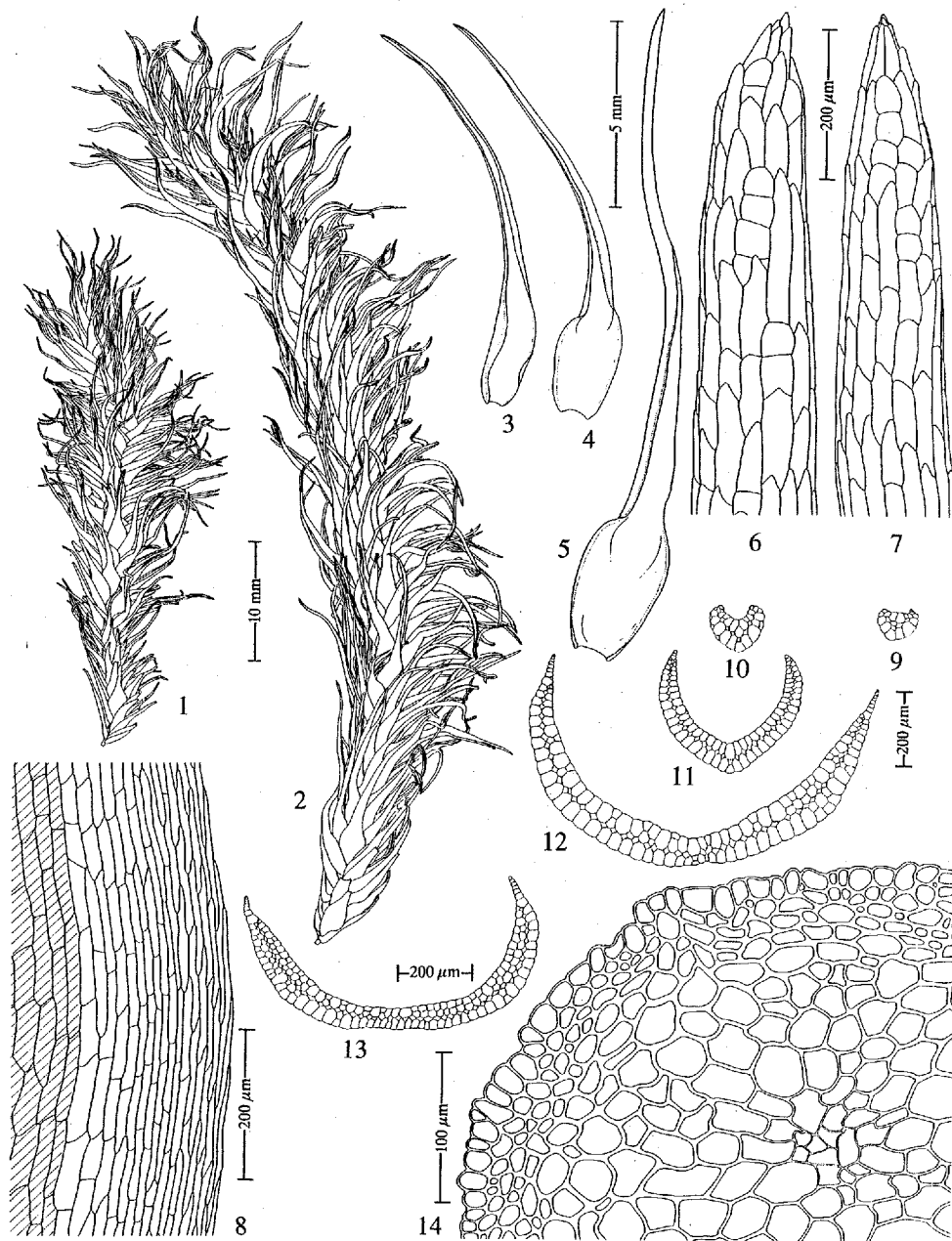


Figure CXXIII. *Leucobryum sumatranum* Broth. ex Fl. 1, 2. Plants. 3-5. Leaves. 6, 7. Leaf apices. 8. Basal cells of leaf (adaxial view). 9-13. Cross-sections of leaf (9, 10, apical; 11, median; 12, 13, basal portions). 14. Cross-section of stem. Figs. 1, 3, 4, 7, 9-14 were drawn from holotype of *L. pulchrum* (H); 2, 5, 6, from holotype of *L. sumatranum* (FH); 8, from Wilde & Wilde-Duyfjes 15066A (L).



Figure CXXIV. *Leucobryum sumatranum* Broth. ex Fl. 1. Branching showing position of perichaetia, and dwarf male plants growing on tomenta enclosed by perichaetial leaves. 2, 4. Dwarf male plants. 3, 5. Branching of dwarf male plants 2 and 4 respectively, showing position of perigonia. 6. Perichaetium with sporophyte. 7, 8. Stem leaves near perichaetium 6 (8, expanded). 9-13. Perichaetial leaves [expanded; numbers show the order of perichaetial leaves from the innermost leaf (number 13)]. 14. Perichaetium. 15. Antheridium. 16. Archegonium. All figures were drawn from Wilde & Wilde-Duyfjes 15066A (L).

alt., 21 Dec. 1924, Winkler 3196 - holotype (H), isotype (L).

Plants robust, whitish tinged with yellow when dry, usually lustrous, forming tufts. Stems to 120 mm long with leaves; central strand well differentiated in cross-sections of stems. Leaves erect to widely spreading, somewhat falcate secund, flexuose and contorted above; 10.0-18.0 x 1.5-2.5 mm, linear lanceolate, gradually narrowed to subtubulous point from oblong to ovate base, smooth on abaxial surface, weakly scabrous at tips due to minutely projecting leucocysts; anatomical structure of leaves similar to those of L. bowringii except for size and number of cell rows at marginal parts; laminae and borders at shoulder parts in 7-18 rows of narrowly rectangular to linear cells.

Dioicous. Dwarf male plants growing on tomentum enclosed by perichaetial leaves; independent normal male plants not observed. Perichaetia terminal on short lateral branches; inner perichaetial leaves around mature sporophytes ca. 0.3 times longer than ordinary leaves near the perichaetia; archegonia ca. 1.5 mm long. Setae 18-23 mm long. Capsules horizontal to inclined, ovoid to ellipsoid; urns 1.8-2.1 mm long, 0.9-1.0 mm wide.

Representative specimens examined: Payaly Peninsula, Pahang, Cemeran Highlands, 4800 ft. alt., 3 Apr. 1930,

Holttum 23381 (L); Selangor, G. Nuang, E. of Kuala Lumpur, ca. 4900 ft. alt., 23 Mar. 1960, Meijer B12226, B12277 (L). Borneo, Sarawak, 4th Division, Gunong Mulu National Park, G. Mulu, 4°05'N 114°55'E, 1320-1400 m alt., 27 May 1978, Touw 20909 (L); ditto, ca. 1900 m alt., 30 May 1978, Touw 21097 (L). Sumatra, Atjeh, Gunung Leuser Nature Reserve, Climbing Gunung Bandahara, ca. 6 km NE of Kampung Seldok (Alas Valley), ca. 25 km N of Kutatjane, ca. 1900 m alt., 20 Feb. 1975, Wilde & Wilde-Duyfjes 15066A (L).

Habitat: On humus and soil in mossy montane regions.

Distribution: Malay Peninsula, Borneo, Sumatra.

The present species is characterized by (1) robust plants, (2) long, linear and lustrous leaves, and (3) perichaetia terminal on short lateral branches.

This curious and beautiful species is quite similar to L. bowringii in many aspects, except for the robust habits and the formation of perichaetia terminal on short lateral branches.

12. Leucobryum sericeum Broth. ex Geh. (Fig. CXXV-CXXVII, CXLII: 3)

Biblioth. Bot. 44: 26, t. 4 (1898) = Leucobryum bowringii var. sericeum (Geh.) Dix., Ann. Bryol. 5: 24 (1932). Type: Borneo, Mt. Paojem, 1876, Teysmann (sub no. 11140) - holotype (H).

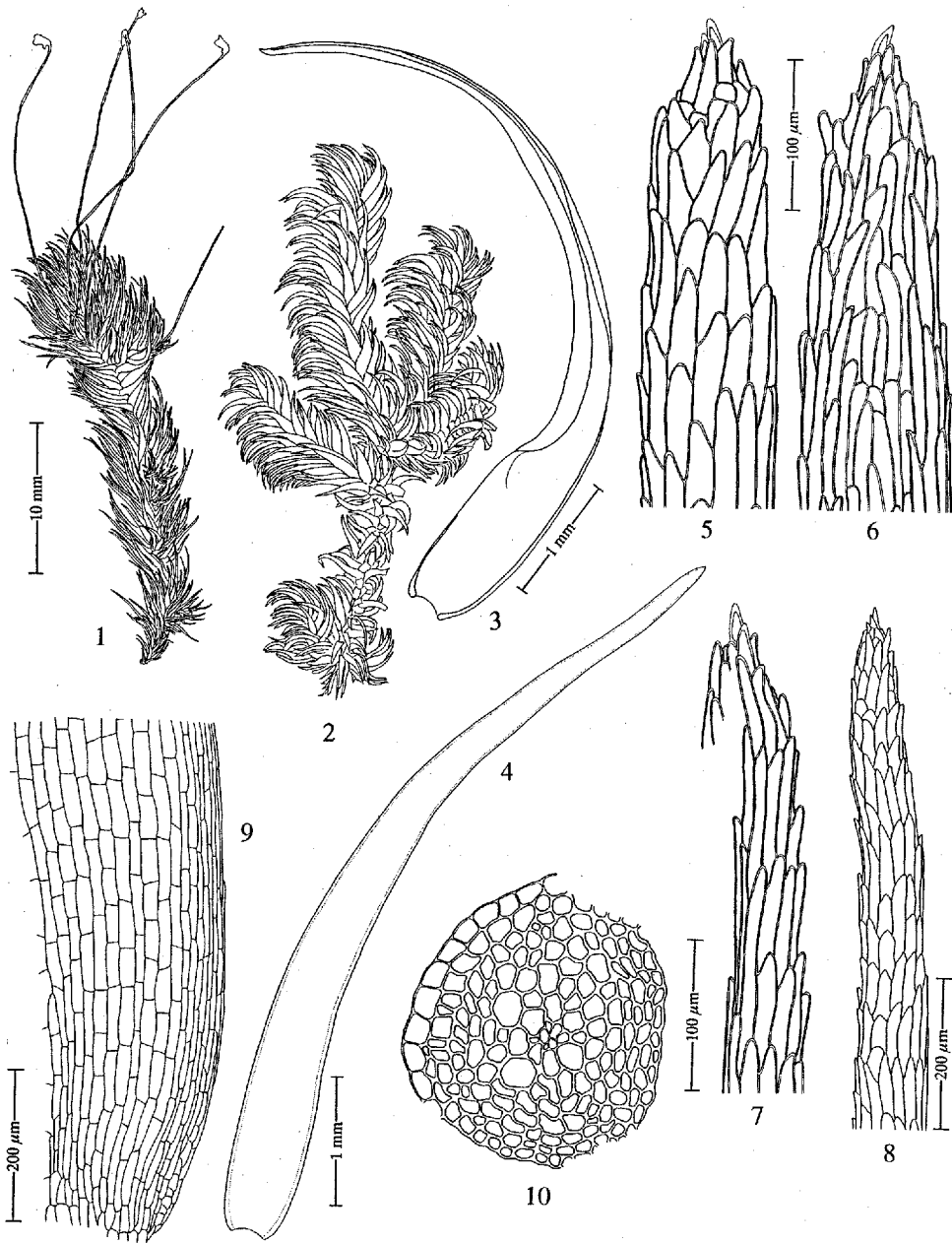


Figure CXXV. *Leucobryum sericeum* Broth. ex Geh. 1, 2. Plants. 3, 4. Leaves (4, expanded). 5-8. Leaf apices (6, adaxial view; 7, lateral view). 9. Leaf base (abaxial view). 10. Cross-section of stem. Figs. 1 was drawn from Deguchi 22292 (KOCHI); 2-10, from holotype of *L. sericeum* (H).

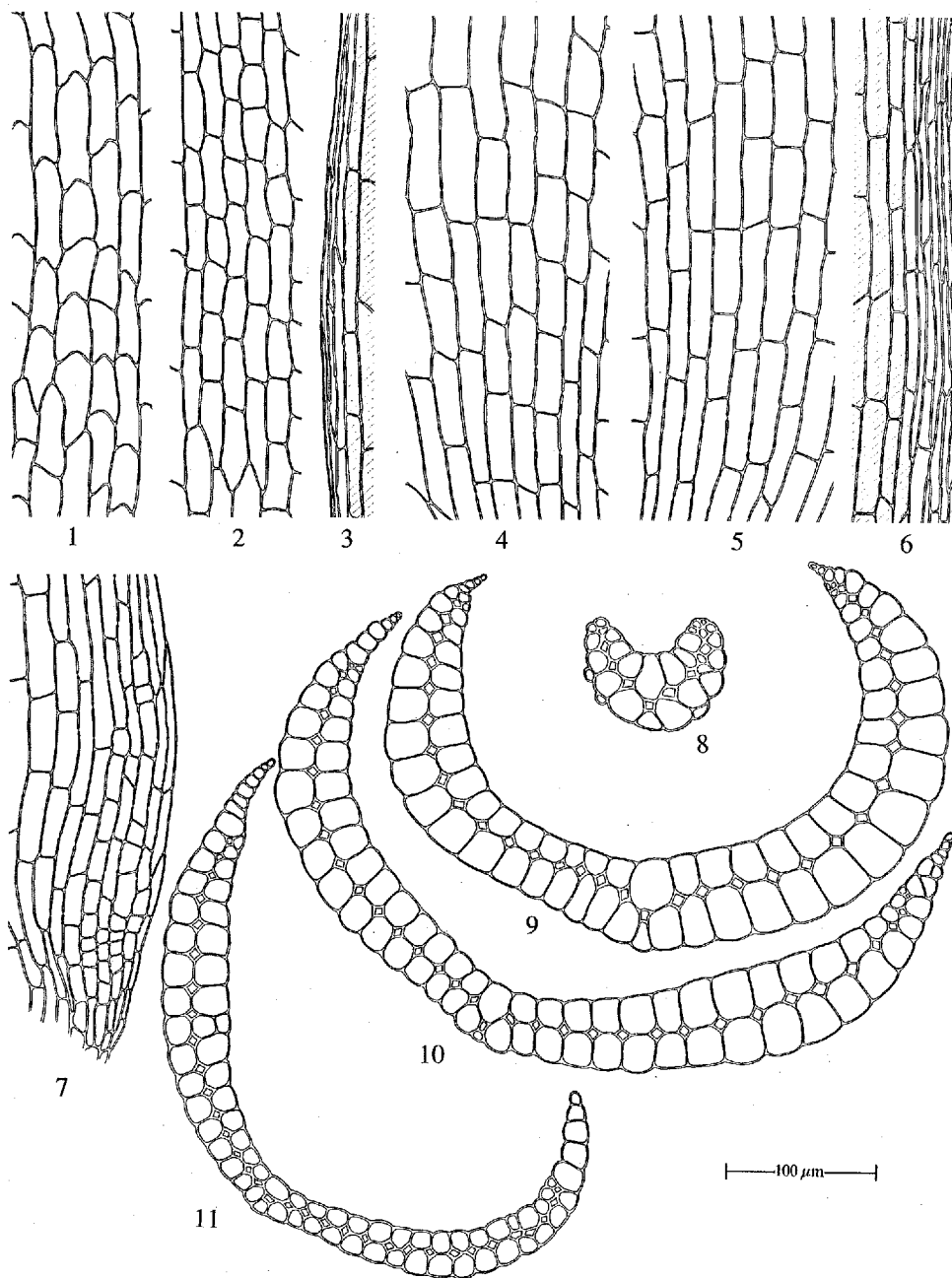


Figure CXXVI. *Leucobryum sericeum* Broth. ex Geh. 1-3. Median cells of leaf (1, 3, abaxial view; 2, adaxial view). 4-7. Basal cells of leaf (4, 7, abaxial view; 5, 6, adaxial view). 8-11. Cross-sections of leaf (8, apical; 9, median; 10, 11, basal portions). All figures were drawn from holotype of *L. sericeum* (H).



Figure CXXVII. *Leucobryum sericeum* Broth. ex Geh. 1, 2. Branching showing position of perichaetia (1, dwarf male plants growing on tomenta enclosed by perichaetial leaves). 3. inner perichaetial leaf showing formation of tomentum on abaxial side. 4-6. Rhizoid on abaxial side of inner perichaetial leaf, which forms tomentum. 7. Stem leaf. 8-10. Perichaetial leaves [numbers show the order of perichaetial leaves from the innermost leaf (number 10)]. 11. Archegonium. 12. Paraphysis. Figs. 1, 7-10 were drawn from Deguchi 22292 (KOCHI); 2-6, from holotype of *L. sericeum* (H).



Plants whitish when dry, forming compact cushions. Stems to 35 mm long with leaves; central strand well differentiated in cross-sections of stems. Leaves strongly or slightly falcate secund; 6.5-7.4 x 0.5-0.7 mm, (shape), gradually narrowed to subtubulous point from oblong base, papillosely prorate from the apex to 1/10 of the leaf length on abaxial surface; laminae and borders consisting of 5-8 rows of narrowly rectangular to linear cells near base, the differentiation between laminal cells and border cells indistinct; in cross-sections near leaf base leucocysts almost in homostrosic, sometimes 2 cell layers on adaxial side; abaxial leucocysts hardly decurrent on stems.

Dioicous. Dwarf male plants growing on tomentum enclosed by perichaetial leaves; independent normal male plants not observed. Perichaetia usually terminal on short lateral branches, sometimes terminal on stems; inner perichaetial leaves around mature sporophytes almost in half length of the ordinary leaves near the perichaetium; archegonia 0.9-1.0 mm long. Setae 23-24 mm long. Capsules inclined to horizontal, ovoid to ellipsoid; urns 1.2-1.3 mm long, ca. 0.8 mm wide.

Representative specimens examined: Philippines, Romblon, Romblon Prov., NW slope of Mt. Guitinguitin, near Barrio Jao-Asan, Sibuyan Island, 100-200 m alt., 12 Mar. 1980, Deguchi 22292 (KOCHI). Borneo, Sarawak, Kuching, Bako

Nat. Park, 1960, Meijer B12396 (L). Sulawesi, Powerstation Larona, 24 km from Malili, direction Soroako, 2°15'-3°S 121°-121°45'E, 18 June 1979, Hennipman 5924B (L). Seram, Kecamatan Kairatu, Tihulale, en route from the upper elevation to the top of Gunung(Mt.) Totaniwel, 3°29'-31'S 128°30'E, 1100 m alt., 19 Aug. 1986, Akiyama 15833 (KYO, HIRO). Ambon, Liang, 3°31'S 128°18'E, 340 m alt., 13 July 1986, Akiyama 14251 (KYO, HIRO). Aru Islands, P. Wokam, Dosinamalaoe, 26 May 1938, Buwalda 5056 (L). New Guinea, Sorong, 15 Jan. 1950, Hellendoorn 93A (L).

Habitat: Usually on rotten logs, occasionally on tree trunks or tree base.

Distribution: Philippines, Borneo, Sulawesi, Seram, Ambon, Aru Islands, New Guinea.

The present species is characterized by (1) differentiated central strand of stems, (2) falcate linear leaves, (3) papillosely prorate abaxial surface of leaves at apical parts, (4) nearly homostrosic construction at leaf bases, and (5) perichaetia usually terminal on short lateral branches.

Because of the linear leaves the present species had been treated as L. bowringii var. sericeum by Dixon (1932b), or as a synonym of L. bowringii by Enroth (1989). However, L. sericeum and L. bowringii are clearly and easily

distinguished from each other by the proration of apical parts of leaves and the position of perichaetia.

13. Leucobryum sanctum (Brid.) Hampe (Fig. CXXVIII-CXXXIII, CXL: 3)

Linnaea 13: 42 (1839).

Basionym: Dicranum glaucum Hedw. var. sanctum Brid., Bryol. Univ. 1: 811 (1827). Type: Java, Blume s. n. – holotype (B).

Leucobryum auriculatum C. Müll. in Geh., Biblioth. Bot. 13: 2 (1889). Type: New Guinea, Fly River (Branch), Bauerlen (sub no. 149) – holotype (not seen).

Leucobryum papuense Par., Ind. Bryol.: 752 (1896). Type: New Guinea, 23 June 1875, Naumann s. n. – lectotype (H).

Plants whitish tinged with brown when dry, forming loose tufts. Stems to 70 mm long with leaves; central strand well differentiated in cross-sections of stems, the central strands consisting thin-walled small cells and surrounded with 2-3 rows of thin-walled large cells. Leaves widely spreading, somewhat squarrose (Fig. CXXVIII: 5); 5.3-7.1 x 1.0-1.5 mm, narrowly lanceolate to lanceolate, gradually narrowed to subtubulous point from oblong and clearly keeled base, acute to bluntly mucronate, papillose prorate from the apex to 1/10 of the leaf length on abaxial

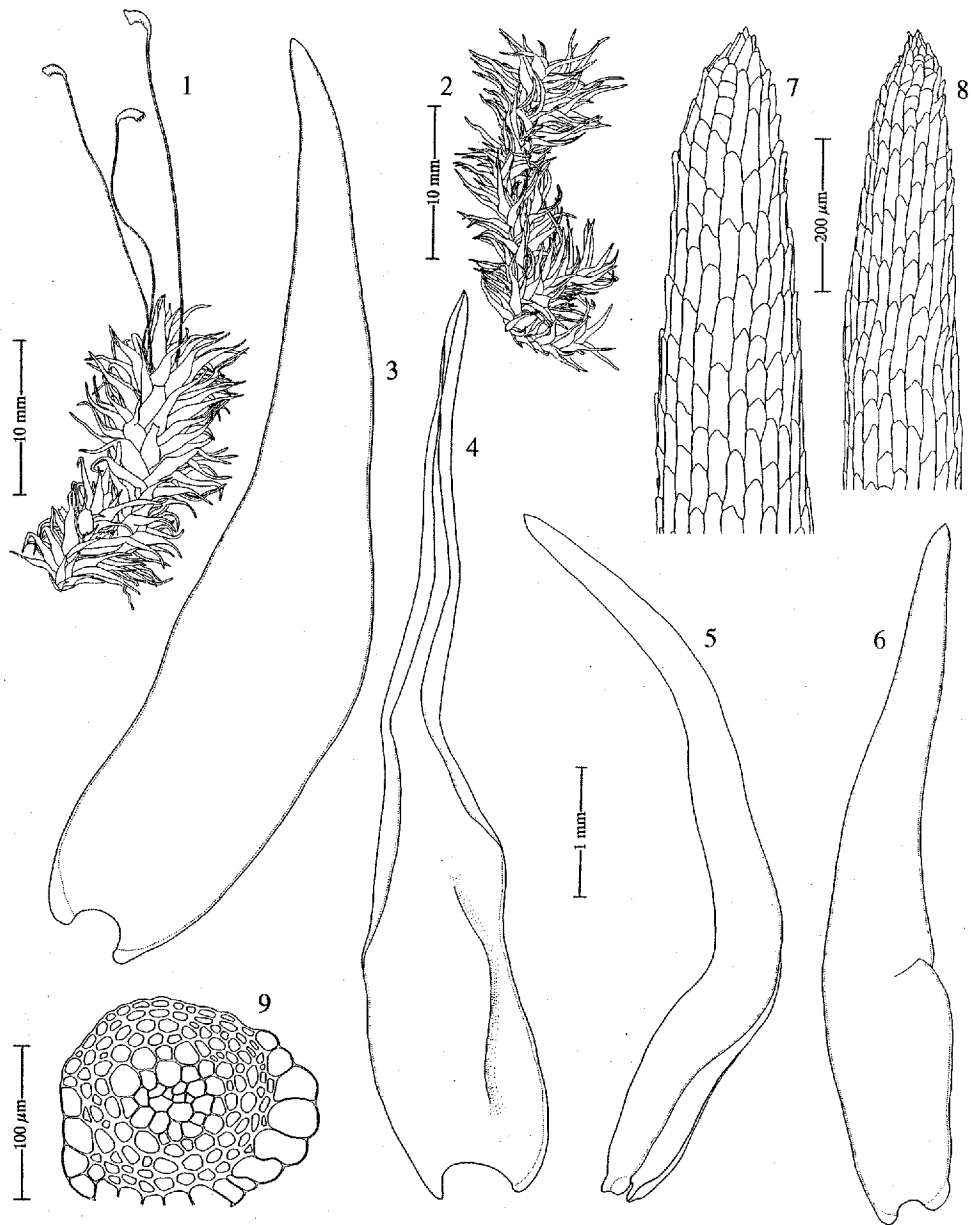


Figure CXXVIII. *Leucobryum sanctum* (Brid.) Hampe. 1, 2. Plants. 3–6. Leaves (3, 6, expanded). 7, 8. Leaf apices. 9. Cross-section of stem. Figs. 1, 4, 8 were drawn from holotype of *Dicranum glaucum* var. *sanctum* (B); 2, 5–7, 9, from lectotype of *L. papuense* (H); 3, from Hale & Banaag 25749 (NICH).

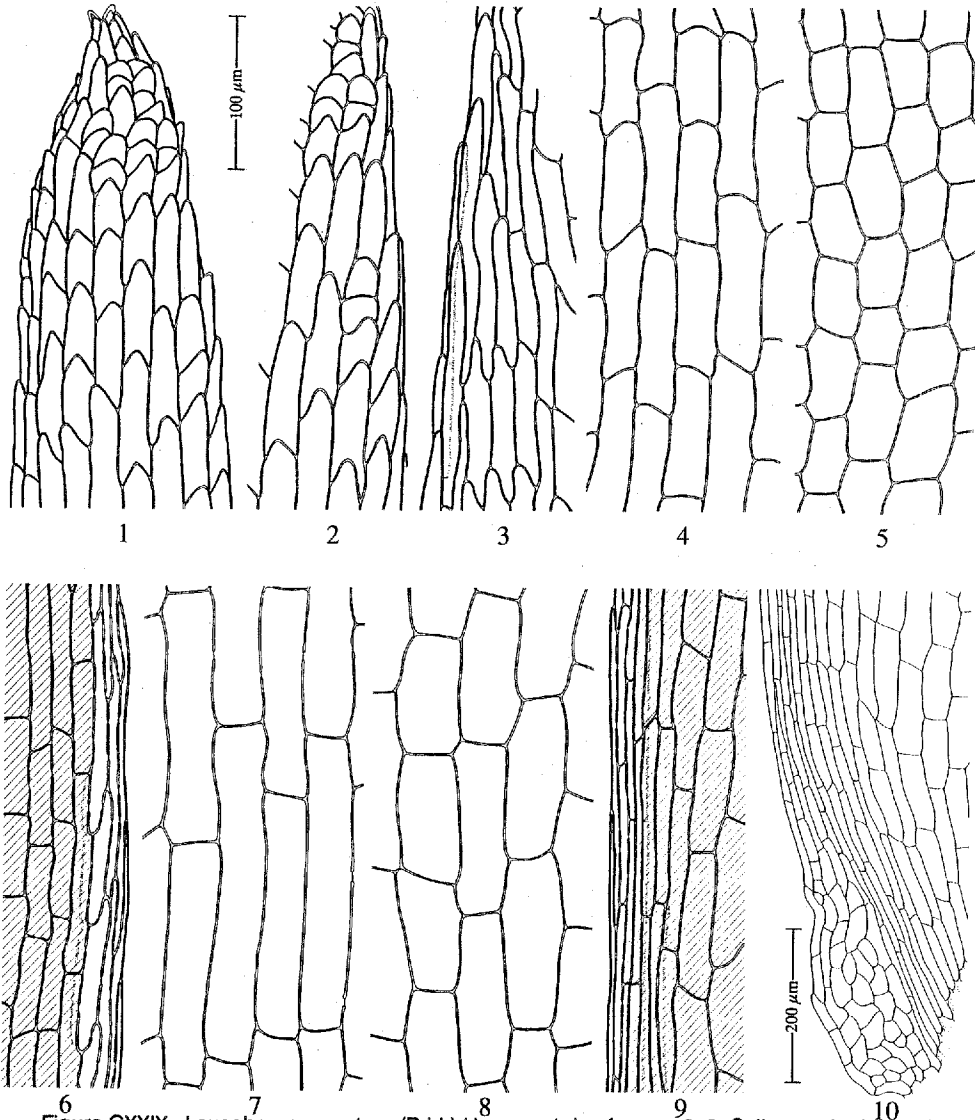


Figure CXXIX. Leucobryum sanctum (Brid.) Hampe. 1. Leaf apex. 2, 3. Cells near leaf apex (2, abaxial view; 3, adaxial view). 4-6. Median cells of leaf (4, 6, abaxial view; 5, adaxial view). 7-10. Basal cells of leaf (7, abaxial view; 8-10, adaxial view). All figures were drawn from holotype of Dicranum glaucum var. sanctum (B).

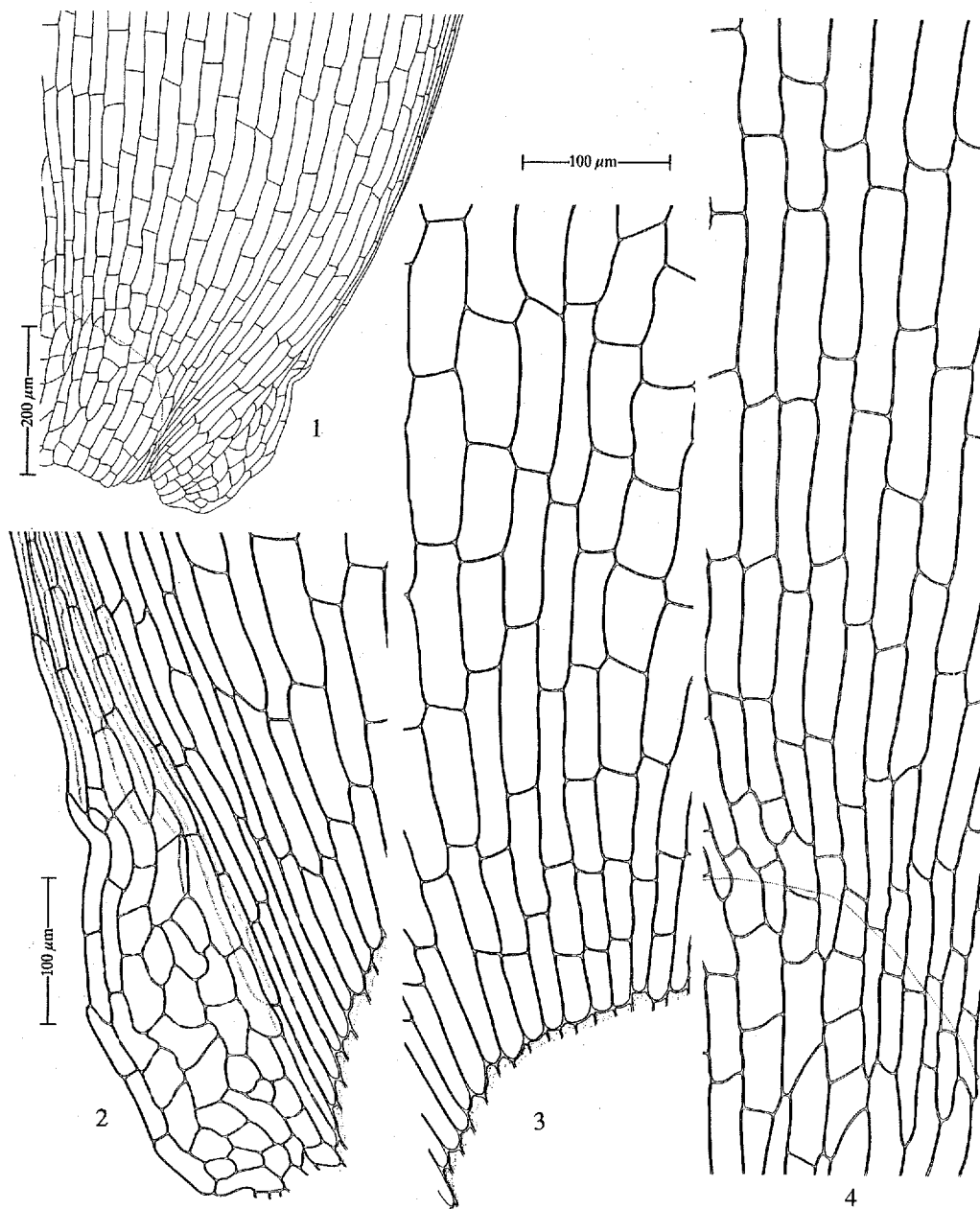


Figure CXXX. *Leucobryum sanctum* (Brid.) Hampe. 1–4. Basal cells of leaf (1, 4, abaxial view; 2, 3, adaxial view). All figures were drawn from holotype of *Dicranum glaucum* var. *sanctum* (B).

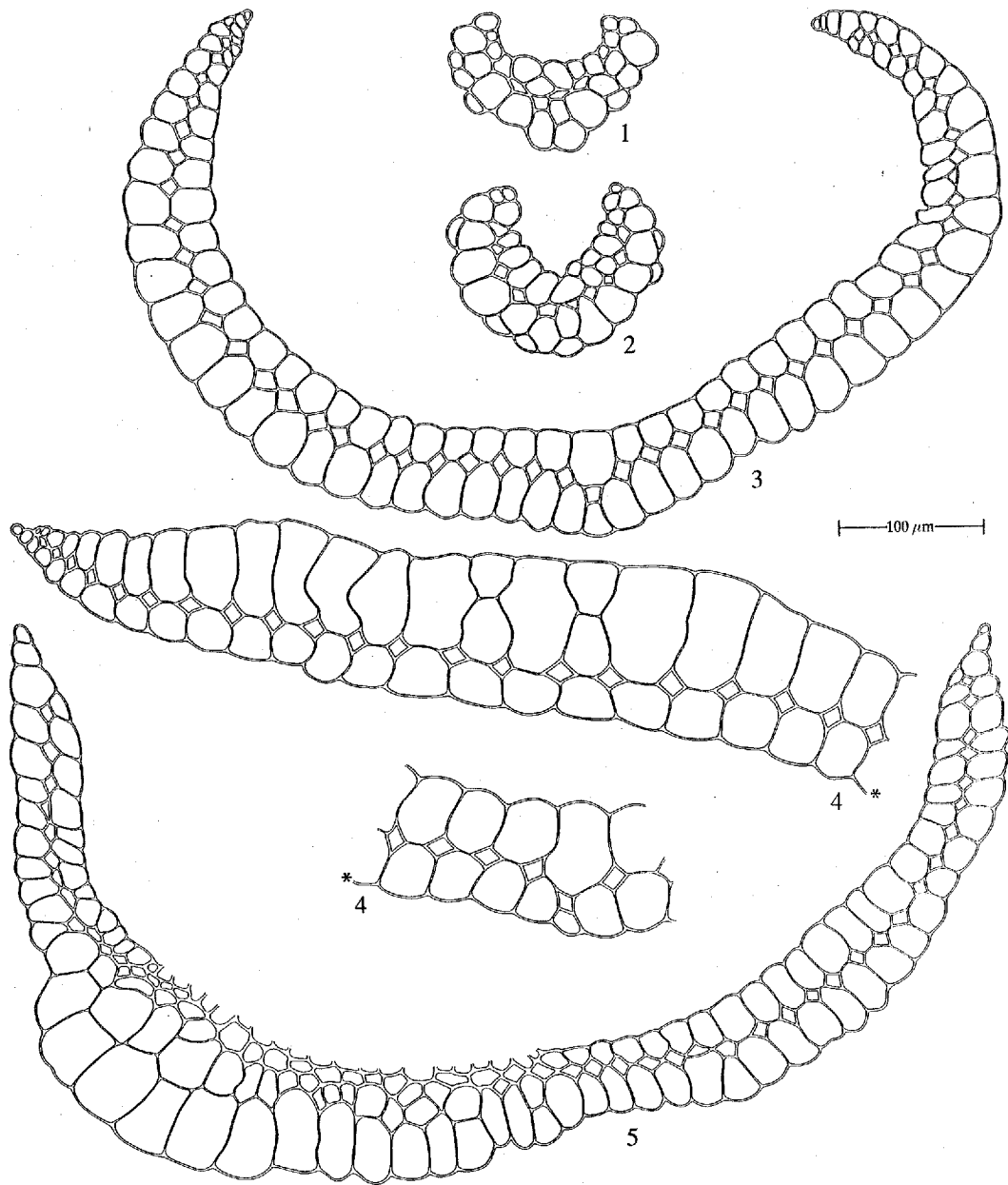


Figure CXXXI. *Leucobryum sanctum* (Brid.) Hampe. 1-5. Cross-sections of leaf (1, 2, apical; 3, median; 4, 5, basal portions). All figures were drawn from holotype of *Dicranum glaucum* var. *sanctum* (B).

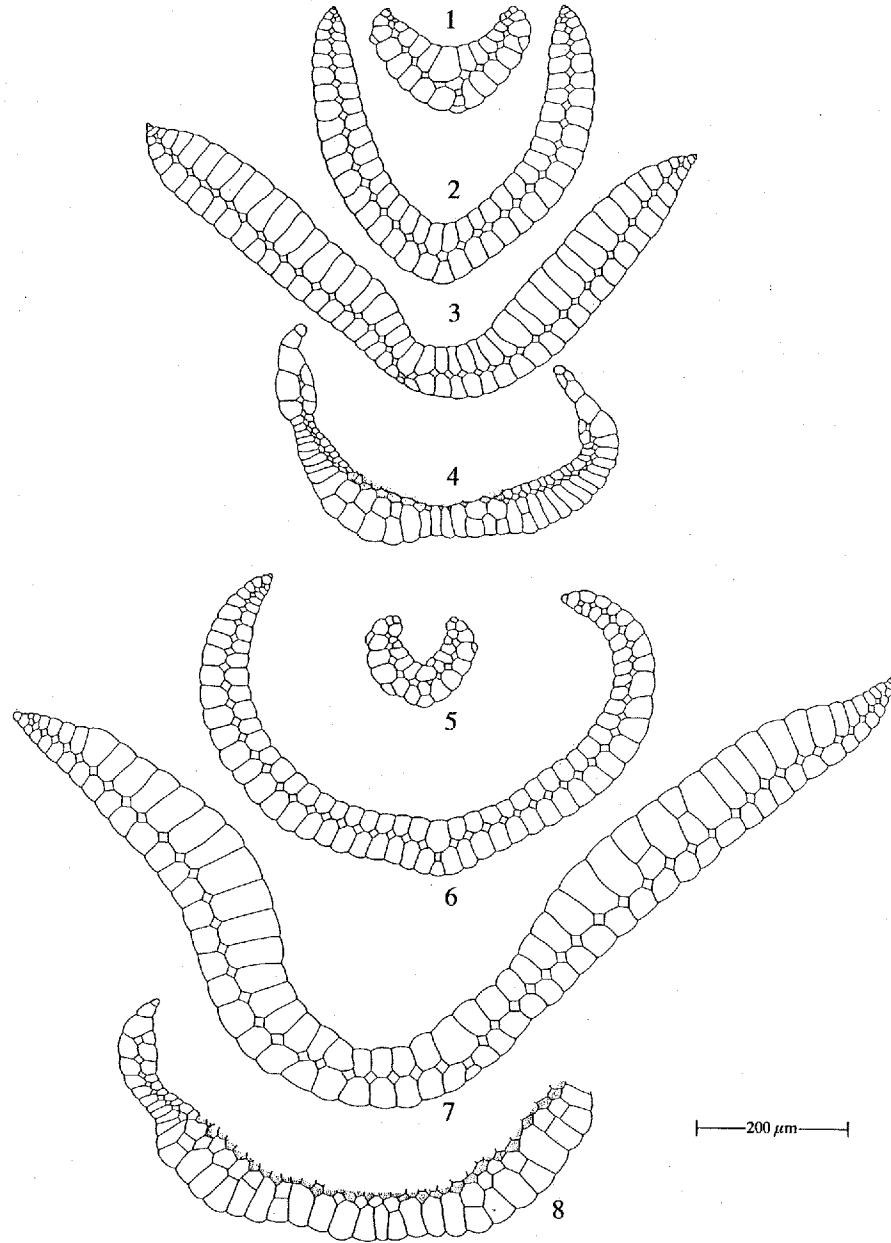


Figure CXXXII. *Leucobryum sanctum* (Brid.) Hampe. 1-8. Cross-sections of leaves (1, 5, apical; 2, 6, median; 3, 4, 7, 8, basal portions). Figs. 1-4 were drawn from lectotype of *L. papuense* (H); 5-8, from holotype of *Dicranum glaucum* var. *sanctum* (B).



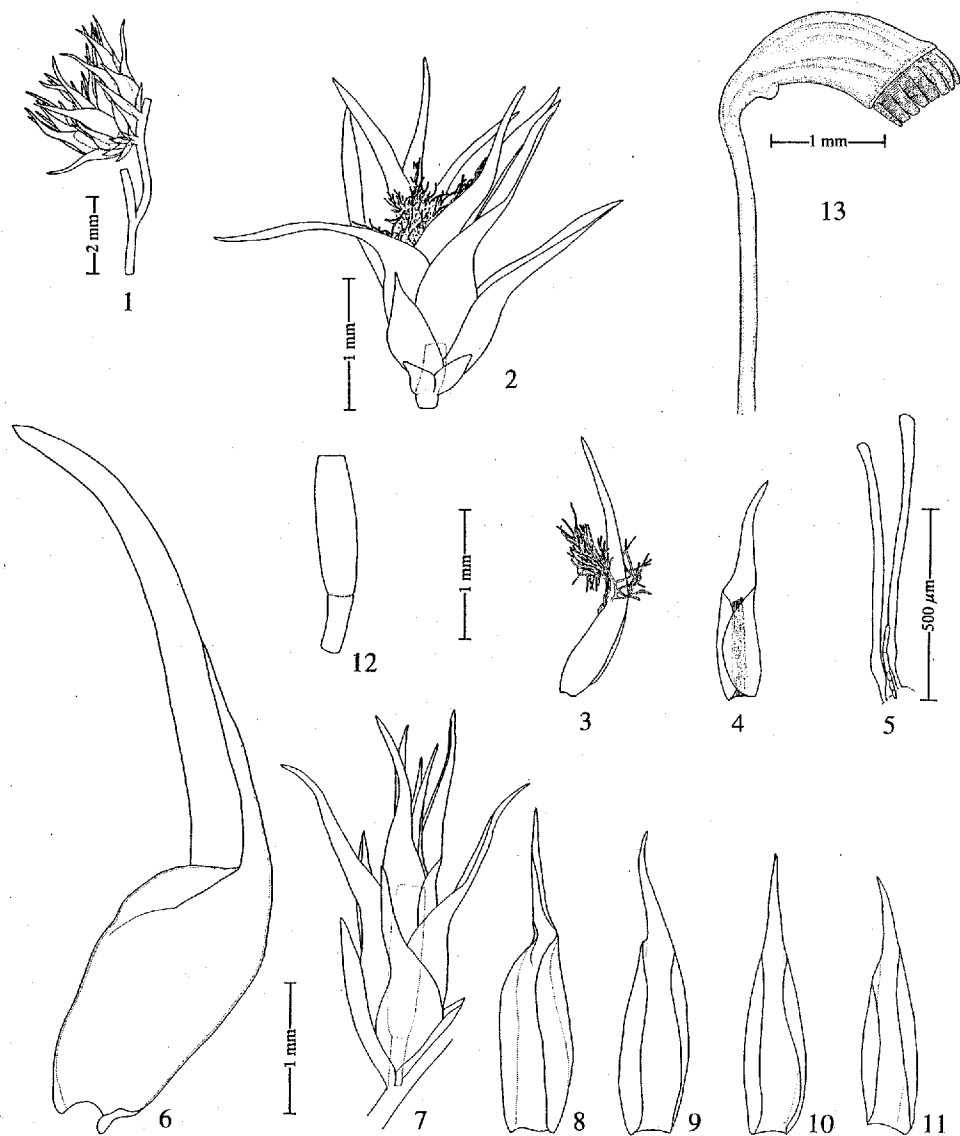


Figure CXXXIII. *Leucobryum sanctum* (Brid.) Hampe. 1. Branching showing position of perichaetia. 2. Perichaetium with tomentum. 3, 4. Inner perichaetial leaves (3, with tomentum on adaxial side) 5. Archegonia. 6. Stem leaf near perichaetium 7. 7. Perichaetium with sporophyte. 8-11. Inner perichaetial leaves from perichaetium 7 [numbers show the order of perichaetial leaves from the innermost leaf (number 11)]. 12. Vaginula. 13. Capsule. Figs. 1-12 were drawn from lectotype of *L. papuense* (H); 13, from holotype of *Dicranum glaucum* var. *sanctum* (B).

surface; laminae and borders consisting of 2-4 rows of narrowly rectangular to linear cells near base, the differentiation between laminal cells and border cells indistinct; abaxial leucocysts at leaf bases not subdivided, narrowly rectangular in surface view (Fig. CXXX: 4); alar parts distinctly auriculate (Fig. CXXX: 1, 2), consisting of 1 cell layered leucocysts; in cross-sections near leaf base chlorocysts distinctly in hypocentric, the leucocysts in 1-2 cell layers on adaxial side and 1 cell layer on abaxial side at the thickest part; abaxial leucocysts distinctly decurrent on stems; in cross-sections at insertional parts to stem usually 2 cell layers of leucocysts at the thickest part (Fig. CXXXI: 5, CXXXII: 4, 8).

Dioicous. Dwarf male plants growing on tomentum enclosed by perichaetial leaves; independent normal male plants not observed. Perichaetia terminal on short lateral branches; inner perichaetial leaves around mature sporophytes small, ca. 0.3 times longer than ordinary leaves near the perichaetia; archegonia ca. 0.7 mm long. Setae 25-30 mm long. Capsules horizontal, ellipsoid, strongly to slightly curved and asymmetrical, distinctly strumose (Fig. CXXXIII: 13); urns 1.3-1.5 mm long, ca. 0.8 mm wide.

Representative specimens examined: Thailand, Prachinburi, Khao Yai National Park, Kluey Mai (Orchid) Waterfall, 14°30'S 101°30'E, 650-680 m alt., 19 Feb. 1966,

Touw 12421 (L). Cambodia, Province de Koh Kong, Chékô, 11 Mar. 1965, Kira et al. 110a (HIRO). Malay Peninsula, Bukit Timar Nature Reserve, Taban Circle, 16 Apr. 1966, Sinclair 10885 (L). Philippines, Luzon, Cagayan Prov., ALSA logging area, south of Sta. Ana., ca. 100 m alt., July/Aug. 1964, Hale & Banaag 25749 (NICH). Borneo, E Kutai, Peak of B. papan, 200 m alt., 2 July 1952, Meijer B1345 (L). Nunukan Island, N of Tarakan, Nov./Dec. 1953, Meijer B4670 (L). Sulawesi, G. Paka-paka, Sept. 1913, Rachmat 681 (L). Sumatra, Ketambe, valley of Lau Alas, near tributary of Lau Ketambe, ca. 35 km NW of Kutatjane, 200-400 m alt., 5 Feb. 1975, Wilde & Wilde-Duyfjes 14528 (L). Enggano Islands, between Kajaäpoe and Kiah, 5°25'S 102°15'E, 4 July 1936, Lütjeharms 5396 (L). Mentawai Islands, N. Pagai, Sikakap, 7 July 1953, Borssum Waalkes & Pleyte 2890 (L). Banka Island, S. selan, Bt. Raja, Nov. 1917, Bünnemayer 2010 (L). Lesser Sunda Islands, W. Flores-Manggarai, 12 Mar. 1981, Schmutz 4851 (L). Seram, Kecamatan(District) Bula, Gunung(Mt.) Simfakan, 3°14'S 130°32-33'E, 10-100 m alt., 2 Mar. 1985, Akiyama 10839 (KYO, HIRO). New Guinea, Vogelkop Peninsula, Tamrau Range, Gunung Bagimata, 0°40'S 132°40'E, 1250-1500 m alt., 1 Jan. 1978, Zon s. n. (L). Woodlark Island, S. Selan, Bt. Raja, Nov. 1917, Bünnemayer 2010 (L). Caroline Islands, Ponape, Mt. Ninanri, 2550 ft. alt., 17 Aug. 1949, Glassman 2887 (L).

Habitat: On soil, humus, rocks and logs.

Distribution: India, Thailand, Cambodia, Malay Peninsula, Philippines, Borneo, Sulawesi, Sumatra, Java, Lesser Sunda Islands, Seram, New Guinea, Caroline Islands, Fiji.

The present species is characterized by (1) well differentiated central strand of stems composed of small thin-walled cells and surrounded with large thin-walled cells, (2) widely spreading somewhat falcate secund leaves, (3) clearly keeled basal parts of leaves, (4) papillosely prorate abaxial surface of apical parts of leaves, (5) distinctly auriculate alar parts of leaves, (6) hypocentric position of chlorocysts in cross-sections near leaf bases, and (7) perichaetia terminal on short lateral branches.

L. neo-caledonicum Duby ex Besch. from New Caledonia is closely related to L. sanctum and L. arfakianum, but differs in having distinctly hypocentric chlorocysts at leaf apices in cross-sections and absence of auriculate alar parts. The distinctions between L. sanctum and L. arfakianum will be discussed under the latter species.

14. Leucobryum arfakianum C. Müll. ex Geh. (Fig. CXXXIV-CXXXVIII, CXLI: 5)

Biblioth. Bot. 44: 5, t. 3 (1898) = Leucobryum sanctum var. arfakianum (C. Müll. ex Geh.) A. Eddy, Malesian Mosses 2:

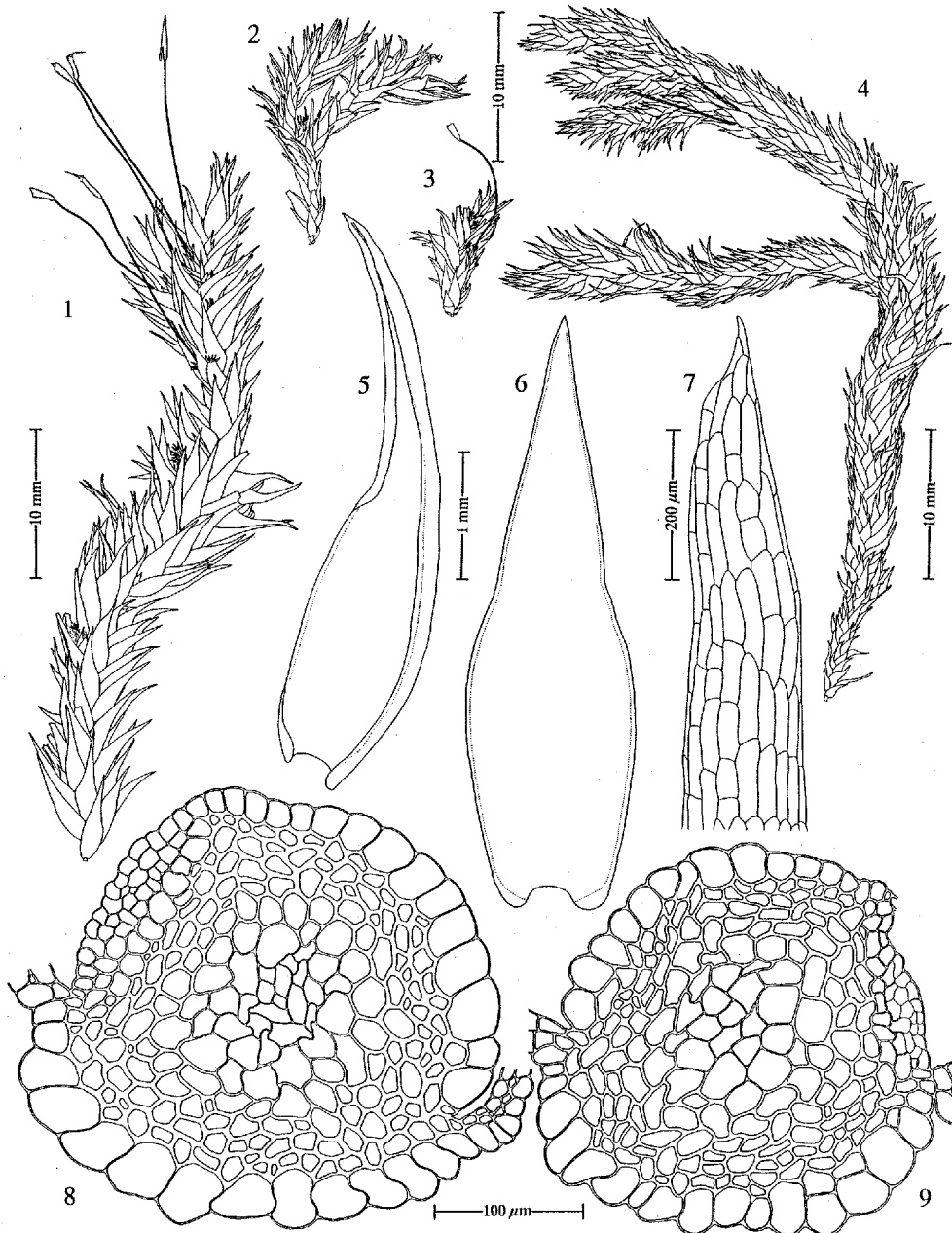


Figure CXXXIV. *Leucobryum arfakianum* C. Müll. ex Geh. 1–4. Plants. 5, 6. Leaves (6, expanded). 7. Leaf apex. 8, 9. Cross-sections of stems. Fig. 1 was drawn from lectotype of *L. subsanctum* (H); 2, 3, from Loria s. n., in hb. C. Müller 743, labeled as *L. brevisetum* (H); 4–7, 9, from isolectotype of *L. arfakianum* (F); 8, from holotype of *L. papuense* var. *pendulum* (L).

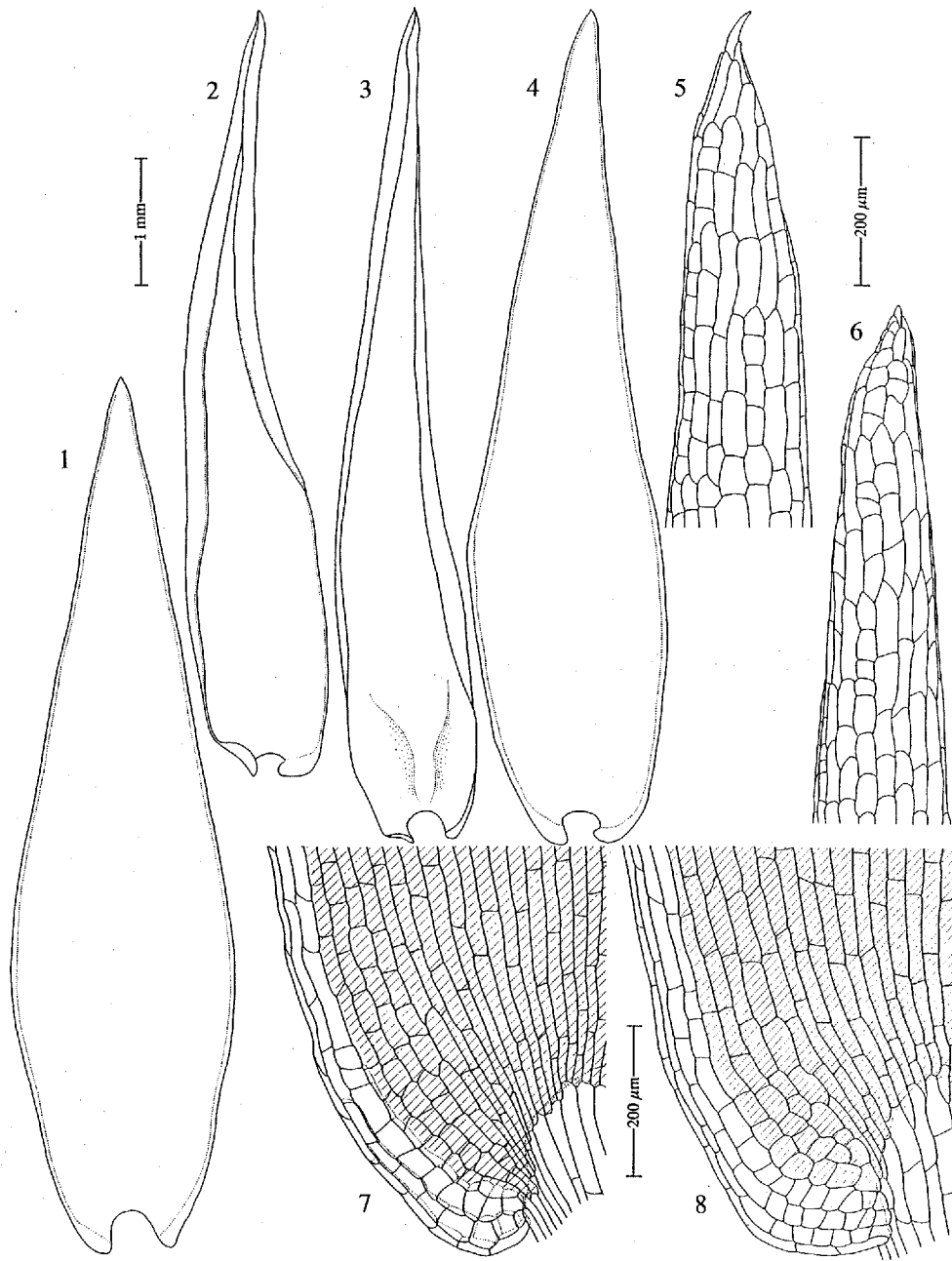


Figure CXXXV. *Leucobryum arfakianum* C. Müll. ex Geh. 1–4. Leaves (1, 4, expanded). 5, 6. Leaf apices. 7, 8. Leaf bases (abaxial view). Figs. 1 was drawn from lectotype of *L. subsanctum* (H); 2, 6, from Loria s. n., in hb. C. Müller 743, labeled as *L. brevisetum* (H); 3–5, 7, from holotype of *L. papuense* var. *pendulum* (L); 8, from isolectotype of *L. arfakianum* (FI).

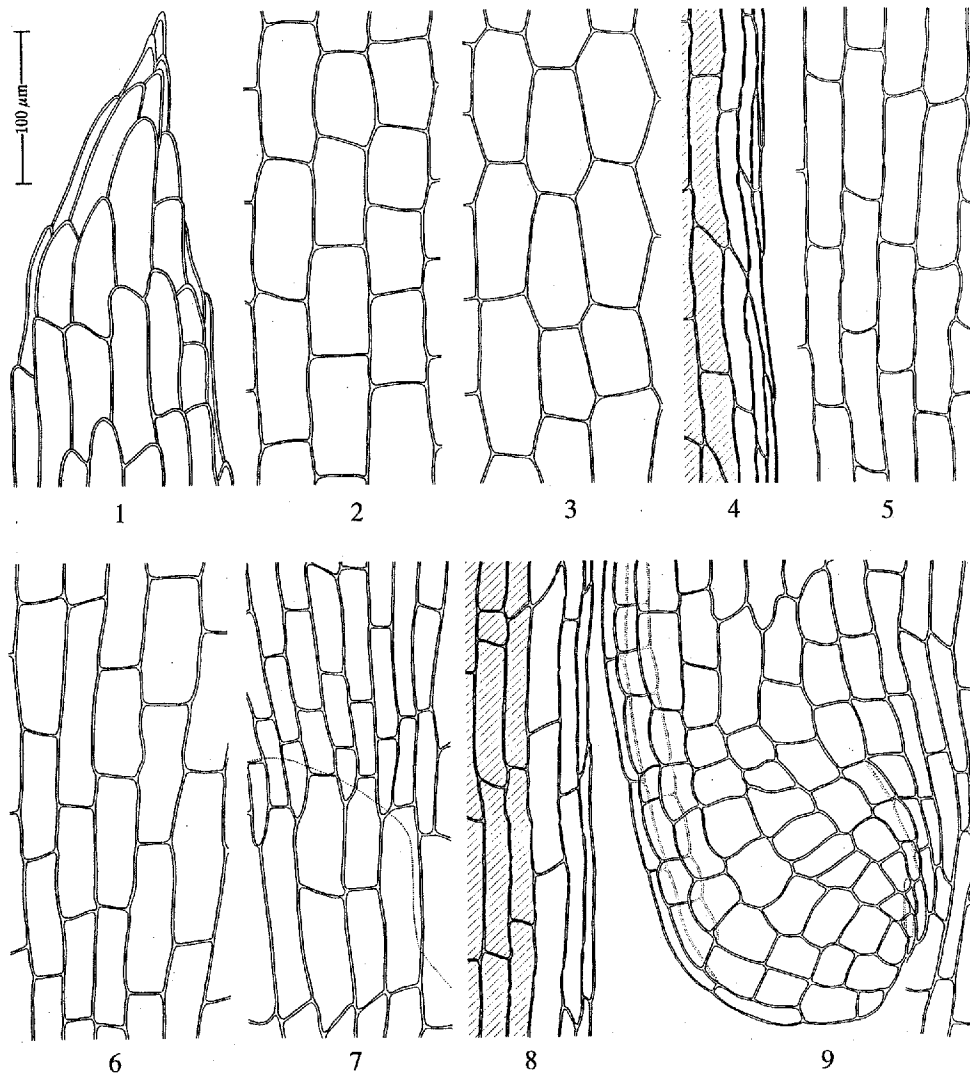


Figure CXXXVI. *Leucobryum arfakianum* C. Müll. ex Geh. 1. Leaf apex. 2-4. Median cells of leaf (2, 4, abaxial view; 3, adaxial view). 5-9. Basal cells of leaf (5, 7-9, abaxial view; 6, adaxial view). All figures were drawn from isoelectotype of *L. arfakianum* (FI).

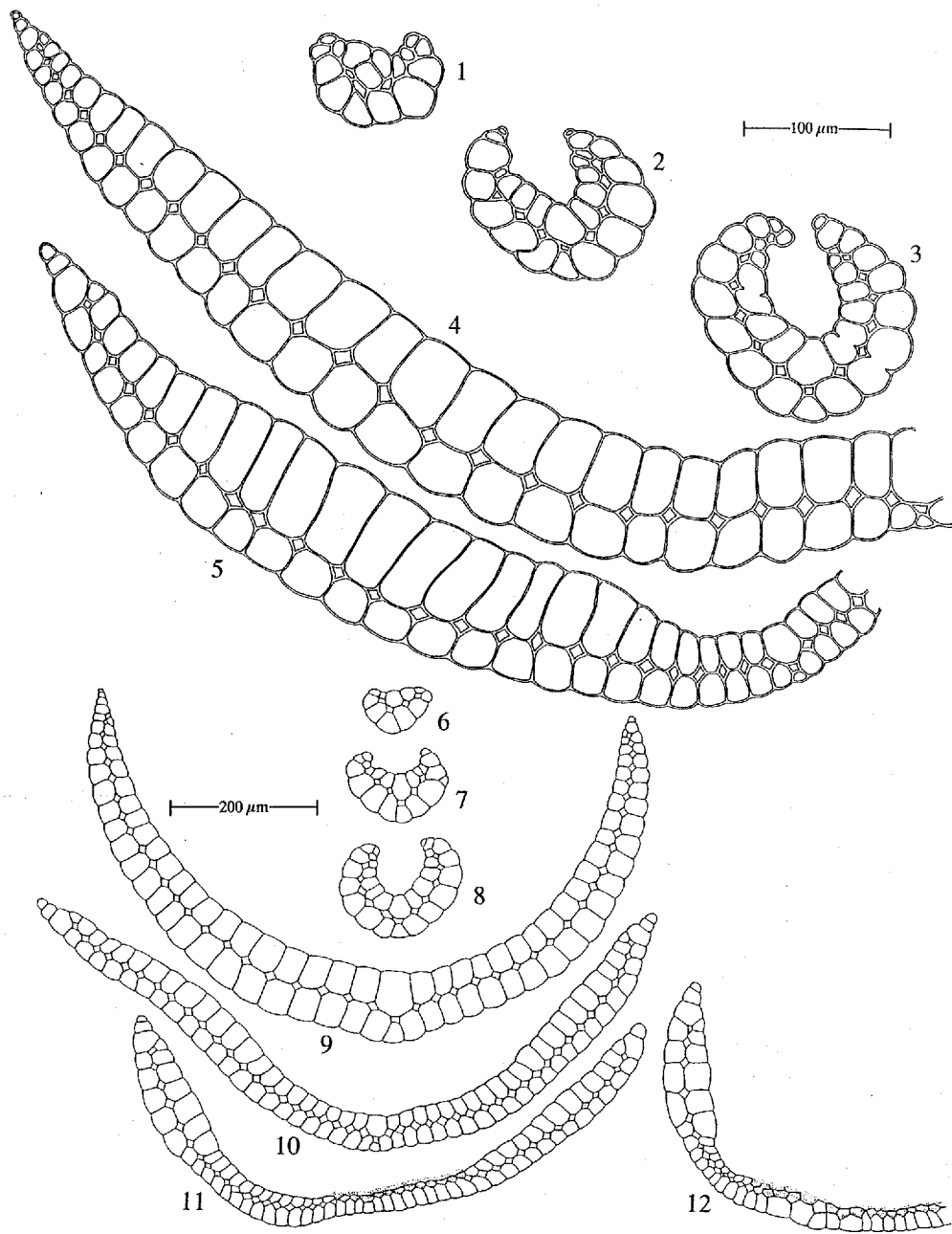


Figure CXXXVII. *Leucobryum arfakianum* C. Müll. ex Geh. 1-12. Cross-sections of leaves (1-3, 6-8, apical; 4, 9, median; 10-12, basal portions). All figures were drawn from isolectotype of *L. arfakianum* (FI).



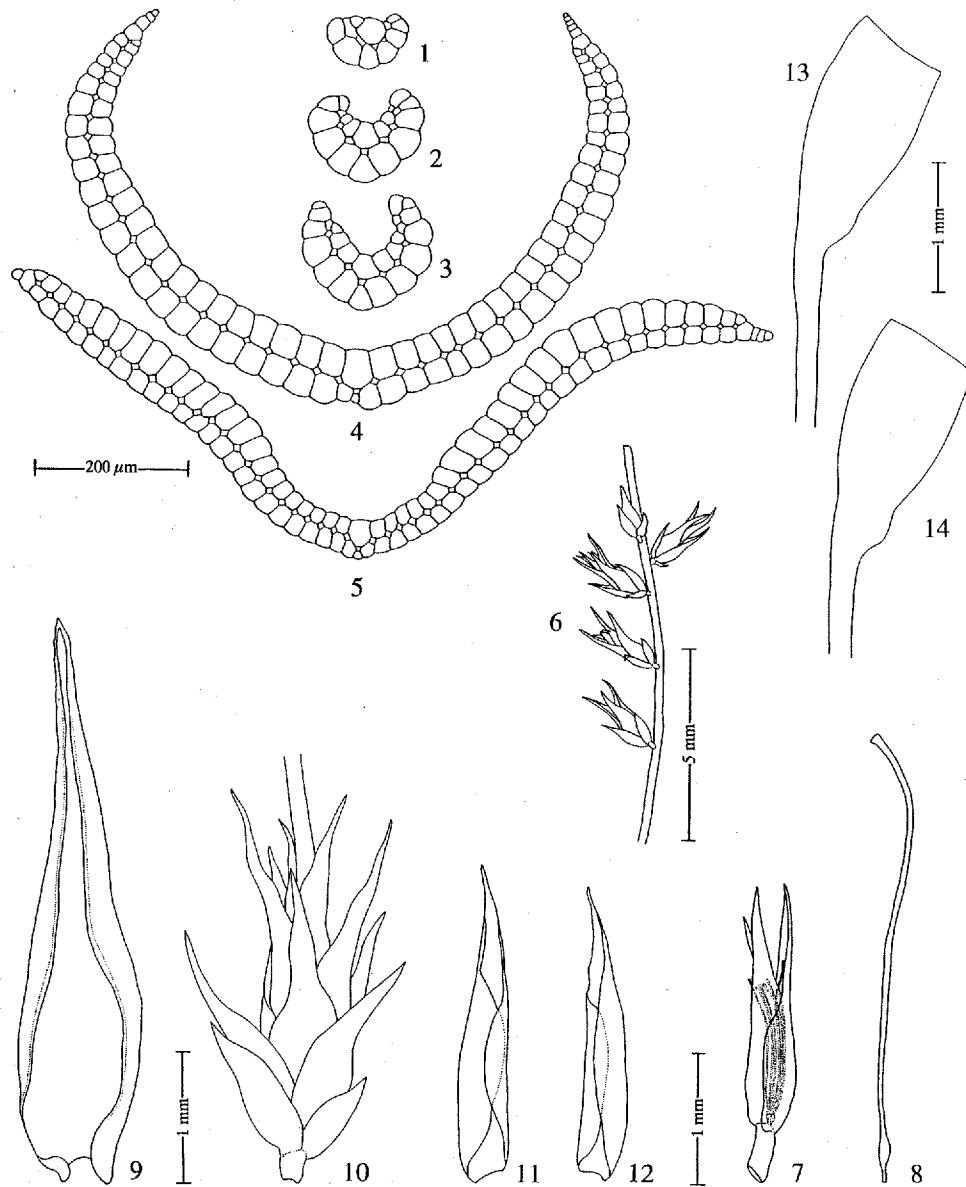


Figure CXXXVIII. *Leucobryum arfakianum* C. Müll. ex Geh. 1-5. Cross-sections of leaf (1-3, apical; 4, median; 5, basal portions). 6. Branching showing position of perichaetia. 7. Perichaetium. 8. Archegonium. 9. Stem leaf near perichaetium. 10. Perichaetium with sporophyte. 11, 12. Inner perichaetial leaves from perichaetium. 13, 14. Capsules. Figs. 1-8 were drawn from holotype of *L. papuense* var. *pendulum* (L); 9-12, from isoelectotype of *L. arfakianum* (Fl); 13, 14, from lectotype of *L. subsanctum* (H).

15, f. 173 (1990). Type: New Guinea, Mt. Arfak ad Hatam, 5-7000 ft. alt., July 1875, Beccari 163 - isoelectotype (FI).

Leucobryum subsanctum Broth., Philipp. J. Sc. 2: 339 (1907). Type: Philippines, Mindoro, Mt. Halcon, 6500 ft. alt, on cliffs, Nov. 1906, Merrill 6161 - lectotype (H). Philippines, Luzon, Province of Bataan, summit of Mt. Mariveles, on trees, Oct. 1903, Merrill 3540, 3549 - paratypes (H). Philippines, Mindoro, Mt. Halcon, 4500 ft. alt., on prostrate logs, Nov. 1906, Merrill 6208 - paratype (H).

Leucobryum papuense var. pendulum Zant., Nova Guinea, Botany 16: 275 (1964). Type: New Guinea, Star Mts., Mt. Antares, bivouac 40, 2400 m alt., in hollow trunk of tree in mossy forest, pendulous, 18 July 1959, Zanten 621 - holotype (L), isotype (NICH).

Plants whitish tinged with brown when dry, usually pendulous from tree trunks or rarely from rock cliffs. Stems to 60 mm long with leaves; central strand well differentiated in cross-sections of stems, the central strands consisting thin-walled small cells and surrounded with 2-3 rows of thin-walled large cells. Leaves appressed to erect spreading; 4.1-6.6 x 1.1-1.7 mm, lanceolate, gradually narrowed to subtubulous point from oblong and weakly keeled base, acute, smooth on abaxial surface at apical parts; laminae and borders consisting of 2-6 rows of

narrowly rectangular to linear cells near base, the differentiation between laminal cells and border cells indistinct; abaxial leucocysts at leaf bases not subdivided, narrowly rectangular in surface view; alar parts auriculate, consisting of 1 cell layered leucocysts; in cross-sections near leaf base chlorocysts distinctly in hypocentric, the leucocysts almost in 1 cell layer on both sides; abaxial leucocysts distinctly decurrent on stems; in cross-sections at insertional parts to stem usually 1 cell layers of leucocysts at the thickest part (Fig. CXXXVII: 11, 12).

Dioicous. Dwarf male plants growing on tomentum enclosed by perichaetial leaves; independent normal male plants not observed. Perichaetia terminal on short lateral branches; inner perichaetial leaves around mature sporophytes small, ca. 0.5-0.6 times longer than ordinary leaves near the perichaetia; archegonia 1.0-1.2 mm long. Setae 10-15 mm long. Capsules erect to suberect, ellipsoid, nearly symmetrical, indistinctly strumose (Fig. CXXXVIII: 13, 14); urns ca. 1.7 mm long, ca. 0.8 mm wide.

Representative specimens examined: Philippines, Mindanao, 11 Oct. 1965, Robbins 4028 (L). Thailand, Nakornsrihamarat, granitic massive Khao(Mt.) Luang, 8°30'N 99°45'E, 1700-1740 m alt., 5 Feb. 1966, Touw 11860 (L). Sumatra, Climbing Gunung Bandahara, ca. 6 km NE of Kampung Seldok (Alas Valley), ca. 25 km N of Kutatjane, ca. 2000 m

alt., 20 Feb. 1975, Wilde & Wilde-Duyfjes 15096D (L).  
Borneo, West Coast Res., Mt. Tambuyokon, ca. 15 miles NE of  
Kinabalu Peak, 6000-7000 ft. alt., 6 July 1961, Meijer  
B11215 (L). Sulawesi, Roroka Timbu, 0°30'-1°30'S 119°30'-  
120°30'E, 2000-2250 m alt., 18 May 1979, Hennipman 5514 (L).  
Seram, Kecamatan Tehoru, Manusela National Park, en route  
from Wae Nua to Gunung(Mt.) Mapahue, 3°15'S 129°29'E, 830 m  
alt., 21 July 1986, Akiyama 14787 (KYO, HIRO). New Guinea,  
Moresby, Moroka, July 1893, Loria s. n., det. C. Müller sub.  
no. 743, as Leucobryum brevicaule C. Müll. n. sp. (H).

Habitat: Usually on tree trunks, rarely on rocks or  
soil in montane forest.

Distribution: Philippines, Thailand, Sumatra, Borneo,  
Sulawesi, Seram, New Guinea.

The present species is differentiated from closely  
related L. sanctum by (1) appressed to erect spreading  
leaves, (2) weakly keeled basal parts of leaves, (3) smooth  
abaxial surface of apical parts of leaves, (4) almost  
homostrosic leucocysts in cross-sections of leaf bases, (5)  
one cell layered leucocysts at decurrent part on stem, and  
(6) erect to suberect capsules.

## IX. Distribution

The geographic distribution of the taxa treated in this study are classified into the following patterns.

1. Temperate to cool temperate regions of Northern Hemisphere: L. glaucum (Fig. CXL: 1).
2. Southwest Europe to Asia: L. juniperoideum (Fig. CXL: 2).
3. Eastern Asia: L. scabrum (Fig. CXLI: 3), L. boninense (Fig. CXLI: 4).
4. Eastern India to Eastern Asia: L. humillimum (Fig. CXLI: 2).
5. Southeast Asia to Eastern Asia: L. javense var. javense (Fig. CXLI: 1), L. bowringii (Fig. CXLII: 1).
6. Southeast Asia: L. arfakianum (Fig. CXLI: 5), L. javense var. novae-guineae (Fig. CXLI: 7), L. javense var. cyathifolium (Fig. CXLI: 8), L. aduncum var. aduncum (Fig. CXLII: 2), L. sericeum (Fig. CXLII: 3), L. aduncum var. teysmannianum (Fig. CXLII: 4), L. sumatranum (Fig. CXLII: 5).
7. Southeast Asia to South Pacific Islands: L. sanctum (Fig. CXL: 3), L. aduncum var. scalare (Fig. CXL: 4), L. chlorophyllosum (Fig. CXL: 5).
8. Endemic areas
  - a. South India: L. imbricatum (Fig. CXLI: 9).

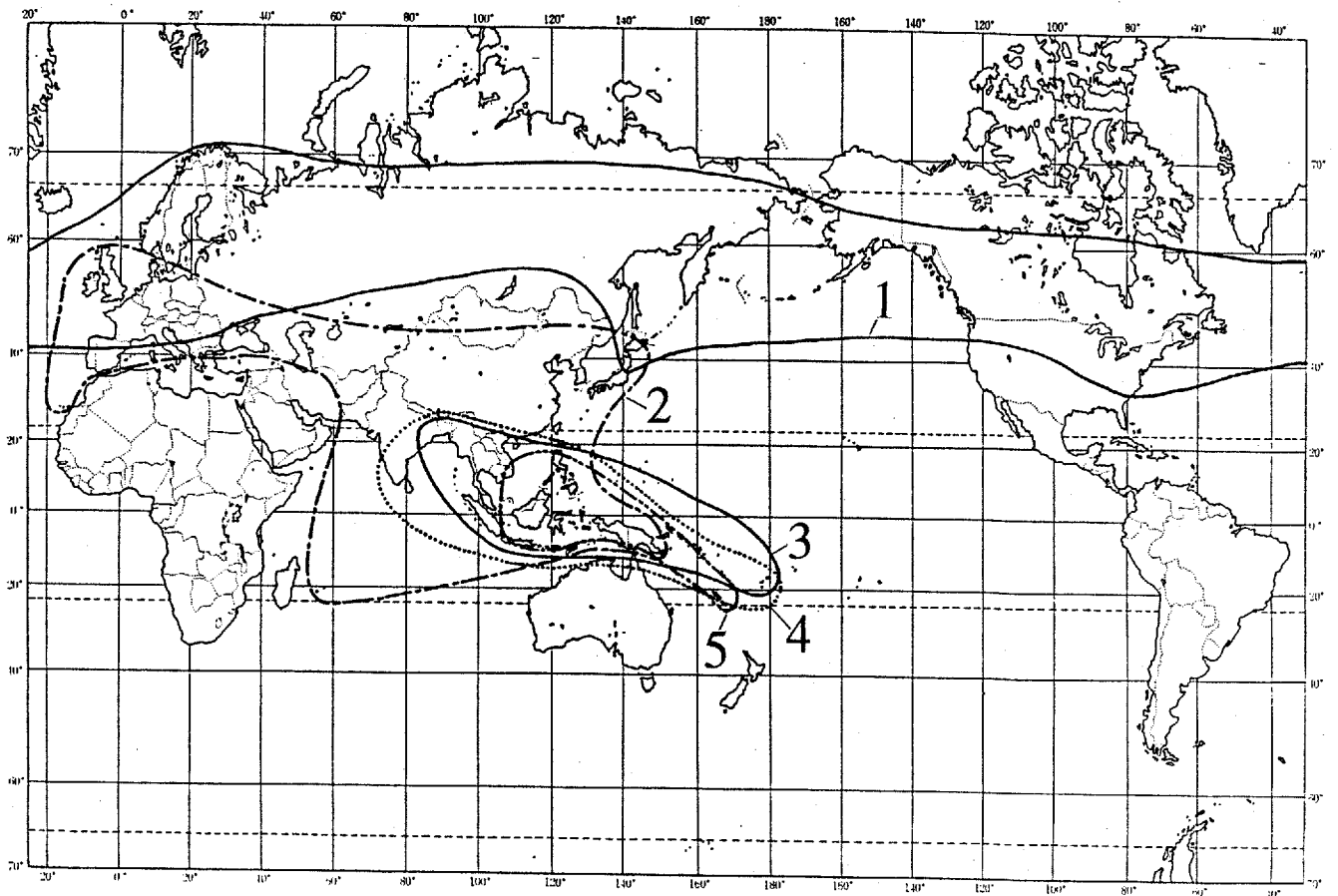


Figure CXXXIX. Distribution of 5 taxa of *Leucobryum*. 1. *L. glaucum* (Hedw.) Aongstr. in Fries. 2. *L. juniperoideum* (Brid.) C. Muell. 3. *L. sanctum* (Brid.) Hampe. 4. *L. aduncum* var. *scalare* (C. Muell. ex Fl.) A. Eddy. 5. *L. chlorophyllosum* C. Muell.

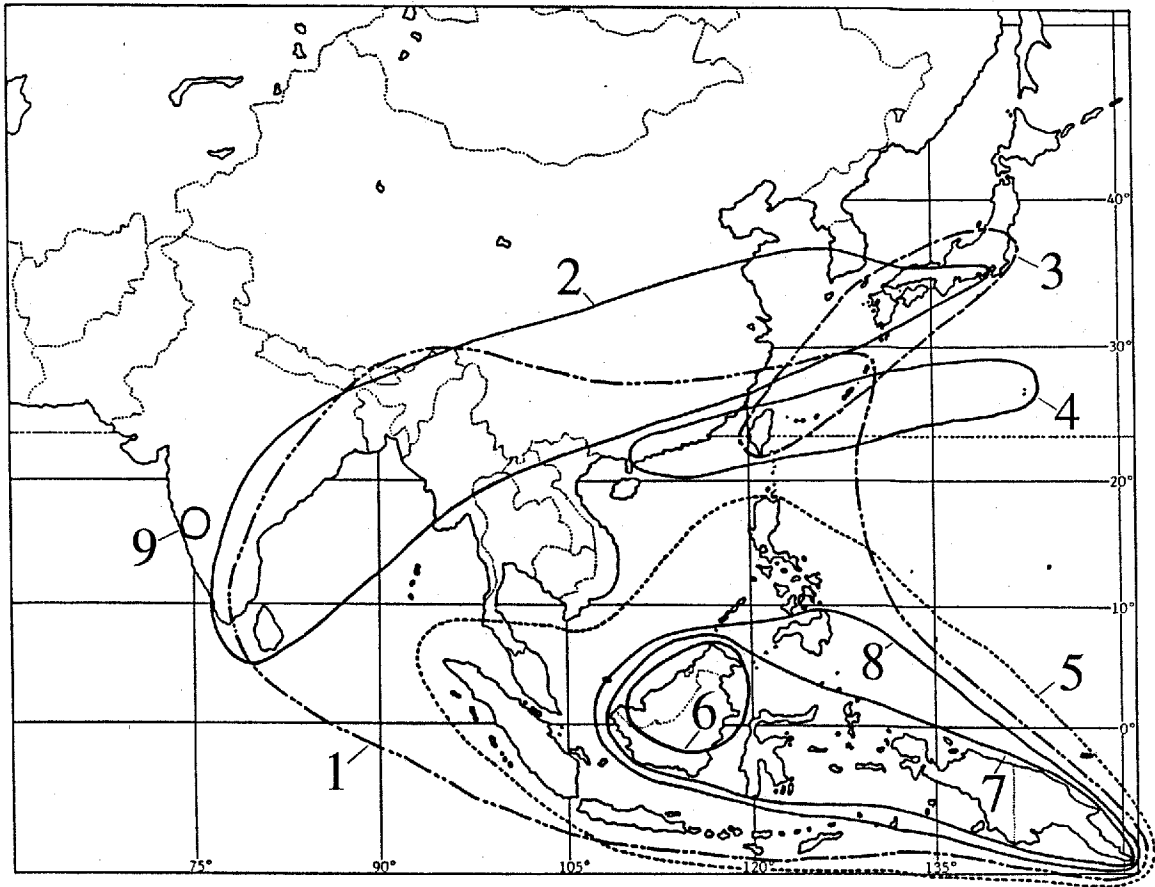


Figure CXL. Distribution of 9 taxa of *Leucobryum*. 1. *L. javense* (Brid. ex Schwaegr.) Mitt. var. *javense*. 2. *L. humillimum* Card. 3. *L. scabrum* Lac. 4. *L. boninense* Sull. & Lesq. 5. *L. arfakianum* C. Muell. ex Geh. 6. *L. uncinatum* Fl. 7. *L. javense* var. *novae-guineae* (Bartr.) T. Yamaguchi. 8. *L. javense* var. *cyathifolium* (Dix.) T. Yamaguchi. 9. *L. imbricatum* Broth.

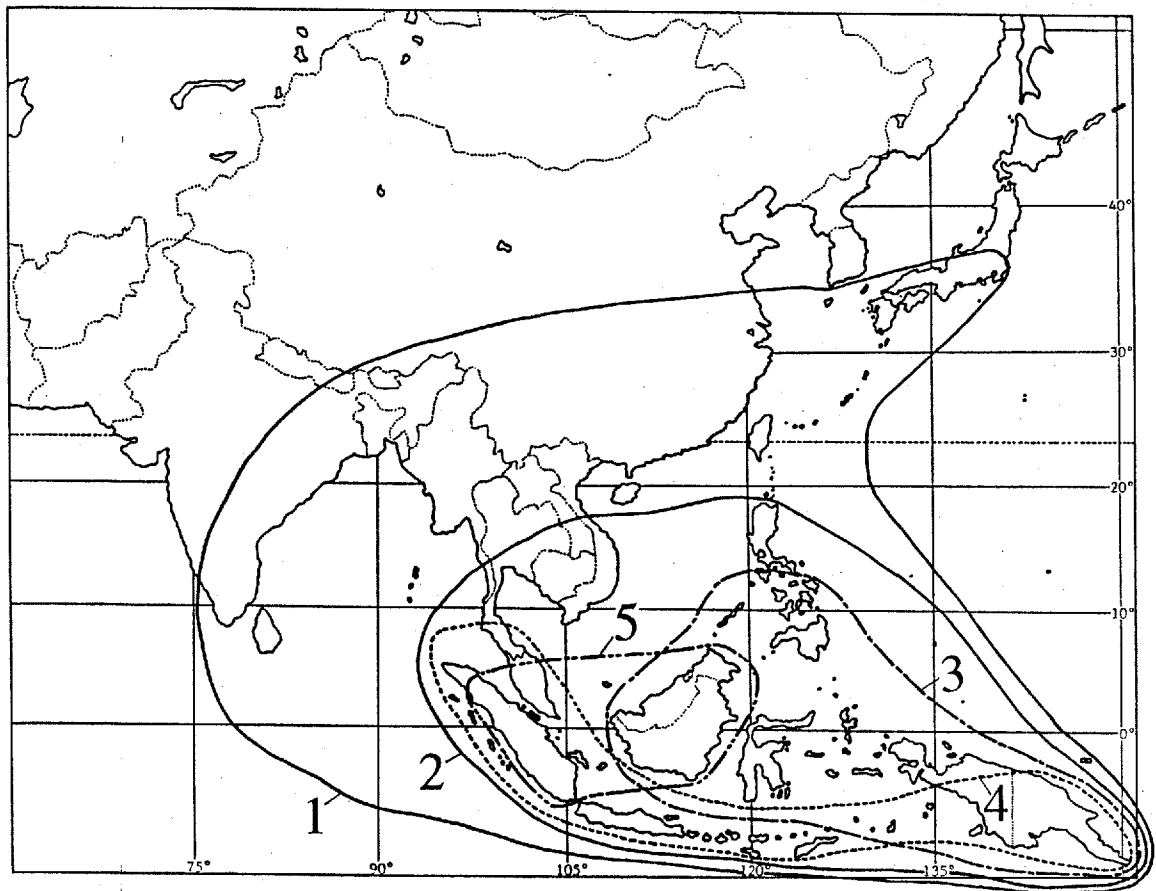


Figure CXLI. Distribution of 5 taxa of *Leucobryum*. 1. *L. bowringii* Mitt. 2. *L. aduncum* Dozy & Molk. var. *aduncum*. 3. *L. sericeum* Broth. ex Geh. 4. *L. aduncum* var. *teysmannianum* (Dozy & Molk.) T. Yamaguchi. 5. *L. sumatranum* Broth. ex Fl.



b. Borneo: L. javense var. uncinatum (Fig. CXLI: 6).

#### X. Excluded species

1. Leucobryum candidum (Brid. ex P. Beauv.) Wils., Fl. Nov. Zel. 2: 64 (1854).

The present species was reported from southeast Asia by Zanten (1964, Johnson (1964) and Eddy (1990). However, I could not find the present species among the specimens examined. This species should be excluded from the Asian bryoflora.

2. Leucobryum pachyphyllum C. Müll., Flora 82: 435 (1896).

The present species was reported from New Guinea by Fleischer (1912). However, I could not find the present species among the specimens examined. I considered that the present species should be excluded from the Asian bryoflora.

3. Leucobryum siamicum Besch. in Ren. & Card., Bull. Soc. R. Bot. Belg. 42(1): 42 (1905).

I carefully examined the holotype specimen of L. siamicum deposited in PC, and found the following characters: (1) mucronate leaf apices, (2) 2-3 layered leucocysts on adaxial side in cross-sections near leaf apices and (3) homostrosic construction of leucocysts at

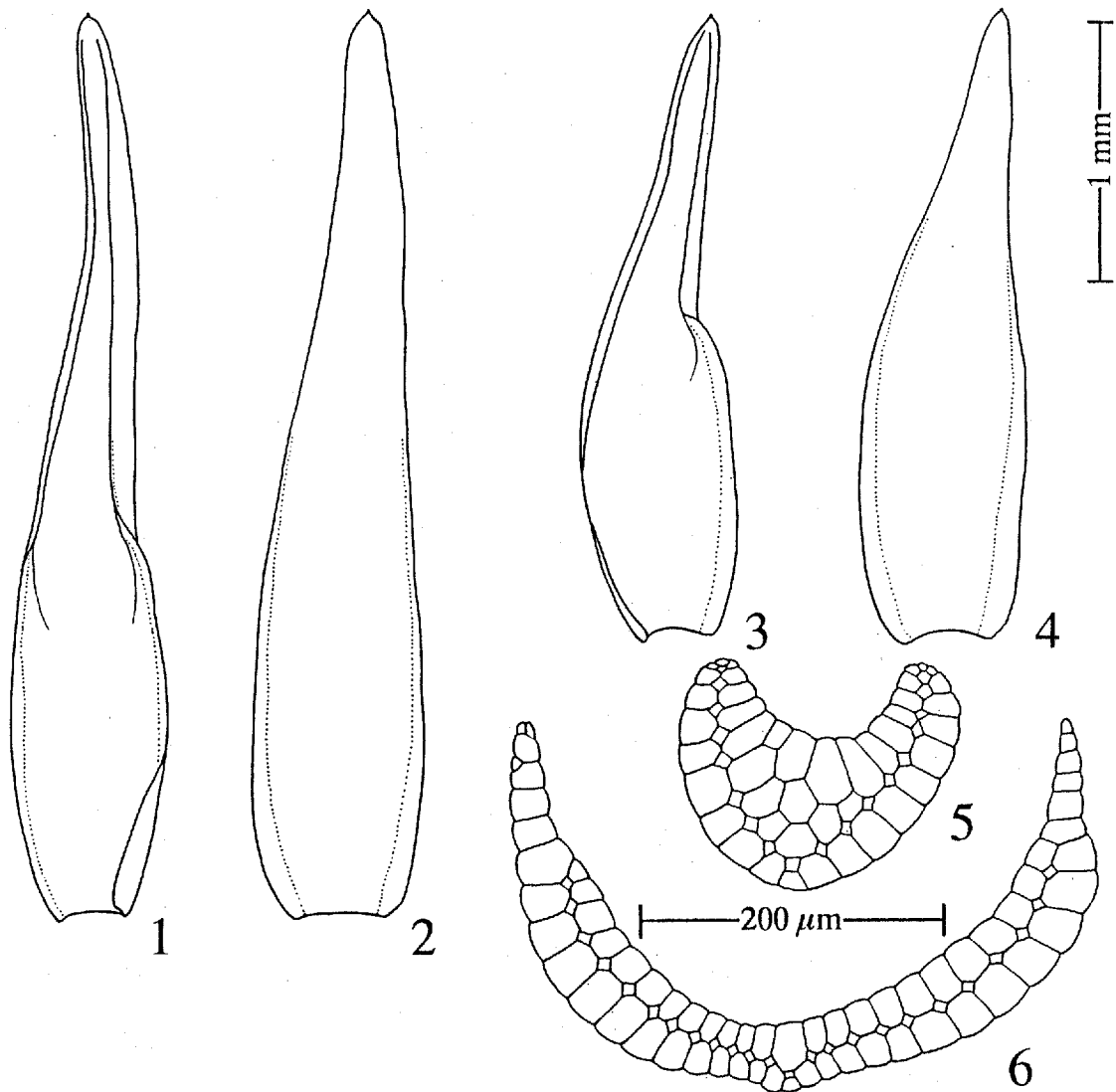


Figure CXLII. *Schistomitrium apiculatum* (Dozy & Molk.) Dozy & Molk. 1-4. Leaves (2, 4, expanded). 5, 6. Cross-sections of leaf (5, apical; 6, basal portions). All figures were drawn holotype of *L. siamicum* (PC).

leaf bases (Fig. CXXXIX). From these characters, L. siamicum is identical with Schistomitrium apiculatum (Dozy & Molk.) Dozy & Molk.

Schistomitrium apiculatum (Dozy & Molk.) Dozy and Molk., Musci Fr. Archip. Indici 3: 68, t. 24, 25 (1846).

Leucobryum siamicum Besch. in Ren. & Card., Bull. Soc. R. Bot. Belg. 42(1): 42 (1905), syn. nov. Type: Siam, without collector name (in herb. Renauld) – holotype (PC).

#### XI. Summary

Based on a taxonomic revision of the genus Leucobryum in Asia, examining about 3000 specimens including types, the following important taxonomic characters were newly recognized: (1) central strand of stem, (2) proration of abaxial side of leaf acumina, (3) decurrency of abaxial leucocysts, (4) ratio between thickness of the thickest part and thickness of the median furrow in the cross-sections of leaves, (5) position of perichaetia, (6) ratio between length of the matured inner perichaetial leaf and length of the stem leaf near the perichaetium, (7) length of archegonia, (8) presence of normal male plants, and (9) growing position of dwarf male plants. Among 78 taxa which had been reported from Asia, 33 taxa were newly reduced to synonyms, 4 taxa were newly reduced to lower status, 2 taxa

were excluded from Asian bryoflora, 4 taxa were combined with other genera, and the following 19 taxa were recognized as Asian Leucobryum. (1) Leucobryum javense (Brid. ex Schwägr.) Mitt., (2) L. javense var. cyathifolium (Dix.) T. Yamaguchi, stat. nov., (3) L. javense var. novae-guineae (Bartr.) T. Yamaguchi, stat. nov., (4) L. javense var. uncinatum (Fl.) T. Yamaguchi, stat. nov., (5) L. scabrum Lac., (6) L. aduncum Dozy & Molk., (7) L. aduncum var. teysmannianum (Dozy & Molk.) T. Yamaguchi, stat. nov., (8) L. aduncum var. scalare (C. Müll. ex Fl.) A. Eddy, (9) L. chlorophyllosum C. Müll., (10) L. boninense Sull. & Lesq., (11) L. juniperoideum (Brid.) C. Müll., (12) L. humillimum Card., (13) L. imbricatum Broth., (14) L. glaucum (Hedw.) Ångstr. in Fries, (15) L. bowringii Mitt., (16) L. sumatranum Broth. ex Fl., (17) L. sericeum Broth. ex Geh., (18) L. sanctum (Brid.) Hampe and (19) L. arfakianum C. Müll. ex Geh. An identification key was constructed on the basis of the morphological characters. For each species synonymy was given together with pertinent literature along with its type, detailed description and illustration, discussion on taxonomical status, selected specimens examined and geographical distribution.

### XIII. Literature cited

- Ando, H. & A. Matsuo 1984. Applied bryology. In W. Schultze-Motel (ed.), *Advances in bryology*, vol. 2: 133-224, figs. 4-6. J. Cramer, Vaduz.
- Andrews, A. L. 1947. Taxonomic notes, VI. The Leucobryaceae. *Bryologist* 50: 319-326.
- Bartram, E. B. 1953. Additional mosses from northeastern New Guinea. *Svensk. Bot. Tidskr.* 47(3): 397-401.
- Bartram, E. B. 1957. Mosses of eastern Papua, New Guinea. *Brittonia* 9: 32-56.
- Bartram, E. B. 1960. Musci. In B. Maguire & J. J. Wurdack (eds.), *The botany of the Guayana Highland*, part IV. *Mem. New York Bot. Gard.* 10(2): 2-10.
- Bescherelle, E. 1873. Flore bryologique de la Nouvelle-Calédonie. *Ann. Sci. Nat. Bot. sér. 5*, 18: 184-245.
- Bescherelle, E. 1893. Nouveaux documents pour la flore bryologique du Japon. *Ann. Sci. Nat. Bot. sér. 7*, 17: 327-393.
- Bescherelle, E. 1897. Revision de genre Ochrobryum. *J. de Bot.* 11: 138-153.
- Bescherelle, E. 1898. *Bryologiae japonicae supplementum*, I. *J. de Bot.* 12: 285-299.

- Blackstock, T. H. 1987. The male gametophores of Leucobryum glaucum (Hedw.) Ångstr. and L. juniperoideum (Brid.) C. Müll. in two Welsh woodlands. J. Bryol. 14: 535-541.
- Bonnot, E. 1964. Le Leucobryum juniperoideum (Brid.) C. Müll. dans la bryoflore française. Bull. Soc. Bot. Fr. 111: 151-164.
- Bridel, S.-E. de 1798. Muscologia recentiorum, vol. 2, pars 1: 1-222, pls. 1-6. C. G. Ettinger, Gotha.
- Bridel, S.-E. de 1826. Bryologia universa, vol. 1(1): 1-746. Joh. Ambros. Barth, Leipzig.
- Bridel, S.-E. de 1827. Bryologia universa, vol. 1(2): 747-856. Joh. Ambros. Barth, Leipzig.
- Brotherus, V. F. 1899a. Contributions to the bryological flora of southern India. Report on a collection of mosses made by Dr. J. L. Walker in Coorg. Rec. Bot. Surv. India 1(12): 311-329.
- Brotherus, V. F. 1899b. Neue Beiträge zur Mossflora Japans. Hedwigia 38: 204-247
- Brotherus, V. F. 1901. Leucobryaceae. In A. Engler & K. Prantl (eds.), Die natürlichen Pflanzenfamilien, Teil 1, Abt. 3, Hälfte 1: 342-351. Wilhelm Engelmann, Leipzig.
- Brotherus, V. F. 1907. Musci halconenses. Philipp. J. Sci. 2: 339-343.

- Brotherus, V. F. 1924. Dicranales. In A. Engler & K. Prantl (eds.), Die natürlichen Pflanzenfamilien, ed. 2, Band 10: 155-228. Wilhelm Engelmann, Leipzig.
- Brotherus, V. F. 1928. Musci. In E. Irscher (ed.), Beiträge zur Kenntnis der Flora von Borneo. Mitt. Inst. Allg. Bot. Hamburg 7: 115-140.
- Brotherus, V. F. 1929. Musci. In H. Handel-Mazzetti (ed.), Symbolae sinicae, Teil IV: 1-147, Taf. I-V. Verlag von Julius Springer, Wien.
- Bruch, P., W. P. Schimper & W. T. von Gümbel 1847.  
Oncophorus. Bryologia europaea, vol. 1, fasc. 41: 1-5, pls. 1, 2. E. Schweizerbart, Stuttgart.
- Burrell, W. H. 1907. Leucobryum glaucum Schp. Bryologist 10: 108-111.
- Cardot, J. 1899. Nouvelle classification des Leucobryaceae. Rev. Bryol. 26: 1-8, pl. 1.
- Cardot, J. 1901. Recherches anatomiques sur les Leucobryacées. Mem. Soc. Sci. Nat. Cherbourg 32: 1-84, pls. 1-19.
- Cardot, J. 1905. Mousses de l'île Formose. Beih. Bot. Centralb. 19: 85-148, f. 1-39.
- Castaldo, R., R. Ligrone & R. Gambardella 1979. A light and electron microscope study on the phylloids of Leucobryum candidum (P. Beauv.) Wils. Rev. Bryol. Lichénol. 45: 345-360.

- Correns, C. 1899. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge: 1-472. Verlag von Gustav Fischer, Jena.
- Crosby, M. R. & R. E. Magill 1981. A dictionary of mosses: 1-43. Missouri Botanical Garden, St Louis.
- Crum, H. A. 1976. Mosses of the Great Lakes Forest: 1-404. Braun-Brumfield, Ann Arbor.
- Crum, H. A. & L. E. Anderson 1981. Mosses of eastern North America, vol. 1: 1-663. Columbia University Press, New York.
- Crum, H. A. & W. C. Steere 1957. The mosses of Porto Rico and the Virgin Islands. New York Academy of Science, Scientific Survey of Porto Rico and the Virgin Islands 7(4): 393-599.
- Crundwell, A. C. 1972. Leucobryum juniperoideum (Brid.) C. Müll. in Britain. J. Bryol. 7: 1-5.
- Crundwell, A. C. 1979. Rhizoids and moss taxonomy. In G. C. S. Clarke & J. G. Duckett (eds.), Bryophyte systematics: 347-363. Academic Press, London.
- Deguchi, H. 1979. A revision of the genera Grimmia, Schistidium and Coscinodon (Musci) of Japan. J. Sci. Hiroshima Univ. ser. b, div. 2, 16(2): 121-256.
- Dixon, H. N. 1922. The mosses of the Wollaston Expedition to Dutch New Guinea, 1912-13; with some additional mosses



- from British New Guinea. J. Linn. Soc. Bot. 45: 477-510, pls. 28, 29.
- Dixon, H. N. 1923. Studies in the bryology of New Zealand, with special reference to the herbarium of Robert Brown, of Christchurch, New Zealand, 3. Bull. New Zealand Inst. 3: 75-152, pls. 7, 8.
- Dixon, H. N. 1924. The student's handbook of British mosses, ed. 3: 1-582, pls. 1-63. Wheldon & Wesley, London.
- Dixon, H. N. 1932a. On the moss flora of Siam. J. Siam Soc., Nat. Hist. suppl. 9(1): 1-51.
- Dixon, H. N. 1932b. Contributions to the moss flora of Sumatra. Ann. Bryol. 5: 17-50.
- Dixon, H. N. 1933. Mosses of Hong Kong. Hong Kong Nat. suppl. 2: 1-31, pls. 1, 2.
- Dixon, H. N. 1938. Notes on the moss collections of the Royal Botanic Garden, Edinburgh. Not. R. Bot. Gard. Edinburgh 19(95): 279-302.
- Dozy, F. & J. H. Molkenboer 1845. Musci frondosi inediti archipelagi indici, fasc. 3: 53-90, pls. 21-30. H. W. Hazenberg & Soc., Leiden.
- Dozy, F. & J. H. Molkenboer 1854. Musci frondosii. In F. A. W. Miquel (ed.), Plantae junghuhnianae, fasc. 3: 312-341. A. W. Sythoff, Leiden.
- Dozy, F. & J. H. Molkenboer 1855. Bryologia javanica, vol. 1, fasc. 3: 17-24, pls. 11-15. A. W. Sythoff, Leiden.

- Eddy, A. 1990. A handbook of Malesian mosses, vol. 2.  
Leucobryaceae to Buxbaumiaceae: 1-256. British Museum  
(Natural History), London.
- Edwards, S. R. 1979. Taxonomic implications of cell patterns  
in haplolepidous moss peristomes. In G. C. S. Clarke &  
J. G. Duckett (eds.), *Bryophyte systematics*: 317-346.  
Academic Press, London.
- Ellis, L. T. 1985. A taxonomic revision of Exodictyon Card.  
(Musci: Calymperaceae). *Lindbergia* 11: 9-37.
- Enroth, J. 1989. The bryophytes of Sabah (North Borneo) with  
special reference to the BRYOTROP transect of Mount  
Kinabalu, IV. Leucobryaceae (Bryopsida). *Willdenowia*  
18: 529-554.
- Enroth, J. 1990. Bryophyte flora of the Huon Peninsula,  
Papua New Guinea, XXXVI. Leucobryaceae (Musci). *Acta*  
*Bot. Fennica* 139: 65-120.
- Fleischer, M. 1899. Neue javanische Fissidens-Arten und  
Varietäten, herausgegeben in Musi-Archipelagi Indici.  
*Hedwigia* 38(Beibl.): 125-128.
- Fleischer, M. 1904. Die Musci der Flora von Buitenzorg, vol.  
1: 1-379. E. J. Brill, Leiden.
- Fleischer, M. 1912. Laubmoose. *Nova Guinea* 8: 735-753, t.  
119-124.
- Fleischer, M. 1923. Die Musci der Flora von Buitenzorg, vol.  
4: 1104-1729. E. J. Brill, Leiden.

- Florschütz, P. A. 1964. The mosses of Suriname, part 1: 1-271. E. J. Brill, Leiden.
- Fries, E. M. 1846. Summa vegetabilium scandinavie, sectio prior: 1-258. E. typographia Academica, Uppsala.
- Geheeb, A. 1889. Neue Beiträge zur Moosflora von Neu-Guinea. Biblioth. Bot. 13: 1-13.
- Geheeb, A. 1898. Weitere Beiträge zur Moosflora von Neu-Guinea. Biblioth. Bot. 44: 1-29.
- Grout, A. J. 1905. Mosses with a hand-lens and microscope, ed. 2: 1-208. Published by author, New York.
- Grout, A. J. 1937. Leucobryaceae. Moss Flora of North America, north of Mexico, vol. 1, part 2: 97-99, pl. 52. published by author, New York.
- Hampe, G, E, L. 1839. Relation über die von dem Reisenden C. Beyrich auf seiner letzten Reise in Nord America gesammelten Laubmoose. Linnaea 13: 39-48.
- Héban, C. 1977. The conducting tissues of bryophytes: 1-157, pls. 1-80. J. Cramer, Vaduz.
- Hedwig, J. 1801. Species muscorum frondosorum: 1-17, 19-353, pls. 1-77. Sumtu Joannis Ambrosii Barthii, Leipzig.
- Herzog, T. 1926. Geographie der Moose: 1-439, t. 1-8. Verlag von Gustav Fischer, Jena.
- Holmgren, P. K. & N. H. Holmgren & L. C. Barnett. 1990. Index herbariorum, part I. The herbaria of the world, 8

- ed. *Regnum Vegetabile* 120: 1-693. New York Botanical Garden, New York.
- Horikawa, Y. 1935. *Symbolae florae bryophytae orientalis-  
asiae*, V. *Bot. Mag. Tokyo* 49: 211-263.
- Imura, S. & Z. Iwatsuki 1990. Classification of vegetative  
diaspores on Japanese mosses. *Hikobia* 10: 435-443.
- Inoue, H. (ed.) 1980. *Koke Engei no Subete* (All about moss  
horticulture): 1-215. Nikko Shoten, Tokyo. (in  
Japanese)
- Iwatsuki, Z. 1966. Critical re-examination of the Asiatic  
mosses reported by Sullivant and Lesquereux in 1857 and  
1859. *J. Hattori Bot. Lab.* 29: 53-69.
- Iwatsuki, Z. 1977. Bryological miscellanies, XXIII-XXIV. *J.  
Hattori Bot. Lab.* 43: 357-364.
- Iwatsuki, Z. & A. Noguchi 1979. Critical re-examination of  
Japanese mosses mainly described by Eikichi Ihsiba. *J.  
Hattori Bot. Lab.* 45: 365-373.
- Iwatsuki, Z. & T. Suzuki 1982. A taxonomic revision of the  
Japanese species of *Fissidens* (Musci). *J. Hattori Bot.  
Lab.* 51: 329-508.
- Jaeger, A. 1873. *Genera et species muscorum*, part 3. *Ber. S.  
Gall. Naturw. Ges.* 1871-72: 309-490.
- Johnson, A. 1964. An account of the Malaysian Leucobryaceae.  
*Gard. Bull. Straits Settlem. ser. 3*, 20: 315-360.

- Kawai, I. 1980. Systematic studies on the conducting tissue of the gametophyte in Musci. (11) Anatomical characteristics of stems in some species of Leucobryaceae. Sci. Rep. Kanazawa Univ. 25(1): 31-42.
- Kindberg, N. C. 1898. European and N. American Bryineae, part 2: 153-410. C. V. Zickerman, Linköping.
- Ligrone, R. 1985. Studies on the leaf structure in some species of Leucobryaceae. III. Leucobryum sanctum (Brid.) Hampe and Leucobryum sp. (Leucobryaceae). J. Bryol. 411-416.
- Meusel, H. 1935. Wuchsformen und Wuchstypen der europäischen Laubmoose. Nova Acta Leopoldina neue Folge, 3(12): 123-277.
- Mitten, W. 1859. Musci indiae orientalis. J. Proc. Linn. Soc. Bot. suppl. 1: 1-171.
- Müller, C. 1845. Beiträge zu einer Flora der Aequinoctial-Gegenden. Laubmoose. Linnaea 18: 667-709.
- Müller, C. 1851. Synopsis muscorum frondosorum omnium hucusque cognitorum, part 2, fasc. 9, 10: 511-772. Sumptibus Alb. Foerstner, Berlin.
- Müller, C. 1854. Musci neilgherienses, II. Bot. Zeit. 12: 556-559, 569-574.
- Müller, C. 1869. De muscorum ceylonensium collectione. Linnaea 36: 1-40.

- Müller, C. 1884. Die auf der Expedition S. M. S. "Gazelle" von Dr. Naumann gesammelten Laubmoose. Bot. Jahrb. 5: 76-88.
- Müller, C. 1896. Bryologia hawaiiica. Flora 82: 434-479.
- Ochi, H. 1959. A revision of the Bryaceae in Japan and the adjacent regions: 1-124. Biological Institute, Faculty of Liberal Arts, Tottori University, Tottori.
- Palisot de Beauvois, A. M. F. J. 1805. Prodrôme des cinquième et sixième familles de l'Aéthéogamie: 1-114. De l'imprimerie de Fournier fils, Paris.
- Paris, E. G. 1896. Index bryologicus, part 3: 645-964. Apud Paul Klincksieck, Paris.
- Plitt, C. C. 1909. Asexual reproduction of Leucobryum glaucum. Bryologist 12: 79-81.
- Potier de la Varde, R. A. L. 1917. Contribution à la flore bryologique de l'Annam. Rev. de Bot. 29: 289-304, pls. 1-4.
- Proctor, M. C. F. 1979. Structure and eco-physiological adaptation in bryophytes. In G. C. S. Clarke & J. G. Duckett (eds.), Bryophyte systematics: 479-509. Academic Press, London.
- Proctor, M. C. F. 1982. Physiological ecology: water relations, light and temperature responses, carbon balance. In A. J. E. Smith (ed.), Bryophyte ecology: 333-381. Chapman & Hall, London.

- Renauld, F. & J. Cardot 1905. Musci exotici novi vel minus cogniti, 10. Bull. Soc. R. Bot. Berg. 41(1): 7-122.
- Robinson, H. 1965a. Notes on Leucobryaceae in Central America. Bryologist 68: 89-93.
- Robinson, H. 1965b. Venezuelan bryophytes collected by Julian A. Steyermark. Acta Bot. Venezuelica 1(1): 73-83.
- Robinson, H. 1985. The structure and significance of the leucobryaceous leaf. Monogr. Syst. Bot. Missouri Bot. Gard. 11: 111-120.
- Robinson, H. 1990. A functional evolution of the Leucobryaceae. Tropical Bryology 2: 223-237.
- Saito, K. 1975. A monograph of Japanese Pottiaceae (Musci). J. Hattori Bot. Lab. 39: 273-537.
- Salazar Allen, N. 1989. A preliminary report of rhizoidal heads in Leucobryum martianum. Bryologist 92: 493-494.
- Sande Lacoste, C. M. van der 1866. Musci frondosii. In G. A. W. Miquel (ed.), Prolusis florae japonicae. Ann. Mus. Bot. Lugd. Bat. 2: 292-300.
- Schimper, W. P. 1856. Corollarium bryologiae europaeae: 1-140. Sumptibus librariae E. Schweizerbart, Stuttgart.
- Schwägrichen, C. F. 1823. Species muscorum frondosorum, supplementum primum, suppl. 2, vol. 1(1): 1-86, pls. 101-125. Sumtu Joannis Ambrosii Barth, Leipzig.

- Scott, G. A. M. & I. G. Stone 1976. The mosses of  
southeastern Australia: 1-495. Academic Press, London.
- Sullivant, W. S. 1846. Musci alleghanienses: 1-87. Columbus.
- Sullivant, W. S. & L. Lesquereux 1859. Characters of some  
new mosses collected by C. Wright in the North Pacific  
Exploring Expedition, under the command of Captain John  
Rogers. Proc. Amer. Acad. Arts Sci. 4: 276-282.
- Thériot, I. 1919. Mousses de l'Annam. Recueil Publ. Soc.  
Havraise, Etud. Div. 1919: 33-47.
- Thériot, I. 1929. Une poignée de mousses cambodgiennes. Rev.  
Bryol. n. sér., 2: 17-20.
- Thériot, I. 1936. Reliquiae boissierianae. Bull. Soc. Bot.  
Genève sér. 2, 26: 76-91.
- Une, K. 1985a. Sexual dimorphism in the Japanese species of  
Macromitrium Brid. (Musci: Orthotrichaceae). J. Hattori  
Bot. Lab. 59: 487-513.
- Une, K. 1985b. 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. 1985c. Factors restricting the formation of normal  
male plants in the isosporous species of Macromitrium  
(Musci: Orthotrichaceae) in Japan. J. Hattori Bot. Lab.  
59: 523-529.



- Vitt, D. H. 1984. Classification of the Bryopsida. In R. M. Schuster (ed.), *New manual of bryology*, vol. 2: 696-795. Hattori Botanical Laboratory, Nichinan.
- Warnstorff, C. 1915. *Bryophyta nova europaea et exotica*. *Hedwigia* 57: 62-131.
- Wijk, R. van der, W. D. Margadant & P. A. Florschütz 1959. *Index muscorum*, vol. 1 (A-C). *Regnum Vegetabile* 17: 1-548.
- Wijk, R. van der, W. D. Margadant & P. A. Florschütz 1962. *Index muscorum*, vol. 2 (D-Hypno). *Regnum Vegetabile* 26: 1-535.
- Wijk, R. van der, W. D. Margadant & P. A. Florschütz 1964. *Index muscorum*, vol. 3 (Hypnum-O). *Regnum Vegetabile* 33: 1-529.
- Wijk, R. van der, W. D. Margadant & P. A. Florschütz 1967. *Index muscorum*, vol. 4 (P-S). *Regnum Vegetabile* 48: 1-604.
- Wijk, R. van der, W. D. Margadant & P. A. Florschütz 1969. *Index muscorum*, vol. 5 (T-Z, Appendix). *Regnum Vegetabile* 65: 1-922.
- Williams, R. S. 1913. *Dicranaceae, Leucobryaceae*. *North American Flora*, vol. 15, part 2: 77-166. New York Botanical Garden, New York.

- Williams, R. S. 1931. Musci. In H. A. Gleason (ed.),  
Botanical results of the Tyler-Duida expedition. Bull.  
Torrey Bot. Club 58: 501-503, pls. 44, 45.
- Wilson, W. 1854. Musci. In J. D. Hooker (ed.), Flora novae-  
zelandiae, part 2: 57-125.
- Woesler, A. 1935. Zur Zwergmännchenfrage bei Leucobryum  
glaucum Schpr. 1. Planta 24: 1-13.
- Wyatt, R. & L. E. Anderson 1984. Breeding systems in  
bryophytes. In A. F. Dyer & J. G. Duckett (eds.), The  
experimental biology of bryophytes: 39-64. Academic  
Press, London.
- Yamaguchi, T. & Z. Iwatsuki 1987. New Caledonian Leucobryum  
(Musci). J. Hattori Bot. Lab. 63: 473-491.
- Yamaguchi, T. & Z. Iwatsuki 1988. The scientific name of  
Leucobryum neilgherrense from Japan. Hikobia 10: 235-  
238. (In Japanese with English summary)
- Yamaguchi, T. & Z. Iwatsuki 1991. New Caledonian  
Leucophanoideae (Musci: Calymperaceae). Hikobia 11: 37-  
42.
- Zanten, B. O. van 1964. Mosses of the Star Mountains  
Expedition. Nova Guinea 16: 263-368, pls. 22-36.